



On Forest Spatial Dynamics with Gap Formation

SUSANNA C. MANRUBIA AND RICARD V. SOLÉ

Complex Systems Research Group, Departament de Física i Enginyeria Nuclear, Universitat Politècnica de Catalunya, Sor Eulàlia d'Anzizu s/n. Campus Nord, Mòdul B5, 08034 Barcelona, Spain

(Received on 9 October 1996, Accepted in revised form on 24 January 1997)

In “Forest Spatial Dynamics with Gap Expansion: Total Gap Area and Gap Size Distribution” by Kubo and co-workers, a cellular automata model of gap formation is introduced. The authors claim that their model is able to recover some of the features of the real clearing dynamics, and apply their results to a plot of a tropical rainforest in Panama. Using an analytic approximation to the model, they are able to obtain two real observations that can be compared with real systems: the global density of gaps ρ_0 and the local density of gaps q_{00} . Nevertheless, the gap size distribution is in most cases well fit by an exponential function, although the real rainforest analysed fits clearly to a power-law. Some previous work introduced the Forest Game (FG), a model of rainforest dynamics that included gap formation. The FG has been tested with a plot of gap patchiness in the same rainforest. The FG is able to account for the exact distribution that the map presented by Kubo and co-workers displays, and we show that their model may give compatible distributions under certain conditions. Some other comments about this paper and the two models might be relevant for the general discussion about gap dynamics modelling.

© 1997 Academic Press Limited

A simple model of lattice-structured forest has been introduced by Kubo *et al.* (1996). The most general model (KIF, from now on) is a cellular automata with four free parameters. The authors work with a two-state system: each cell might be in a state “gap” (0) or in a state “tree” (+), following their notation. The rate of transition from a gap to a non-gap or vice versa is most probably determined and controlled by some parameters that depend on the global and the local density of gaps and trees. To be specific,

- $+ \rightarrow 0$ with probability $P_a = d + \frac{\delta}{z} n(0)$
- $0 \rightarrow +$ with probability $P_b = b + \frac{\beta}{z} n(+)$

where z is the coordination number of the lattice ($z = 2$ in a one-dimensional system and $z = 4$ in a two-dimensional system with Neumann neighborhood); $n(0)$ and $n(+)$ are the number of neighboring sites in state gap or non-gap, respectively, and d , b ,

δ and β are the free parameters of the model. As can be seen in the definition of the dynamical rules, d and b can be thought of as the probabilities of a tree falling or of a tree germinating, and both may acquire a dependence of the global densities in the system. On the other hand, a constraint may be introduced because of the closeness of trees that are able to produce seeds for new individuals or protection against external disturbances (mainly wind). These processes are taken into account by means of β and δ . In particular, the authors discuss a very interesting observation performed, among others, over the real rainforest in Barro Colorado Island (Panama): the transition rate of a non-gap (defined as a tree taller than 20 m in their plot) to a gap in 1984 increases with the number of gaps surrounding it in 1983 [data from Hubbell & Foster (1986)]. This means that it is reasonable to introduce a parameter δ that weights this influence.

By using the so-called pair approximation (Harada

& Iwasa, 1994), the authors derive a closed dynamical system for the total density of gaps ρ_0 and the local gap density $q_{0,0}$ as a function of the system parameters (see equation 7a and 7b in Kubo *et al.*, 1996). This approximation is able to fit quite well with the results from the simulations, not only the two quantities ρ_0 and $q_{0,0}$ but also the gap size distributions obtained under certain conditions that will be discussed later.

Nevertheless, some problems arise when the authors attempt to recover the pattern displayed by a real rainforest. A certain amount of useful data to test the models has been provided by Hubbell & Foster (1986). Among these data, some maps of the gap patchiness in a neotropical forest in Barro Colorado Island (BCI) have been analysed. In figure 7 of Kubo *et al.* (1996), a map of 50 ha. of BCI is represented and reproduced in our Fig. 1(a). It gives information about gap formation in two consecutive years, 1983 and 1984, which allows the authors to make a direct estimation of their variables d , δ and b . A Neumann neighborhood is shown to be the best election to fit the observed data, so the authors use it to evaluate δ , $q_{0,0}$ and ρ_0 . In BCI map, a gap is defined as a site (of size $5 \times 5 \text{ m}^2$ in the real forest) where the height of the trees is lower than 20 m. Then, the global and local densities ρ_0 and $q_{0,0}$ can be directly computed from the map (they chose to evaluate them over the 1983 plot). The determination of the set of parameters $\mathcal{P}_{\text{KIF}} = \{d = 0.024, \delta = 0.276, b = 0.177\}$ and the set of expected outputs $\mathcal{O} = \{\rho_0 = 0.331, q_{0,0} = 0.580\}$ is a good way of testing their model. If given \mathcal{P}_{KIF} they obtain \mathcal{O} , this would be a first sign of a good approximation to the real system. However, as they admit, none of the variants introduced in the general model is able to recover the real data. Using the expected values, they can obtain two values of b and β that (in the pair approximation) give the desired result. But this can be done for *any* two values of ρ_0 and $q_{0,0}$: they have two equations with two parameters to be fixed. Their final conclusion is that the current spatial pattern is not at equilibrium, so one guesses that waiting long enough, their claim is that BCI would achieve the values predicted by their model.

Some time ago (Solé & Manrubia, 1995a, b; Manrubia & Solé, 1996) a new model of gap and tree dynamics (the Forest Game, FG) was introduced. This model intended to explain the pattern observed in a map of BCI that had been published in a paper by Welden *et al.* (1991) [see Fig. 1(b)] and in some other tropical rainforests, where power-law distributions of gap sizes and tree heights have been found [see for instance data in Gentry (1990)]. Some possible implications related to the appearance of these power-laws will be discussed later. The map that

appeared in Welden *et al.* (1991) considered a gap area of height below 10 m in 1983, 1984 or in both years. The study of this spatial pattern has been thorough and some conclusions were drawn from it: the spatial forest structure is multifractal with a wide spectrum of different gap sizes; the distribution of gap sizes follows a very well-defined power law, and the gap-gap correlation function is also a power law (Manrubia and Solé, 1996). The FG was able to account not only for the qualitative, but also for the quantitative features of BCI.

Our model is a cellular automaton with periodic boundary conditions. Each cell might be in a state represented by a real number between zero and a maximum height h_c that intends to mimic the height of the tree occupying that site. Each tree is allowed to grow, to fall and create a gap, and to be born if the cell is empty. In the FG, interaction among nearest trees takes place at two levels. First, there is a competition for resources (light, nutrients, space, . . .) that influences the rate of growth. Second, each time a tree falls, it may form a gap in the canopy depending on its biomass. Define $h(i, j; t)$ as the height at time

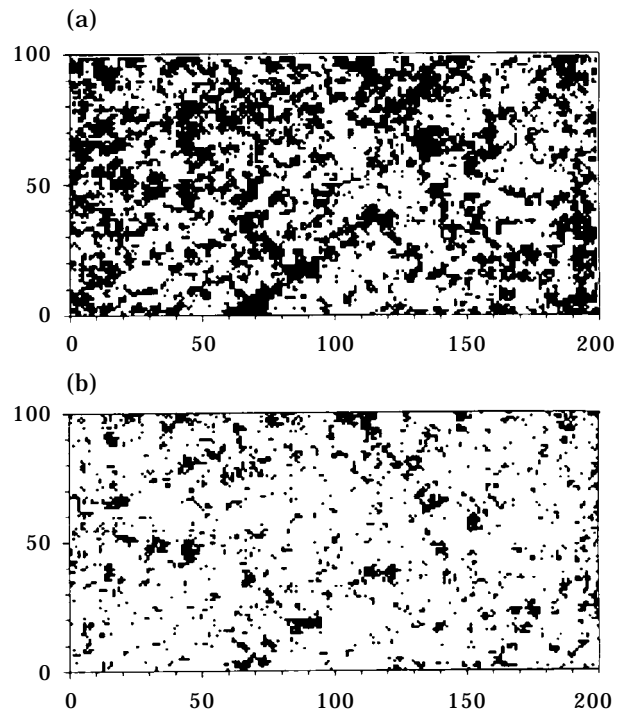


FIG. 1. Two maps of Barro Colorado Island with a different definition of “gap”, or low canopy points, represented as black dots. (a) Trees lower than 20 m are considered gaps. Data from Hubbell & Foster (1986). (b) Trees lower than 10 m are gaps. Data from Welden *et al.* (1991). In both maps, black sites fit the previous criteria in years 1983 and/or 1984. The axes display the size of the plot in pixels. Each pixel represents an area of $5 \times 5 \text{ m}^2$, giving thus a total area of 50 ha.

t of an automaton located in site i, j in the lattice. The specific rules of the model are as follows.

- (i) Birth: if $h(i, j; t) = 0$, the $h(i, j; t + 1) = h_0$ with probability p_b .
- (ii) Growth: if $h_c > h(i, j; t) > 0$, then

$$h(i, j; t + 1) = h(i, j; t) + \Theta \left[1 - \left\{ \frac{\gamma}{z} \sum_{\langle kl \rangle} h(k, l; t) \right\} \right]$$

where the sum is restricted to the z nearest neighbors. The function $\Theta(x)$ is zero for $x < 0$ and x for $x > 0$. It also defines the units of the height of our trees, which could be assumed to be in meters.

- (iii) Death: if $h(i, j; t) \geq h_c$ then $h(i, j; t + 1) = 0$, or independent of height, a tree falls down with probability p_d .
- (iv) Gap formation: when a tree $h(i, j; t)$ falls down, a certain variable amount of trees surrounding it are also removed according to the condition

$$h(i, j; t) < \sum_{\langle kl \rangle} h(k, l; t).$$

This mean that an amount of biomass at most equal to the one of the falling tree is also removed in a neighborhood defined by the previous inequality.

Our free parameters are p_b, p_d and γ . The two limiting sizes h_0 and h_c are the minimum and maximum height allowed. A new germinated tree is assigned the minimum height $h_0 = 0.1$ m in our simulations. The maximum height (seldom attained for realistic parameters) is $h_c = 30$ m. On the other hand, it is known that trees standing above the surrounding canopy have a greater probability of falling (Hubbell & Foster, 1986). We work in a square lattice with Moore neighborhood, so the coordination number is $z = 8$. The parameter γ tries to take into account all the competition among nearest trees for resources. It is the main parameter in controlling the distribution of heights in the forest.

The parameter p_b was fixed to value 0.5 in our first simulations. This allowed the construction of a phase space for the model [see for example Solé & Manrubia (1995b)]. There is a very interesting part of this space of parameters where the most complex behaviors are observed. In particular, the values of p_d for which this holds are between 1–2% (mortality per year), in the range calculated to be the average of many tropical rainforests [see for example table 2 in Lieberman *et al.* (1985)] and γ has a wider range, $0.5 < \gamma < 10$. The values of γ cannot be directly computed, but we

observed that the pattern of BCI gaps for height below 10 m was reproduced in all its details (fractality, correlation function and gap distribution) for a value of $\gamma \approx 2$. If the value of p_b is changed, the domain where complex behavior is observed shifts slightly in the phase space, but there is no qualitative change in it.

We have attempted to recover the pattern of Fig. 1(a). To do so, it was necessary to change the parameters in our model. With our definition of gap ($h(i, j) = 0$), it was necessary to increase the mortality per year to obtain a high density of clearings. In our model it is not possible to “redefine” a gap by simply taking taller trees, because height is strongly dependent on γ , and the dynamics of gap formation and tree growth are in some sense decoupled. By using the set of parameters $\mathcal{P}_{FG} = \{p_b = 0.3, p_d = 0.1, \gamma = 1\}$, the density $\rho_0 = 0.36$ is obtained. This is almost the same value that the KIF model gives for the set of parameters \mathcal{P}_{KIF} . It is worth noticing that the values obtained for $q_{0/0}$ with both models differ from that measured in BCI. Both models give $q_{0/0} \approx 0.44$, a value clearly deviating from the 0.58 expected. This is related to the appearance of several gaps “larger than expected by chance” in the real system.

The main point of our comment is related to the actual gap size distribution. This is a very informative measure that can be easily performed over Fig 1(a). In Fig. 2 we have represented in the same plot the distributions obtained from Fig. 1(a), KIF model (parameters \mathcal{P}_{KIF}), FG model (parameters \mathcal{P}_{FG}) and a pure percolation pattern with density $\rho_{PP} = 0.35$. It is very clear that the real distribution is well fit by a power-law with an exponent $\alpha_{BCI} \approx 1.6$ through almost three decades. The FG model gives an exponent equal to this value if we consider statistical fluctuations, $\alpha_{FG} \approx 1.7$. The KIF model also reproduces the spatial distribution of gaps with an exponent close to 1.6. In fact, both ρ_0 and $q_{0/0}$ are averages over Fig. 1(a), thus many different gap distributions could in principle be adjusted to them. However, the distribution of gaps captures some more features of the pattern that we think should be recovered by a reliable model. Both KIF and FG models seem to adjust quite well to the actual gap distribution for small gap sizes. As can be clearly seen, both deviate from BCI distribution for large sizes. Some comments seem to be of interest here. First, although both models give higher distributions than the pure percolation distribution, they do not recover the largest gaps in the real forest. Pure percolation presents a deviation to an exponential distribution because the density that has been fixed is still far from

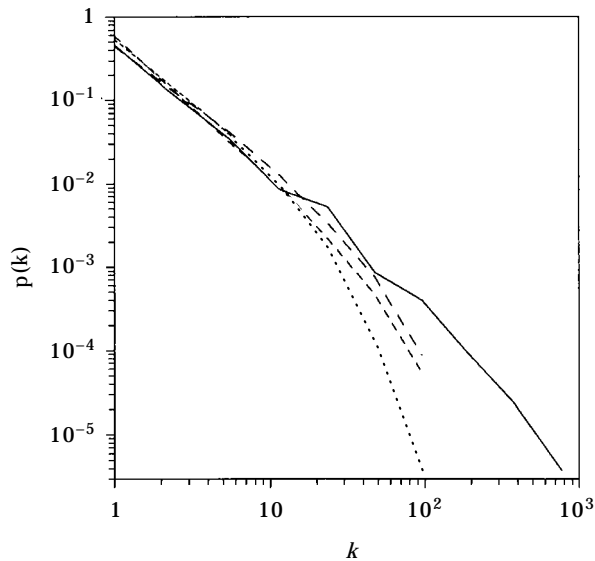


FIG. 2. Normalized gap distribution for Barro Colorado Island (BCI), for the two models Kubo–Iwasa–Furumoto (KIF) and Forest Game (FG), and for a pure percolation (PP) system. k is the size of the gap with Neumann neighborhood, and $p(k)$ is the probability of finding a gap of size k . Real data are well fit by a power-law distribution, $p(k) \propto k^{-z_{\text{BCI}}}$ with an exponent ≈ 1.6 . The simulation for the KIF model was run over a lattice of size 100×100 during 1000 time steps after discarding 200 transients, a period necessary for the system to settle in a statically stationary state. The simulation for the FG was run over a 200×200 lattice and average over 1000 time steps after discarding 500 transients. As can be seen, both models approach closely the BCI distribution for small and medium gap sizes. The parameters used for each simulation are specified in the main text. The distribution for the purely percolating system was obtained by averaging 10 independent configurations of size 100×100 with density $\rho_{\text{pp}} \approx 0.35$. The points in the distributions have been logarithmically binned in boxes of powers of two. Key: — BCI, — — KIF, . . . FG, . . . PP.

the critical percolating point, where power-law distributions with a cut-off only due to finite system size would be observed. The modified models with short-range correlations are not able to avoid this finite size effect. Second, recall the mechanism of gap formation in the models. One (KIF) considers nearest neighbors gap density to adjust the probability of falling or germinating, and another (FG) simply allows the formation of a gap depending on the biomass of a randomly chosen tree. Both mechanisms are similar as seen by comparing the KIF and FG distributions in Fig. 2. Nevertheless, a lack of larger gaps [compared with Fig. 1(a)] is observed. This probably means that *another mechanism* is responsible for the formation of them. A comparison between the two maps in Fig. 1 might give some insight about this problem. If a gap is defined at height 20 m, one realises that the “new” gap sites in Fig. 1(a) [compared with Fig. 1(b)] appear mainly close to gaps present at height 10 m. It could be that the formation

of gaps due to a lack of screening depends on the height of nearest neighbors, next-to-nearest neighbors, and so on. This may explain the appearance of long-range correlations and thus the formation of gaps larger than expected from a simple model as pure percolation (Stauffer & Aharony, 1991). On the other hand, it is our belief that both KIF and FG models belong to the same universality class that pure percolation thus short-range correlations (introduced in the rules of the models) cannot be responsible (close to a critical point) for the formation of a different pattern (Binney *et al.*, 1993). In other words, they will never be able to account for very large gaps with fixed density for any set of parameters. This fact is included in the dynamic rules.

A second step towards the analysis of the spatial gap distribution might be to calculate the fractality of the pattern or the gap–gap correlation function. This last measure is defined as the average number of gaps (located in \mathbf{r}' at a distance $d = |\mathbf{r} - \mathbf{r}'|$ from a site in the gap state (in \mathbf{r})), or

$$C(d) = \frac{1}{N} \sum_{|\mathbf{r}-\mathbf{r}'|=d} \rho(\mathbf{r})\rho(\mathbf{r}')$$

where $\rho(\mathbf{r}) = 1$ for a gap site and is equal to zero for a cell with a tree. The normalization factor is $N = n_n \times \rho_0$, where n_n is the maximum number of neighbors at distance d . The two-point correlation function $C(d)$ is simply the probability for an observer located in a gap of finding a gap when choosing at random a site at distance d . From the definition of $C(d)$, the two values used in the pair approximation are now $C(0) = \rho_0$ and $C(1) = q_{0,0}$. When the system that the models try to recover has an exponentially decaying correlation function [this is the rule far from a critical point, $C(d) \propto e^{-d}$], it is reasonable to attempt an analytic approach to the problem just by taking into account $C(0)$ and $C(1)$ and discarding higher order terms. But when the modeled system is close to a critical point, where $C(d) \propto d^{-z}$, this approximation breaks down, due to the appearance of long-range correlations. This explains the failure of the pair approximation in the case of BCI. The right global and local densities can only be obtained by considering terms in $C(d)$ up to a system’s correlation length [see Binney *et al.* (1993) for further explanation about critical phenomena].

A second point which is worth analysing in some detail concerns the following statement made by Kubo *et al.* (1986), p. 241: “when we observe deviation between the predicted equilibrium composition of the forest and the observed pattern, we may conclude that the current spatial pattern is not at

equilibrium". This is also easy to test in the model. The set of parameters chosen to reproduce the gap patchiness of BCI in Fig. 1(a) fixes the time step of the model to be about 1 year. This is the same election that was performed in the FG. Then, just by looking at the time that the model needs to reach a statistically stable state, one may guess the approximate number of years that BCI would need to set in this state of equilibrium *if the model is going to capture the essential dynamics of the real rainforest*. Beginning with an initial condition far from this equilibrium (empty forest, all sites in gap state), we have calculated the convergence time (in simulation time steps) needed to reach the equilibrium (see Fig. 3). For the KIF model, this time is no more than 50 time steps, that would mean about 50 years. The convergence time is somewhat longer for the FG, due to the multiple states available to each site and to the initial condition: just 50% of minimum size trees randomly scattered in the forest. The variation of ρ_0 with time is depicted in Fig. 3 for two different system sizes, 100×100 and 200×200 , both comparable to the actual size of Fig. 1(a). There are estimations of the time that BCI has remained undisturbed. For example, in Gentry (1990, p. 522): "Radiocarbon dating indicates that the last of these clearings was cut more than 550 years ago, and the phytolith record demonstrates that the forest was never cleared for maize agriculture." This leaves us with an undisturbed forest for at least 500 years, which is more than a factor 10 to the time that KIF model requires to set in an equilibrium state.

It is our belief that models should take into account some other features of real systems that have not been

considered and that might be relevant for their dynamics and the observed macroscopic patterns. Some work has been done in the direction of minimising the number of variables needed to describe these large systems with many degrees of freedom. In particular, it has been conjectured that the interaction among individuals in a rainforest might poise the system to a so-called critical state [Solé and Manrubia, 1995a; see Solé *et al.* (1996) for a review of critical phenomena]. When a system is found in a critical state, it means this system is far from the thermodynamic equilibrium, but this does not mean it is not in a stable state. The very dynamic rules may keep the system in a statistically stationary state, in which the distributions of macroscopic magnitudes are constant in time. This critical state would imply that the rainforest dynamics has as a natural output (1) power-law distributions in relevant magnitudes, including temporal fluctuations and (2) the formation of fractal patterns in space. Some data from real rainforests seem to support this conjecture. In particular, apart from gap distributions, tree height distributions have also been found to follow clear power-laws [Solé and Manrubia (unpublished data) from data in Gentry (1990)]. The conjecture of "criticality" for the rainforest supports the approximation of using minimal models for their description. In a critical state, small details can be skipped if one tries to explain the macroscopic patterns (both in time and in space), and the use of minimal models is completely justified (Binney *et al.*, 1993).

Our concerns about the discussed models are basically dependent on its ability to generate the largest gaps observed in the real rainforest. On the other hand, our previous discussion about criticality does not apply in the KIF case: this model does not poise the system to a critical state, where power laws should be observed. As the authors show, the model gives exponential distributions for a wide set of parameters. In fact, they do not present a single example with a power-law distribution, although we have shown that this is the case for the set of parameters \mathcal{P}_{KIF} . Nevertheless, we think that this model could be very useful perhaps to represent some other type of forests, for instance a case that they report, a subalpine spruce-fir forest with a gap area distribution that has been found to be a negative exponential (Foster & Reiners, 1986). It is clear that the observation of gaps causing more gaps has to be taken into account, but in the modeling of a real forest, the interaction at the level of growth must also be considered. In this sense, the FG and KIF models might complement each other and be a first step towards the understanding of the general problem of

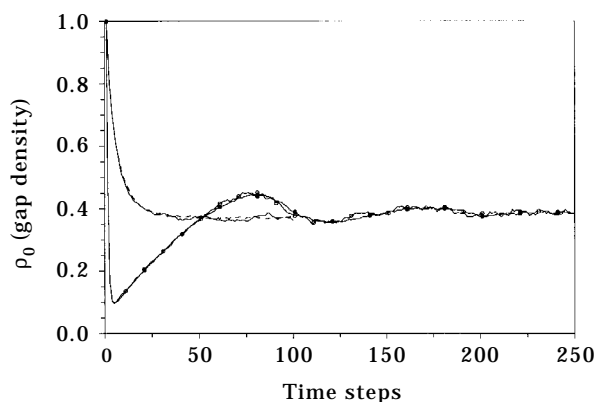


FIG. 3. Convergency of the models to the statistically stable state. As can be seen, the KIF model reaches equilibrium in about 50 time steps, irrespectively of the system size. The FG needs some more time because it is a multistate system and each automaton has a multiplicity of states. Nevertheless, the time required to reach the equilibrium density is about 200 time steps. Key: — $N_{\text{KIF}} = 100$, - - - $N_{\text{KIF}} = 200$, - · - · - $N_{\text{FG}} = 200$, · · · · $N_{\text{FG}} = 100$.

not only gap formation, but also the vertical structure of the forest.

The authors wish to thank Jodi Delgado for his kind computer assessment. This work has been supported by a grant DGYCIT PB94-1195.

REFERENCES

1. BINNEY, J. J., DOWRICK, N. W., FISHER, A. J. & NEWMAN, M. E. J. (1993). *The Theory of Critical Phenomena. An Introduction to the Renormalization Group*. Oxford: Clarendon Press.
2. FOSTER, J. R. & REINERS, W. A. (1986). Size distribution and expansion of canopy gaps in a northern Appalachian spruce-fir forest. *Vegetatio* **68**, 109–114.
3. GENTRY, A. H., ed. (1990). *Four Neotropical Rainforests*. Yale: Yale University Press.
4. HARADA, Y. & IWASA, Y. (1994). Lattice population dynamics for plants with dispersing seeds and vegetative propagation. *Res. Pop. Ecol.* **36**, 237–249.
5. HUBBELL, S. P. & FOSTER, R. B. (1986). Canopy gaps and the dynamics of a neotropical forest. In: *Plant Ecology* (Crawley, M. J., ed.), pp. 77–96. Oxford: Blackwell Science.
6. KUBO, T., IWASA, Y. & FURUMOTO, N. (1996). Forest spatial dynamics with gap expansion: total gap area and gap size distribution. *J. theor. Biol.* **180**, 229–246.
7. LIEBERMAN, D., LIEBERMAN, M., PERALTA, R. & HARTSHORN, G. S. (1985). Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. *J. Ecol.* **73**, 915–924.
8. MANRUBIA, S. C. & SOLÉ, R. V. (1996). Self-organized criticality in rainforest dynamics. *Chaos, Solitons & Fractals*, Vol. 7, **4**, 523–541.
9. SOLÉ, R. V. & MANRUBIA, S. C. (1995a). Are rainforests self-organized in a critical state? *J. theor. Biol.* **173**, 31–40.
10. SOLÉ, R. V. & MANRUBIA, S. C. (1995b). Self-similarity in rain forests: Evidence for a critical state. *Phys. Rev. E* **51**, 6250–6253.
11. SOLÉ, R. V., MANRUBIA, S. C., LUQUE, B., DELGADO, J. & BASCOMPTE, J. (1996). Phase transitions and complex systems. *Complexity* **4**, 13–26.
12. STAUFFER, D. & AHARONY, A. (1991). *Introduction to Percolation Theory*, 2nd edn. London: Taylor & Francis.
13. WELDEN, C. W., HEWETT, S. W., HUBBELL, S. P. & FOSTER, R. B. (1991). Sapling survival, growth and recruitment: relationship to canopy height in a neotropical forest. *Ecology* **72**, 35–50.