



Out of Equilibrium Dynamics

A quantitative theory of vegetation patterns based on plant structure and the non-local F–KPP equation

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ABSTRACT

The theory of vegetation patterns presented rests on two hypotheses: (i) the *self-organization hypothesis* that attributes their cause to interactions intrinsic to vegetation dynamics; (ii) the *complementary self-assembly hypothesis* that attributes their large spatial scale to the proximity of their dynamical conditions with a critical point. A non-local version of the F–KPP equation allows us to formulate these hypotheses in terms of individual plant properties. Both general and parsimonious, this formulation is strictly quantitative. It only relies on structural parameters that can be measured with precision in the field. Quantitative interpretation of observations and of the predictions provided by the theory is illustrated by an analysis of the periodic patterns found in some Sub-Saharan regions.

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Avant-propos

C'est une des conférences de Paul Clavin à Bruxelles, événements scientifiques et humains toujours mémorables, qui nous a fait connaître l'équation F–KPP, ou *équation de Fisher–Kolmogorov, Petrovsky, Piscounov*, comme paradigme des ondes chimiques et des fronts de flamme [1,2]. Introduit initialement en dynamique de population, c'est dans son domaine d'origine qu'on retrouvera ici ce paradigme, mais sous une forme non-locale. Cette formulation, comme sa version classique, combine simplicité et puissance explicative. L'image riche et clarifiée qu'elle renvoie des phénomènes d'auto-organisation de la végétation, se révèle aussi prédictive et quantitative.

1. Introduction

When in 1950, he discovered the first known vegetation patterns (cf. Fig. 1), Macfadyen concluded in regard to their origin as follows:

“The study of the first two patterns, of which I have been able to find no previous recognition, is not conveniently pigeon-holed under any one accepted branch of knowledge, and the phenomena are thus awkward to classify. They are manifestly within the province of botany and ecology; the essential background concerns geomorphology and meteorology; the causes as I believe, must be investigated by physics and mathematics.”

At the time, this was a profoundly insightful statement. The first investigation by mathematics however, a computer simulation based on a cellular automata model, only appeared after forty five years [4]. Two years later, suggested by the

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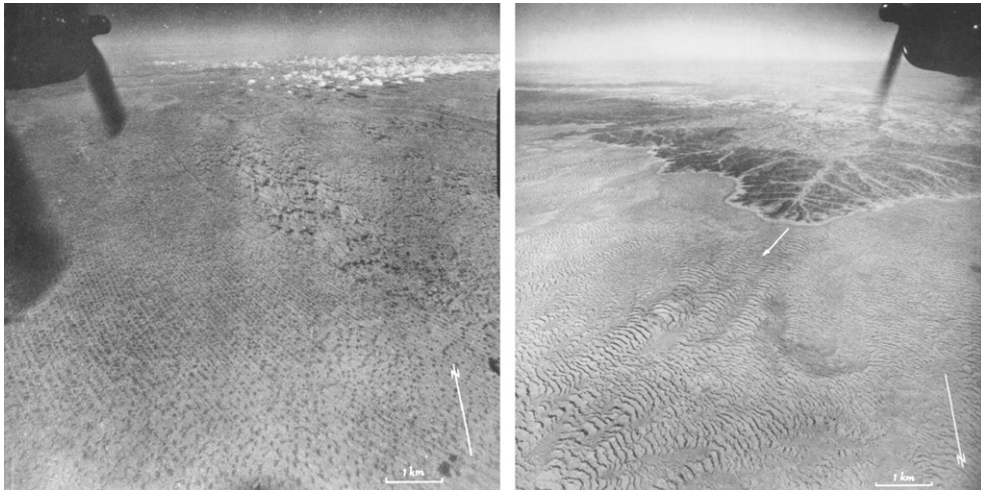


Fig. 1. Vegetation bands and arcs discovered by Macfadyen (British Somaliland, 1950) [3]. Width of vegetated bands: 70 m; width of bare soil bands: 300 m.

F–KPP paradigm and the *self-organization hypothesis*, a time and space continuous evolution equation modeling the non-local interactions specific of vegetation communities was proposed [5]. Its study showed that pattern formation could originate from interactions intrinsic to the vegetation dynamics, so-called *facilitation* and *competition*, rather than from extrinsic, environmental causes considered plausible at the time. By now, this prediction has been vindicated by numerous field investigations.

That the gap in time separating the discovery and first theoretical studies of vegetation patterns was so large, is somewhat surprising. At least in part, it reflects a prudent mistrust, widespread in the field of vegetation ecology, for mathematical treatments, the simplifications that these treatments require and the interpretations deduced from them. This is a domain where the notion of system is fuzzy, where phenomena are interconnected and cannot easily be pulled apart, where mathematics and modeling are weakly constrained by fundamental physical principles. The idealizations that models propose are thus easy to put into question if there is a lack of quantitative confrontation with reliable field data. On the other hand, population behaviors, and vegetation patterns in particular, are non-linear phenomena. There is little chance in succeeding, only by field observations and/or hopefully clever intuitive reasonings, to understand, even only qualitatively, the spectrum of observed behaviors or possible phenomena. Mathematics and modeling are for such exploration indispensable. In fact, they constitute the only dependable tools available. Our aim below is not to present the non-local F–KPP theory as an ultimate truth but to show that its predictions are as close an approximation to the truth as needed within the limit of what quantitative measurements on the terrain have been able to establish.

2. Self-organization, non-local F–KPP equations and the modeling of interactions dependence upon plant structure

The number of models associating vegetation patterns and self-organization has now multiplied. Often, quite different phenomenology and treatments are adopted. They may be broken up into three categories¹:

- (i) The non-local F–KPP approach: it focuses on the relationship between the structure of individual plants and the facilitation–competition interactions existing within plant communities. The biomass density is defined at the individual plant level; the modeling calls for no other state variable [5–7].
- (ii) The reaction–diffusion approach: it emphasizes the influence on vegetation patches of water transport by below ground diffusion and/or above ground run-off. The biomass density is defined at the patch level. Together with the water concentration below ground and/or in some surface ground layer, it constitutes the set of state variables [8–13].
- (iii) The stochastic approach: it focuses on the “constructive” role of environmental randomness as a source of noise induced symmetry breaking transitions triggering pattern formation. These transitions occur when the variance of environmental noise increases while its average value remains constant [14,15].

It is beyond our scope to further compare these three approaches and the models proposed within the framework of each of them. We want to take stock of the first one, the non-local F–KPP approach. Its spirit strives to be both general and parsimonious in view to lend itself to mathematical analysis. Its ambition is to furnish transparent expressions that describe how the spatial organization of plant communities depends on simple plant characteristics, like the crown and rhizosphere size, and to provide in this way both theoretical insight and testable predictions.

¹ The literature mentioned is meant to point out research direction choices and is in no way exhaustive.

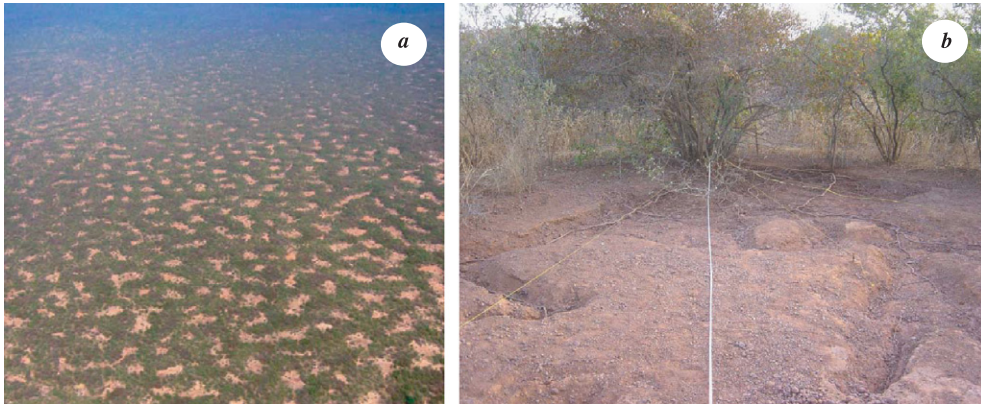


Fig. 2. (a) Sub-Saharan periodic gapped landscape of bare spots distant from approximately 50 m (South-West Niger, shrub species *Combretum micranthum* G. Don). The average crown radius is approximately 1.75 m. (b) Excavated rhizosphere. Roots penetrate to ca. 40 cm depth but their spread can exceed the crown radius by one order of magnitude (reproduced from [16]).

To introduce non-local F–KPP equations and define notations, let us first write the classical (local version) F–KPP equation of population dynamics in a slightly more general way than usual by adding the linear term $-\mu b(\mathbf{r}, t)$ to its right-hand side; $b(\mathbf{r}, t)$ represents the population density at a given point in space \mathbf{r} and time t , μ is the population loss/gain ratio, i.e., the quotient of the biomass density characteristic decay rate divided by its characteristic growth rate (doubling time). In terms of normalized variables, it then reads:

$$\partial_t b(\mathbf{r}, t) = b(\mathbf{r}, t)[1 - b(\mathbf{r}, t)] - \mu b(\mathbf{r}, t) + \nabla^2 b(\mathbf{r}, t) \quad (1)$$

The first term, on the right-hand side, expresses that local growth only depends upon local population density: it is exponential when density is low (cf. first factor) and vanishes at high density when resources are consumed as rapidly as renewed (cf. second logistic factor). The Laplacian on the right-hand side, amounts to admit that the individuals of the population are *animals* whose displacements are a simple random walk (Brownian motion).

We consider communities within which, as shown in Fig. 2, and as it is often the case in drylands, a single species accounts for most of the biomass. Being interested in stationary in time, periodic in space, non-uniform biomass distributions, the major ingredient that needs to be incorporated in (1) is the modeling of non-local interactions that plants exert up to some effective distance from the point at which they are located: when confronted with drought, they strive to increase their water resources by spreading their roots over a greater territory. Fig. 2(b) is an example showing that in a shallow soil context, this lateral spread may extend beyond the radius of the aerial structure (crown) by an order of magnitude. In terms of structural plasticity, this is an extraordinary performance. However, whereas the lateral expansion of the roots allows for greater water uptake, it significantly increases the degree of *competition* between neighboring plants. This modifies the natural balance between competition and the positive facilitation feedback which favors vegetation development by the accumulation of nutrients in the neighborhood of the plants, the reciprocal sheltering of neighboring plants against climatic harshness, and the provision of shade, which improves the water budget in the soil [17,18]. Keeping unmodified the formal mathematical structure of (1), we rewrite it as

$$\frac{\partial}{\partial t} b(\mathbf{r}, t) = f_1(1 - f_2) - \mu f_3 + \int \Phi_D(|\mathbf{r}'|^2/L_D^2) b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}' \quad (2)$$

where the f_i , with $i = 1, 2, 3$, are positive functions expressing how the vegetation distribution near the locus \mathbf{r} influences, at this point, the processes of growth (f_1), resource uptake (f_2), and population loss (f_3). The integral with a Gaussian kernel Φ_D is a source term meant to represent more realistically than a Laplacian the biomass gains due to seed dispersion and germination. Plants and seeds do not walk randomly. More respect should be paid to this fact, in spite of the desire for idealization and mathematical simplicity.² Before we further precise the terms appearing in (2), two other important points should be mentioned.

First, let us emphasize that the biomass density $b(\mathbf{r}, t)$ refers to individual plants rather than to vegetation patches. The surface element S on which this density is defined, supposed to be uniform for that definition to make sense, is of the order of magnitude of the size of a mature plant. It should be kept in mind, that when the biomass density at a given point \mathbf{r} tends to zero or one, the probability that the surface element S centered on \mathbf{r} be occupied by a mature plant tends to zero or one. The effective radius L_a of S is in general much smaller than the characteristic length of vegetated patches. Feedbacks between neighboring space domains of size S concern thus in the first place mature plant-to-plant interactions.

² This remark applies as well to the integro-differential modeling of propagation adopted in [7] as to the straightforward Laplacian modelings adopted in most reaction–diffusion approaches devoted to vegetation patterns.

Allowing for self-feedback effects, especially for self-competition, seems a questionable idealization from a biological point of view. How its elimination at the level of surface element S can be implemented, and the impact that this elimination has, is the object of Section 5 devoted to the modeling of competition void domains.

Second, in Eq. (2), a priori, there are three distinct processes where plant-to-plant interactions could appear. Only two kinds of interactions however come into play, facilitation and competition. The distance at which competition effectively operates is of the order of rhizosphere size. It inhibits vegetation development, and in accord with well known conditions that must be met for the self-organization hypothesis to be plausible, thus operates at a distance considerably greater than the positive facilitation feedbacks mediated by the crown. This fact however does not determine which of the three functions f_i is associated with facilitation, which is associated with competition and which, since only two feedbacks are involved, can, without significant loss, be put equal to $b(\mathbf{r}, t)$, i.e., its value in F-KPP equation (1). Mathematically, six cases are possible. Considering them in detail would be tedious; not all of them are plausible from a biological point of view; furthermore, for some of them, pattern formation is anyway always impossible. It is sufficient for the following to mention two cases that have been the object of theoretical studies previously and that, interestingly, describe different biological situations. Let us call them the *weak competition case* and the *aggressive competition case*.³ Facilitation is modeled by f_1 in both cases, meaning that it enhances biomass growth. In the weak case, competition inhibits the uptake of resources, it concerns f_2 , but has no influence on biomass loss, i.e., plant mortality. In the aggressive case on the contrary, competition concerns f_3 , operates by enhancing plant mortality and leaves resource uptake unaffected. Presenting these situations as separate alternatives may be an idealization. Reality could be somewhere in between so that competition influences both resource uptake and plant mortality. It turns however out that weak competition better than aggressive competition explains recent field data on the variation of patterns wavelength with aridity, an aspect that will be the subject of a separate publication. In Section 3 and following, we shall therefore focus our discussion on the weak competition case,

$$\frac{\partial}{\partial t} b(\mathbf{r}, t) = f_1(1 - f_2) - \mu b(\mathbf{r}, t) + \int \Phi_D(\mathbf{r}') b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}' \tag{3}$$

that associates facilitation and competition, respectively with f_1 and f_2 .

The first two terms of Eq. (3) correspond to the mathematical structure considered in the first model studied [5]. Beside the addition of the integral term, further elaboration however is indispensable. As before, we represent in f_1 and f_2 the effect of interactions by a mean-field integral of the biomass density distribution,

$$f_i = f_i \left(b(\mathbf{r}, t), \int w_i(|\mathbf{r}'|/L_i) b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}' \right), \quad i = 1, 2 \tag{4}$$

whose kernel $w_i(|\mathbf{r}'|/L_i)$ decreases with distance. But we no longer admit that the parameters L_1 and L_2 controlling this decrease are constant. This simplification neglects their variation in the course of plant development and turns out to be too crude (for a more detailed discussion see [7]). The most convenient remedy, which avoids the complication of introducing supplementary variables, is to represent the age classes of the community, by putting

$$L_i = L_i^0 b(\mathbf{r} + \mathbf{r}', t)^p, \quad i = 1, 2 \tag{5}$$

where p is a positive constant. This allometric ansatz has already been used [13,7]. It expresses in a simple manner that wide-ranging interactions are due to mature plants whose presence at a given point is unlikely if its biomass density tends to zero. The contribution of such points in the integral of (4) is negligible.

A simple guess for f_i would be its immediate identification with the mean-field integral, i.e., to put

$$f_i = \int w_i(|\mathbf{r}'|/L_i) b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}' \tag{6}$$

It is however easy to show [5] (at least for Gaussian or exponential kernels) that plugging this, still linear, expression in (3) cannot give rise to the spatial structures we are looking for. The functions f_i , or at least one of them, must be non-linear with respect to the density. Replacing in (6), $b(\mathbf{r} + \mathbf{r}', t)$ by $b(\mathbf{r} + \mathbf{r}', t) + \Lambda b(\mathbf{r} + \mathbf{r}', t)^2$ is a possibility. Its price is the introduction of a “cooperativity” parameter, Λ , not directly accessible to measurement. This drawback is avoided in the modeling below, where all parameters, i.e., p , L_1^0 , L_2^0 , are accessible by simple measurements concerning directly individual plant structure [19].

Since f_1 , f_2 must be positive definite functions, that one of them must be non-linear and that environmental conditions are supposed isotropic, we set

$$f_1 = b(\mathbf{r}, t) \frac{1}{2\pi} \exp \left(\int w_1(|\mathbf{r}'|/L_1) b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}' \right) \tag{7}$$

$$f_2 = \frac{\int w_2(|\mathbf{r}'|/L_2) b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}'}{\int w_2(|\mathbf{r}'|/L_2) d\mathbf{r}'} \tag{8}$$

³ This terminology was not used before; it is meant to draw attention here to a distinction that becomes more important in the light of recent data.

and let L_1 and L_2 be given by (5). In agreement with field determinations [19], we assume that the kernels w_i are exponentially decreasing functions of \mathbf{r}' :

$$w_i(|\mathbf{r}'|/L_i) = \exp(-|\mathbf{r}'|/L_i), \quad i = 1, 2 \tag{9}$$

For uniform vegetation distributions Eqs. (7), (8) simply become

$$f_1 = b(t) \exp[L_1^0 b(t)^{(2p+1)}], \quad f_2 = b(t) \tag{10}$$

When the uniform mean-field density $b(t)$ is small, mature plants are on the average too far apart to interact, the influence of small (young) plants being essentially negligible, both f_1 and f_2 tend towards their value in the absence of interactions, i.e., $b(t)$ as in the classical F-KPP equation. When the mean-field density increases so that mature plants get close, interactions become important, but the averaging effect of integration cancels out the long range interactions associated with competition; the uniform mean field $f_2 = b(t)$ is unaffected by their presence. For facilitation, on the contrary, whose operation range is small, the averaging effect of integration is less efficient so that the uniform mean-field expression of f_1 still keeps the trace of the existence of interactions.

Let us take the radius L_a of S as space unit, define the dimensionless parameters:

$$e_1 = L_1^0/L_a, \quad e_2 = L_2^0/L_a, \quad \sigma = L_D/L_a, \quad \varepsilon = (L_1^0/L_2^0)^2 \tag{11}$$

and put the kernel of the source term in (3) equal to the Gaussian function

$$\Phi_D(|\mathbf{r}'|^2/\sigma^2) = \frac{d}{\pi} \exp(-|\mathbf{r}'|^2/\sigma^2) \tag{12}$$

where d is a constant. Using expressions (7)–(12), putting $\tilde{\mu} = \mu - d\sigma^2$, Eq. (3) then becomes, for spatially uniform systems:

$$\frac{d}{dt} b(t) = b(t) [1 - b(t)] \exp(e_1^2 b(t)^{2p+1}) - \tilde{\mu} b(t) \tag{13}$$

The stationary states of (13), representing uniform vegetation covers, are (i) the bare soil state $b_0 = 0$, and (ii) the curve $b \in [0, 1]$ solution of

$$\tilde{\mu} = (1 - b) \exp(e_1^2 b^{2p+1}) \tag{14}$$

Let us remark in passing that if one puts $d = 0$ and $e_1^2 = \Lambda$, the loss/gain ratio $\tilde{\mu}$ becomes $\tilde{\mu} = \mu$, and (13), (14) become the evolution and stationary states equations of uniform systems in the aggressive competition case.⁴

3. Vegetation critical point and the complementary self-assembly hypothesis

In Fig. 3(a), the stationary states of (14) are plotted in terms of $\tilde{\mu}$ for $p = 0$. In Fig. 3(b), $p = 1/3$, is the value determined by field measurements for the patterns of Fig. 2(a). It is noteworthy that whatever e_1 and p , all curves b cross the bifurcation point ($b = 0, \mu - d\sigma^2 = 1$) where the bare soil solution b_0 changes stability. At this point, if $p = 0$, the slope $db_s/d\tilde{\mu}$ varies with e_1 while it is independent from e_1 if $p = 1/3$. In fact, for any $p > 0$, it is equal to the slope equal to -1 of the (green) straight line $b_s = 1 - \tilde{\mu}$ representing communities without interactions ($e_1 = 0$). Biologically, this makes sense because as b tends to zero, vegetation becomes sparsely distributed, mature plants are rare and, hence, interactions become negligible. Facilitation then has no effective influence. It is therefore clear that hysteresis, if it appears, should do so *via* a *critical point* corresponding to a density b_c that lies above the abscissa axis $b = 0$, and not *via* a *transcritical bifurcation point* located on the abscissa axis $b = 0$. For $p = 0$, the slope of the curve b at its intersection with $b = 0$ (bare soil) is negative when $e_1 < e_{1c}$, infinite for $e_1 = e_{1c}$ and positive for $e_1 > e_{1c}$. In other words, when $p = 0$, hysteresis appears on the abscissa axis under conditions where the biomass density is zero, where, as mentioned, interactions are non-existent and where edaphic dependent parameters, like μ , should not influence dynamics. One can only conclude from this that setting $p = 0$ is a crude approximation to be avoided. This is certainly so at low biomass density, like in the course of a desertification process. The existence of age classes inside the community plays then a role that can no longer be overlooked.

In $(b, e_1, \tilde{\mu})$ -space, the coordinates of the critical point are:

$$\boxed{b_c = \frac{2p}{1 + 2p}, \quad e_{1c} = \frac{1}{b_c^p}, \quad \tilde{\mu}_c = \frac{b_c e^{b_c}}{2p}} \tag{15}$$

This result is in fact the central, prediction of the approach of vegetation patterns based on the non-local F-KPP equation. A first important aspect of (15) is practical and immediately evident: the sole knowledge of the allometric constant p

⁴ With a redefined dimensionless time scale, which is of no importance as far as uniform stationary states are concerned.

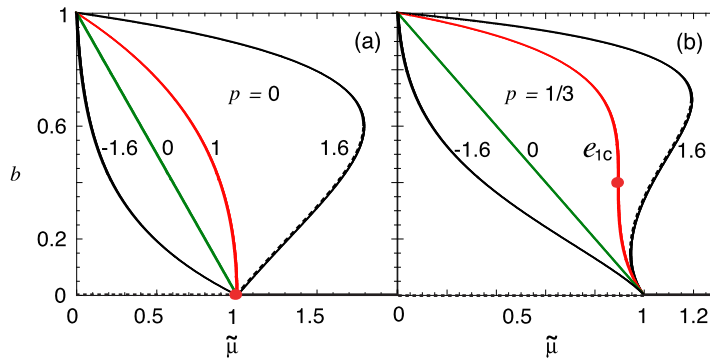


Fig. 3. Uniform stationary solutions (14) vs $\tilde{\mu}$ for the values of e_1 and p indicated. (For interpretation of the references to color, the reader is referred to the web version of this article.)

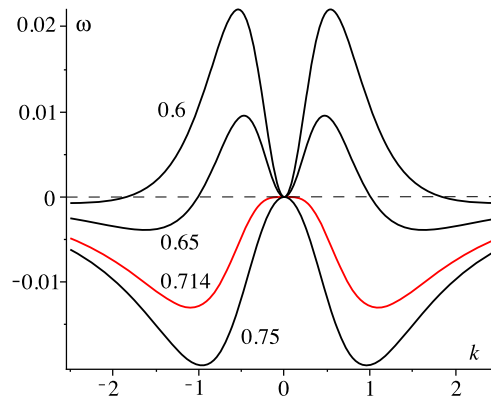


Fig. 4. Eigenvalues of Fourier modes as a function of k for $p = 1/3$, $d = 0$ and the values of ε indicated.

suffices to evaluate the coordinates (15). This phenomenological dimensionless constant integrates numerous functional processes, couplings and environmental edaphic influences. It constitutes their combined, global expression at the level of plant development. A more complete, more detailed description of these intricate interconnections rapidly becomes impenetrable to any feasible mathematical analysis. Furthermore, from the point of view of experimental measurements, quite a number of pertinent factors are probably still unknown, poorly identified and/or extremely difficult to quantify on the terrain. Evaluating the allometric constant p , though it may require arduous work under difficult terrain conditions, is in comparison technically simple and, as we shall show in the next section, yields unambiguous, remarkably predictive information.

But there is a second even more important property of (15) that is specific of the non-local F-KPP equation in the weak competition case. It is illustrated by Fig. 4 that summarizes the linear stability properties of the critical point (15) with respect to the Fourier modes of an arbitrary infinitesimal fluctuation (cf. (A.2)). One sees that at

$$\varepsilon = \varepsilon_{sa} \equiv \frac{1 + 2p}{1 + 4p} \tag{16}$$

i.e., for $\varepsilon = 5/7 \approx 0.714$ when $p = 1/3$ and in the absence of seed dispersion ($d = 0$), the critical point becomes a point of tri-marginal stability where two unstable space periodic modes coalesce at the same time that their wave number vanishes. In other words, for all $\varepsilon < \varepsilon_{sa}$ there exists a finite band of unstable modes whose lower cut-off is $k = 0$. Assuming that the intrinsic dynamics of vegetation patterns proceeds close to this point is the *complementary self-assembly hypothesis*.⁵ It is complementary to the self-organization hypothesis because it solves the most puzzling property of vegetation patterns, namely, that their characteristic length (wavelength) is in general orders of magnitude larger than the size of a plant. What makes the critical point (15) and Eq. (3) especially interesting in that respect, as we shall see in the next section, is that there is no need therefore to introduce other parameters than those already defined so far.

⁵ It may be called that way because physically it amounts to assuming that vegetation patterning can be understood as being an aggregative phase transition in which vegetated domains and bare soil separate like two fluids that become immiscible (cf. [7] for a more complete discussion).

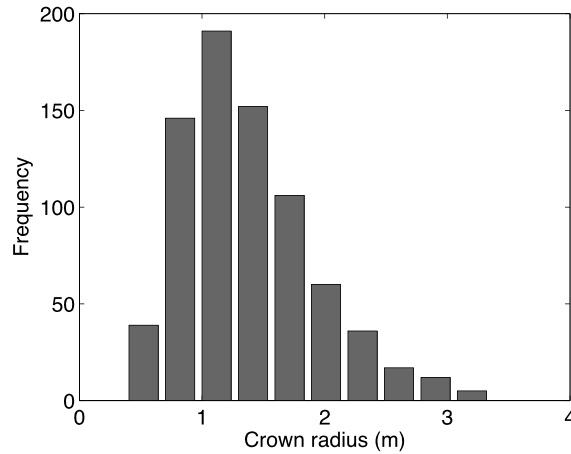


Fig. 5. Crown radius histogram: number of plants as a function of crown size for 750 individuals of *C. micranthum* above 1.5 m height measured in a plot of 0.4 ha representative of the Niger site seen in Fig. 2 (reproduced from [16]).

4. Interpretation and predictions in terms of plants structural parameters

Let us explain the method of quantification applied on the representative Sub-Saharan gapped pattern of Fig. 2(a). Reliable data that suit the theory presented above are available for that system. They establish that the structure and development of the crown and rhizosphere of *Combretum micranthum* nicely fit with the assumption that interactions decrease exponentially with distance. Measurements of the pertinent structural parameters furnish the values [19]:

$$p \approx 1/3, \quad L_1^0 \approx 0.81L_a, \quad L_2^0 \approx 1.27L_a \quad (17)$$

For the structural ratio defined as $\varepsilon = (L_1^0/L_2^0)^2$, this yields the value:

$$\varepsilon \approx 0.41 \quad (18)$$

Fig. 5 shows the frequency histogram of the crown radius of the plants. The most probable and average values, respectively L_M and L_A , read:

$$L_M \approx 1.25 \text{ m}, \quad L_A \approx 1.75 \text{ m} \quad (19)$$

Tentatively, we equate L_a , the radius of the surface element S considered as spatially uniform and earlier introduced as such to define the biomass density $b(\mathbf{r}, t)$, with the most probable crown value, i.e., we put $L_a = L_M$. Taking into account that the wavelength of the pattern (average distance between gaps in Fig. 2(a)) is 50 m, 5 quantities, namely, p , L_a , L_1^0 , L_2^0 , λ , have now known values, fixed by straightforward field measurements. The number of parameters to manage in the non-local F-KPP equation of weakly competitive vegetation (see Eq. (A.1) in Appendix A for its explicit expression) is 6, namely, μ , p , e_1 , e_2 , d , σ . The self-organization hypothesis furnishes for this purpose the usual two equations that determine the conditions for which the crossing of the imaginary axis by a real eigenvalue ω_k , solution of Eq. (A.2), triggers the onset of a pattern having for wavelength $\lambda = 2\pi/k$:

$$\omega_k = 0, \quad \frac{\partial \omega_k}{\partial k} = 0 \quad (20)$$

But as it happens, we have to ask for more than a bifurcation point and marginal stability, we want λ to be very large compared to plant size, i.e., the wave number k must tend to zero. The keystone of the theory, as explained at the end of the preceding section, is to make use therefore of the complementary self-assembly hypothesis. Accordingly, we assume that for $k=0$, the third equation

$$\left(\frac{\partial^2 \omega_k}{\partial k^2} \right)_{k=0} = 0 \quad (21)$$

holds. The interpretation of field data can then proceed as follows. Regarding conditions at which patterning first appears (the transition from uniform vegetation cover to a gapped pattern) we can admit, as a first approximation, that the facilitation range e_1 and the competition range e_2 are given by the coordinates of the critical point. Replacing in (15) the known value $p = 1/3$ of the allometric parameter, we find that

$$e_1 = \left(\frac{5}{2} \right)^{\frac{1}{3}} \approx 1.36 \quad (22)$$

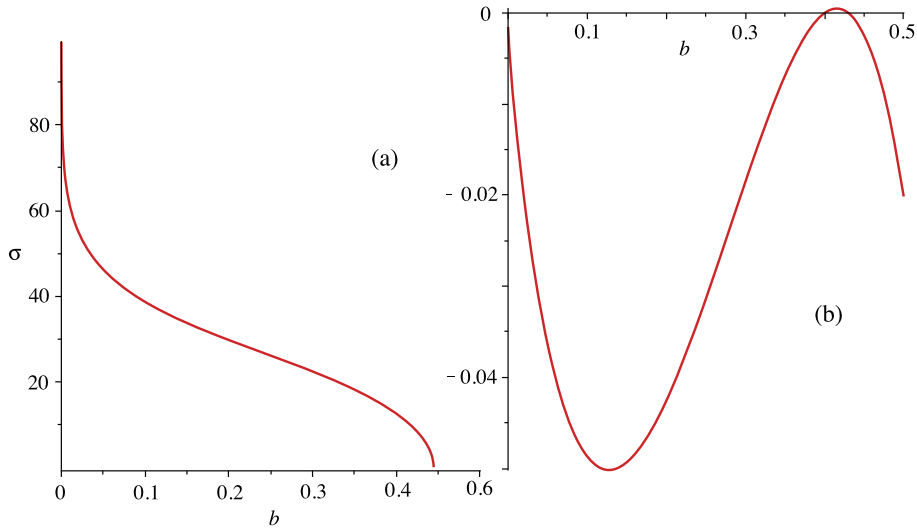


Fig. 6. (a) At $b = 0$ the value of σ diverges while for $b \approx 0.444$ it vanishes; (b) plot of the function of b whose zero corresponds to uniform stationary solutions of (A.1). The root $b \approx 0.430$ corresponds to the marginal stability point for the emergence of patterns having wave number (25).

Using the known value (18) of the structural ratio, fixes the competition range e_2 at

$$e_2 = \frac{e_1}{\sqrt{\varepsilon}} \approx 2.12 \tag{23}$$

Three quantities are still to be determined, the uniform stationary biomass density b , the parameters associated with seed propagation: d and σ . Therefore, we still have at our disposal the two equations (20) provided by the self-organization hypothesis, Eq. (21) provided by the complementary self-assembly hypothesis, and the still unused field data corresponding to the pattern wave number. To exploit (21), we replace the expressions (15), (23) in it and put $k = 0$; solving the expression so obtained for d yields:

$$d = 6 \frac{b_c}{\sigma^4} \left(\frac{1}{\varepsilon} - \frac{1 + 4p}{1 + 2p} \right) e^{b_c} \approx 0.0220 \tag{24}$$

Dealing with gapped patterns that result from the first patterning transition that destabilizes the uniform vegetation cover b when aridity increases, we suppose that the wave number of the pattern represented in Fig. 2 is close to the one of the first mode that becomes unstable. Hence, we set

$$k = 2\pi \left(\frac{L_a}{\lambda} \right) \approx 0.157 \tag{25}$$

Replacing (22)–(25) in the second condition (20) and solving for σ yields an expression depending on the biomass density b . Its graph represented in Fig. 6(a) shows that it is a monotonously decreasing function of b that vanishes for $b \approx 0.444$. In Fig. 6(b) is plotted the function of b obtained by replacing the expression of σ and (22)–(25) in the first condition (20). We see that it possesses two roots for $b \in [0, 1]$. The first one, at $b = b_c = 2/5$ reflects that, at the critical point, b_c is a triple root of (A.2); the second one, at $b \approx 0.430$ is the marginal stability point of the wave number $k = 0.157$ that interests us.

In summary, under the dimensionless form in which they appear in Eqs. (A.1), (A.2) the values of parameters determined for the gapped pattern of Fig. 2 read⁶:

$$k = 0.157, \quad p = 1/3, \quad b = 0.43, \quad d = 0.0220 \tag{26}$$

$$e_1 = 1.36, \quad e_2 = 2.12, \quad \sigma = 3.61 \tag{27}$$

It is interesting to convert the quantities (27) in real space unit. Remembering that L_a has tentatively been put equal to 1.25 m, the most probable value of crown radius L_M in the histogram of Fig. 5, they become:

$$L_1^0 = 1.70 \text{ m}, \quad L_2^0 = 2.65 \text{ m}, \quad L_D = 4.51 \text{ m} \tag{28}$$

⁶ Approximation symbol on floating point values is replaced by equality signs for simplicity. Replacing these values in (14) determines the loss/gain ratio at the marginal stability point: $\tilde{\mu} = 0.89505$.

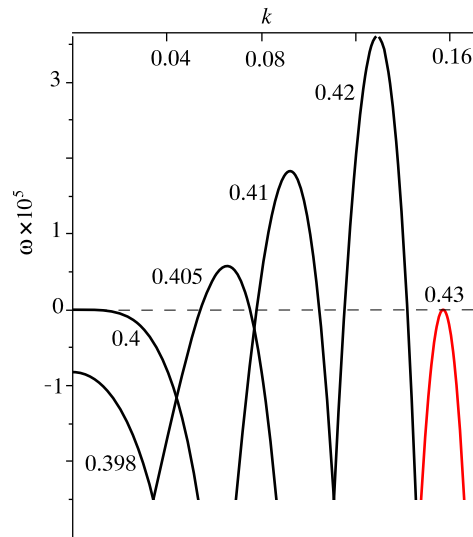


Fig. 7. Influence of increasing aridity on fastest growing mode corresponding to the values of b indicated. The red curve (the last curve on the right) corresponds to the marginal stability point (26), (27).

No room for ambiguity is left in this evaluation. No fitting of data has been performed, no adaptable parameter has been involved or remains at disposal, no alternative to (28) is in fact possible within the framework of the measurements made concerning individual plants and of the non-local evolution equation set up on this basis. The result for L_1^0 is therefore worth to be noted. Especially so when compared with the average crown radius measured on the terrain, i.e., $L_A = 1.75$ m (a relative difference of less than 3%). In other words, for $p = 1/3$, the prediction of the theory is that the effective range over which facilitation operates is nothing else than the average plant crown radius. This makes sense both physically and biologically: at the individual plant level what matters is the *most probable value* of the crown size, at the population level what matters is the *average value* of the crown size. This dichotomy arises because, clearly (see the histogram of Fig. 5) the crown size distribution is not a Gaussian distribution. Concerning the prediction for L_D no quantified field data to compare with seem to exist. Observations suggest that effective values greater than the crown size are plausible; $L_D = 4.51$ m is the prediction of the F–KPP theory.

Fig. 7 exemplifies the dependence of the pattern wavelength upon aridity. It shows, as expected, that in the critical region the community organization is strongly sensitive even to very small aridity increases: a drop of the average uniform biomass density from 0.43 to 0.4 is sufficient for the patterns to switch from the gapped morphology to the spotted morphology. Observations that seem to support this behavior have been reported [20] and will be discussed in a paper in preparation.

5. Influence of competition void domains

At the starting point of our approach, there exists a broad consensus in the field of vegetation ecology that recognizes the existence in plant communities of facilitation and competition effects that play an important role in their organization. These effects are generally considered as well demonstrated at the population level. If so, one may wonder whether or not these effects fade away somewhere between the population and individual plant level. Do self-facilitation and self-competition take place at the individual plant level? The question does not seem to have a simple answer. Positive feedbacks may seem rather plausible, self-competition of a plant with itself may seem to be a notion that biologically speaking does not make much sense. We shall not try to enter in this debate which would only lead us to express more or less subjective opinions. What we can do however, since we have a model, and that is a matter of mathematics involving no subjectivity, is to explore and to quantify the self-feedback component in this model.

We have done that in the case of the interactions associated with competition. Technically, self-competition sneaks into the model through the mean-field integrals. Getting rid of it can be achieved by excluding from the integration domain some neighborhood of radius a_2 around the position \mathbf{r} at which the integral is evaluated. A domain of surface πa_2^2 is then void of competition. The linear stability of uniform vegetation covers can be recalculated under those conditions and the modified eigenvalue equation is given in Appendix A (cf. Eq. (A.4)). Fig. 8 reports results that demonstrate the sensitivity of the critical region with respect to the introduction of competition void domains not only from a quantitative point of view, but also, rather unexpectedly (see Fig. 8(b)), from a qualitative point of view. The situation in the absence of self-competition clearly becomes rapidly even more rich in complex stability problems than before.

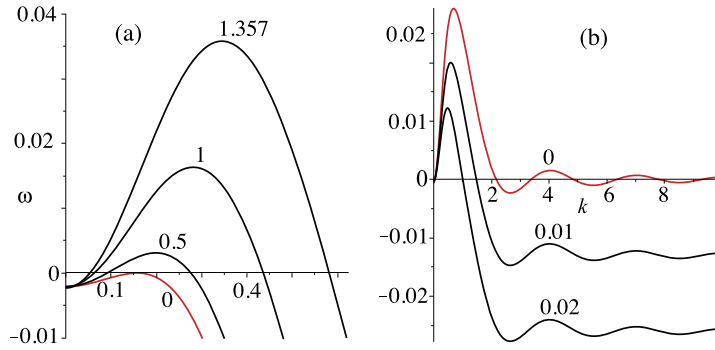


Fig. 8. Influence of competition void domains on the linear stability: (a) effect on the band of unstable modes of increasing values of a_2 ; red: marginal stability curve of gapped pattern for $a_2 = 0$. (b) Putting $a_2 = 2.12$ (the value of e_2), the marginal stability condition now exhibits a succession of separated bands of unstable modes (red curve). As d increases stability is progressively restored. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

6. Conclusion

Biologically speaking, the F-KPP approach provides a reliable quantitative description of vegetation patterns in terms of plant size and development at low and high biomass densities. It highlights the importance of the crown/root ratio, which reflects the plasticity of plant structures and of the allometric parameter p that governs the range of plant interactions during development; it strongly supports the conceptual interpretation that vegetation patterning is a phenomenon whose dynamics has properties similar to those of some phase separation processes. These results are fully supported quantitatively, they have been established within a framework of reliable observations and measurements on the field. Reasonable disagreement on what lies beyond this framework remains possible, but within it the *self-organization hypothesis* and the *complementary self-assembly hypothesis* can be considered as quantitatively tested and vindicated. To that extend the theory of vegetation patterns based on the non-local F-KPP equation is validated and the mechanism of these phenomena is understood.

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Appendix A

Written in explicit form, taking into account expressions (4), (5), (7)–(12) and putting the unit of space equal to L_a , the non-local F-KPP equation (3) describing the spatio-temporal evolution of vegetation in the weak competition case reads:

$$\frac{\partial}{\partial t} b(\mathbf{r}, t) = b(\mathbf{r}, t) \exp\left(\frac{1}{2\pi} \int \exp\left[-\frac{|\mathbf{r}'|}{e_1 b(\mathbf{r} + \mathbf{r}', t)^p}\right] b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}'\right) \left(1 - \frac{\int \exp\left[-\frac{|\mathbf{r}'|}{e_2 b(\mathbf{r} + \mathbf{r}', t)^p}\right] b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}'}{\int \exp\left[-\frac{|\mathbf{r}'|}{e_2 b(\mathbf{r} + \mathbf{r}', t)^p}\right] d\mathbf{r}'}\right) - \mu b(\mathbf{r}, t) + d \int \frac{1}{\pi} \exp\left(-\frac{|\mathbf{r}'|^2}{\sigma^2}\right) b(\mathbf{r} + \mathbf{r}', t) d\mathbf{r}' \tag{A.1}$$

Let

$$\delta b(\mathbf{r}, t) = \frac{1}{2\pi} \int d\mathbf{k} A(\mathbf{k}, 0) \exp(\omega_k t + i\mathbf{k} \cdot \mathbf{r}) \tag{A.2}$$

be the decomposition into Fourier modes of an arbitrary infinitesimal fluctuation perturbing a uniform stationary state solution b of Eq. (14); $A(\mathbf{k}, 0)$ is the initial amplitude of the wave vector of modulus $k \equiv |\mathbf{k}|$. We replace $b(\mathbf{r}, t) = b + \delta b(\mathbf{r}, t)$, in Eq. (A.1), only retain the terms linear in $A(\mathbf{k}, 0)$. Hence, the Fourier mode k is unstable if its eigenvalue

$$\omega_k = -\frac{b \exp(e_1^2 b^{2p+1})}{(1 + k^2 e_2^2 b^{2p})^{3/2}} + \frac{e_1^2 b^{2p+1} [1 + 2p + k^2 e_1^2 b^{2p} (1 - p)] (1 - b) \exp(e_1^2 b^{2p+1})}{(1 + k^2 e_1^2 b^{2p})^{5/2}} - d\sigma^2 [1 - \exp(-\sigma^2 k^2 / 4)] \tag{A.3}$$

is positive.

Eigenvalue value equation governing the linear stability of uniform vegetation covers in the absence of self-competition:

$$\omega_k = \left(-\frac{b(A_1(k) + A_2(k))}{(e_2 b^p + a_2)(1 + e_2^2 k^2 (b^p)^2)} + A_3(k) \right) e^{b e_1^2 b^{2p}} - d \sigma^2 (1 - \exp(-1/4 \sigma^2 k^2)) \quad (\text{A.4})$$

$$A_1(k) = \left(-\frac{K_0}{k} + \frac{e_2 b^p}{\sqrt{1 + e_2^2 k^2 (b^p)^2}} \right) e^{\frac{a_2 b^{-p}}{e_2}} \quad (\text{A.5})$$

$$A_2(k) = -J(1, a_2 k) b^p k e_2 a_2 + a_2 J(0, a_2 k) \quad (\text{A.6})$$

$$A_3(k) = \frac{(b^p)^2 b(1-b) e_1^2 (1+2p + e_1^2 k^2 (b^p)^2 (1-p))}{(1 + e_1^2 k^2 (b^p)^2)^{5/2}} \quad (\text{A.7})$$

$$K_0 = e^{-\frac{a_2}{e_2 b^p}} \sum_{n=1}^{\infty} (\omega_+^n - \omega_-^n) J(n, a_2 k) \frac{1}{\sqrt{\frac{1}{e_2^2 k^2 (b^p)^2} + 1}} \quad (\text{A.8})$$

$$\omega_+ = \frac{1}{e_2 b^p k} + \sqrt{\frac{1}{k^2 e_2^2 (b^p)^2} + 1}, \quad \omega_- = \frac{1}{e_2 b^p k} - \sqrt{\frac{1}{k^2 e_2^2 (b^p)^2} + 1} \quad (\text{A.9})$$

The $J(n, a_2 k)$ represent the Bessel functions of the first kind.

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