



Modelling forest–savanna mosaic dynamics in man-influenced environments: effects of fire, climate and soil heterogeneity

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Received 2 July 2002; received in revised form 26 June 2003; accepted 11 July 2003

Abstract

Forests and savannas are the major ecotypes in humid tropical regions. Under present climatic conditions, forest is in a phase of natural expansion over savanna, but traditional human activities, especially fires, have strongly influenced the succession. We here present a new model, FORSAT, dedicated to the forest–savanna mosaic on a landscape scale and based on stochastic modelling of key processes (fire and succession cycle) and consistent with common field data. The model is validated by comparison between the qualitative emergent behaviour of the model and results of biogeographical field studies. Three types of forest succession are shown: progression of the forest edge, formation and coalescence of clumps in savanna and global afforestation of savanna. The parameters (frequency of savanna fires, climate and soil fertility) appear to have comparable effects and there is a sharp threshold between a forest edge progression scenario and the cluster formation one. Moreover, pioneer seed dispersal pattern and recruitment are determinant: peaked curves near a seed source and far dispersal combine to increase the fitness of the pioneers. © 2003 Elsevier B.V. All rights reserved.

Keywords: Forest–savanna ecotone; Stochastic model; Cellular automata; Fire; Seed dispersal

1. Introduction

In many regions starting from the equatorial belt, evergreen and semi-evergreen tropical forests are progressively replaced by humid savannas (e.g. Tucker et al., 1985) through a landscape of forest–savanna mosaics.¹ The total area presenting a mix of forest

and savannas in 1997 was evaluated by Achard et al. (2002) to ca. 3×10^6 km² (compared to ca. 9×10^6 km² of closed forests). The question of the stability of the border between savannas and forests, and of the influence of men activities in these regions, are crucial. How will that border evolve in the future? Which conditions led to past evolution as reconstructed from paleo-environmental studies? What are the impacts of the different parameters (natural or linked to human activities)? Under different demographic and climatic scenarios, are these landscapes likely to shift towards forest-dominated or savanna-dominated ecosystems?

Field studies already gave partial answers. First, paleo-environmental reconstruction has evidenced dry

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¹ In this paper “forest” will be used for humid tropical forest (evergreen or semi deciduous) and “savanna” for humid savannas (e.g. Guinean savannas in Africa).

periods leading to forest recession in favour of savanna in South America between 7500 and 4500 bp (Servant et al., 1993) and in central Africa between around 4000 and 1200 bp (Vincens et al., 1999). After these major droughts, paleo-environmental reconstruction shows a trend towards the progression of forests over savannas, with a time response of vegetation to climate change of a few centuries. Most of non-climax savannas (found where the climate and the soil conditions would theoretically be suitable to a forest ecotype) are now understood as relicts from drier periods (Aubréville, 1962; Mariotti and Peterschmitt, 1994; Schwartz et al., 1996; Desjardins et al., 1996). Field studies of present savanna-forest boundaries and remote sensing techniques confirm this progression of forest over savanna (e.g. Youta Happi, 1998; Guillet et al., 2001, in Cameroon; Fabing, 2001, in Congo; Ratter, 1992, in Brazil; Puyravaud et al., 1994, in India). Nevertheless, measured forest transgression rates (on the order of a few meters a year, corresponding to a few kilometres per 1000 years) seem small compared to those inferred from paleo-environmental reconstruction.

It is most likely that this discrepancy can be explained by present human action in the transgression zones: savanna burning and land clearing for cultivation. Savanna fires reduce or prevent the settlement of forest species in savannas and subsequent forest encroachment. However, abandoned fields near forests are in general readily colonised by forest (see, e.g. Letouzey, 1968; Guelly et al., 1993). Even slash-and-burn zones can revert to forest if they are not too large, as shown in Brazil by Eden (1986) (cited by Eden and McGregor, 1992). Because of higher soil nutrient levels, forest encroachment seems to be faster on pastures and agricultural zones derived from forest clearing than on older savannas (Eden and McGregor, 1992; King et al., 1997). Moreover, field experiments of reforestation of cleared forest zones show forest development in these zones even when they are burnt frequently (e.g. Brookman-Amisshah et al., 1980; Moreira, 2000). Derived savanna only persists when clearings are intentionally maintained (Dounias, 2000; King et al., 1997) or when land-use results in soil impoverishment (Hopkins, 1992), generally in densely populated regions (Fabing, 2001).

Our goal is to obtain a better understanding of forest transgression, and to determine the key processes and the main parameters. We show how parameter changes

lead to the different patterns of transgression described in the literature: regression of forest; linear progression of forest edge (de Foresta, 1990); formation of clumps of forest in savanna (Gautier, 1989); afforestation of a whole zone (Eden and McGregor, 1992). Some other questions remain partly unexplored: to what extent is afforestation favoured by the presence of collapsed or active termite mounds? To what extent are transgression dynamics determined by the pioneer species involved, and especially by their seed shadow patterns? To answer these questions, we built a model dedicated to forest-savanna ecotone dynamics.

As is often the case in ecological problems, different processes are involved at different scales, and modellers have to choose one level of description. In global models, the dynamics of the forest and savanna is considered at such a large scale that local processes such as seed dispersal, fires, and human activities are excluded (Peng, 2000, see however, Moorcroft et al., 2001; Thonicke et al., 2001). On the other hand, some models of savanna vegetation study tree/grass interaction and consider the fate of individuals (e.g. Menaut et al., 1990). We aimed towards a model describing elementary processes (succession cycle, fires in savanna) and inputs (soil structure, climate) of the Forest Savanna Transgression (FORSAT) at an intermediate level of description (mesoscale). Information from the individual level (microscale) is evaluated as stochastic processes with a small number of parameters. The emergent behaviour at the larger scale (macroscale) is compared to field observations. Models were already developed at this scale for dry forest-savanna ecotone (e.g. Loehle et al., 1996; Li, 2002) but not for the humid tropics.

Our model, FORSAT is spatially explicit at a landscape scale and well suited for comparison with remote sensing data. Although all examples given here concern the Central African tropics, the model has a global scope. After describing the approach chosen to model forest transgression, we present a comparison between its qualitative emergent behaviour and biogeographical observation of the ecotone dynamics to illustrate and validate the model. Then we explore the model behaviour with simple parameters, especially the effect of climate and fire frequency on the rate and type of transgression. Finally, we explore the changes induced by the presence of collapsed termite mounds, and the influence of pioneer tree seed shadows. More

extensive applications to specific field studies will be presented in forthcoming papers.

2. Hypotheses and description of the model

FORSAT is a vegetation model of a landscape mosaic of forests and savannas in the humid tropics. To construct such a model, one must determine: (1) the key processes for the system (here, savanna fires and the succession cycle or settlement of forest trees species in grassland); (2) the vegetation state variables relevant to these processes; (3) the appropriate framework in which these hypotheses can be included; and (4) the rules of the dynamics. As for any ecological model, two constraints need to be clearly identified beforehand: the availability of sets of initial conditions (e.g. remote sensing data, quadrat-based field observations or GIS data) and the parsimony of the model, i.e. the limitation of the numbers of parameters.

2.1. Key processes

As mentioned above, we consider that the key processes for the system are savanna fires and the succession cycle or settlement of forest trees species in grassland. The question of soil water is important in drier systems such as the sub-sahelian tree and shrubs savannas, while it does not play a role in tropical humid regions (excepted maybe for floodplain forests and water logged savannas as those found in parts of South America). Menaut et al. (1990), for instance, have written that: “apart from the case of water-logged savannas [. . .], no evidence yet shows that tree clumps are bound to particular soil conditions”.

2.2. Vegetation states

The process of forest recruitment in savanna has been often described and appears to be similar throughout the tropics (Letouzey, 1968, p. 230). Light-demanding tree species of the dense forest (e.g. *Albizia* spp. in Cameroon) defined by Letouzey (1968) as pioneers, play an important role. Their seeds sprout easily in open savanna, generally near a forest gallery edge or a relict forest patch. As they grow and their crowns develop, the herbaceous cover is shaded and reduced. The floristic composition changes, with the

appearance of ferns, undergrowth plants, and progressively, shade-tolerant tree species. Eventually, these replace the light-demanding species and the savanna patch is turned into a dense forest.

The impact of fire varies with the vegetation type. Herbaceous cover burns when it is dry enough, but it regenerates afterwards. The chance for a pioneer tree to resist fire increases as it grows, with an important threshold when its crown overgrows the herbaceous cover (Menaut et al., 1990) and is therefore more likely to escape fire. Dense forest stands are well protected from fires because of low or absent herbaceous cover and humid microclimatic conditions (Biddulph and Kellman, 1998; Belsky and Amundson, 1992); however, a late fire in a long dry season can penetrate dense forest, but it generally leaves enough trees for a quick reestablishment.

Thus, we can define four groups of species that correspond to four vegetation stages, distinguished by their biological structure and their sensitivity to fire: (i) ‘*Herbs*’ is dominated by grasses and herbs (either savanna grasslands with a sparse shrubby vegetation or low understory vegetation in forest clearings); (ii) ‘*Young Pioneers*’ is dominated by seedlings or bushes of forest woody pioneer species: it is the first stage in the colonisation by the forest; (iii) ‘*Adult Pioneers*’ is dominated by seed producing pioneer trees with crowns above understory species, that therefore can escape fire; (iv) ‘*Forest*’ corresponds to patches of dense forest where the herbaceous cover is low and the structure, if not the species cohort, has reached an equilibrium. These four vegetation stages have decreasing susceptibility to burn when reached by a fire. What we here call stages of vegetation are similar to plant functional types (PFTs), in the sense that trees are defined by their roles in the particular issue of forest transgression over savanna, which are played by different species in different parts of the tropics.

2.3. Choice of a model frame

We have modelled this system with a Von Neumann object analogous to a cellular automaton. Cellular automata (CA) have been used in ecological modelling for a long time (see Balzter et al., 1998 for a review). In CAs, space and time are discrete. The variables describing the system can take only a finite set of possible values, and each cell evolves according to the same

updating rule. The FORSAT model is not a CA stricto sensu, as it allows for interactions between cells that are not in the direct neighbourhood, as will be detailed in subsequent sections.

The variable, or state, is the vegetation type. In addition to the vegetation states described above ('Herbs', 'Young Pioneers', 'Adult Pioneers', 'Forest'), we consider a 'Sterile' state, where no vegetation can ever grow, representing rocks or roads, for instance.

Space is modelled as a two-dimensional grid with 5-m-sided square cells. In each cell, the vegetation is considered homogeneous. Data from real sources can therefore easily be included. The time step is 1 year, during which the dynamics of succession and fire propagation through the savanna are simulated. The time variable is t and the space variable, \vec{r} .

To conform to the constraint of parsimony, processes are modelled stochastically. This is a way to deal with processes that are poorly known in detail or complicated to model deterministically, by limiting the numbers of parameters. So each cell is assigned a probability to turn into the next state in the succession cycle. These probabilities are related to biological processes and properties, such as rates of seed dispersal and sprouting, growth and mortality.

Two additional external inputs are included: climate and soil fertility. The climate factor summarises the influence of both the mean rainfall and the duration of the dry season. It is identical for the entire simulated landscape, and has the notation $c(t)$. Depending on the nature of the soil, the encroachment of forest species is favoured or penalised. To model this aspect, we have introduced a soil fertility parameter associated with each cell: the higher this parameter, the more fertile the area. It has the notation $s(\vec{r}, t)$. These environmental variables are normalised so that values around unity represent neutral conditions, values superior to unity denote conditions favourable to forest, and values inferior to unity, harsh conditions.

2.4. Succession cycle

During the cycle a fraction of randomly chosen sites changes states. The transition probability from state i to state j , $P^{i \rightarrow j}$, is the product of a basic transition probability in the absence of environmental variability, called $p^{i \rightarrow j}$, times an environmental 'reductor', function of the different factors considered (climate,

nature of the soil, etc.), called $v^{i \rightarrow j}$

$$P^{i \rightarrow j}(\vec{r}, t) = p^{i \rightarrow j}(\vec{r}, t) \times v^{i \rightarrow j}(c(t), s(\vec{r}, t)) \quad (1)$$

Transition rates depend on the type of process that is involved. The cycle is summarised in Fig. 1.

2.4.1. Recruitment of pioneers

The recruitment of pioneer species in a herbaceous cover encompasses the biological processes of reproduction, seed dispersal and establishment. Three approaches can be combined to model this aspect:

1. *Homogeneous seedling recruitment* over the whole space, so that the basic probability of appearance of the pioneers does not depend upon time or space:

$$p^{h \rightarrow yp}(\vec{r}, t) = p_0^{h \rightarrow yp}; \quad (2)$$

where $hc \rightarrow yp$ indicates the transition from the 'Herbs' state to the 'Young Pioneers' state.

2. *Spatially explicit recruitment*: The probability of transition from 'Herbs' to the 'Young Pioneers' state is directly influenced by the presence of seed producers in a neighbourhood. Let $f(r)$ denote the seed shadows, that is the probability of successful dispersal events of pioneer seeds at a distance r from a parent tree. We assume that the basic probability of transition of a 'Herbs' site to 'Young Pioneers' is simply the sum of the probabilities induced by surrounding trees. Thus,

$$p^{h \rightarrow yp}(\vec{r}) = \sum_{\vec{r}'/\text{state is } f \text{ or } ap} f(|\vec{r} - \vec{r}'|), \quad (3)$$

where the sum is restricted to the sites in the 'Forest' or 'Adult Pioneers' states.

3. *A patch model approach*: The simulated space is divided into N identical patches. In each patch i , the number n_i of dispersers ('Adult Pioneers' and 'Forest' cells) is computed. Then, to every savanna cell of a patch j is assigned the same basic transition probability, depending on the distance between the two patches i and j , through the function f described above, weighed by the number n_i of dispersers. Taking into account all possible cells i , one finds

$$p^{h \rightarrow yp}(\vec{r}, t) = \sum_{z'=1}^N n(z') f(|\vec{r}_z - \vec{r}_{z'}|). \quad (4)$$

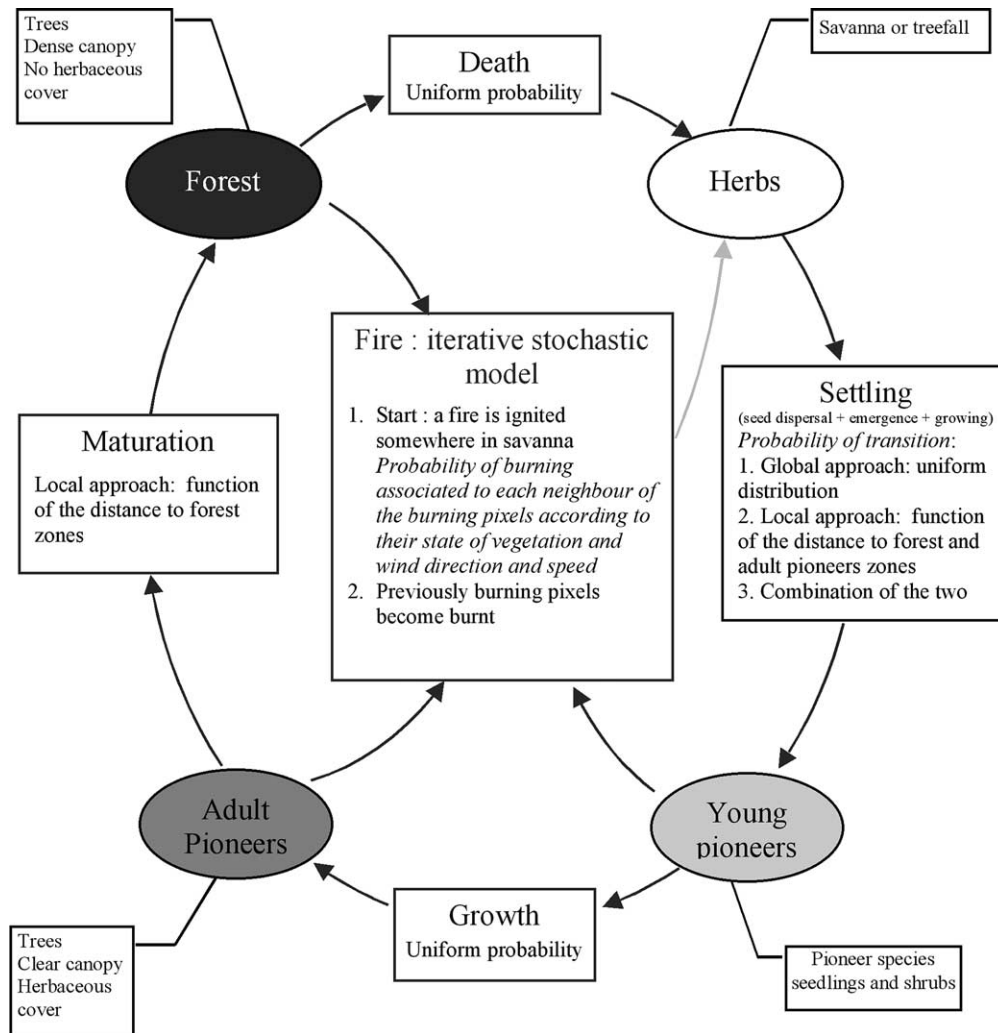


Fig. 1. Summary of the two key processes modelled in FORSAT each year: succession and fire, which acts as a shortcut to the 'Herbs' state.

The patch approach permits us to account for spatially explicit seedling recruitment, in restraining the computation time to reasonable values.

By combining the three approaches we can explicitly describe short-range dispersal events with the local approach and model the long-range dispersal, representing rare but important events, using either the global or the patch approach.

2.4.2. Growth of pioneer species

The basic probability of growth of young pioneers in trees, is considered as independent of the location

and constant. So, every 'Young Pioneers' cell has the basic transition probability:

$$p^{yp \rightarrow ap}(\vec{r}, t) = p_0^{yp \rightarrow ap} \tag{5}$$

2.4.3. Transition to forest

The basic transition from the 'Adult Pioneers' state to the 'Forest' state involves the dispersal of shade tolerant species, many of which have short-ranged dispersal modes. The probability of transition from the 'Adult Pioneers' to the 'Forest' state is also modelled with spatially explicit rules, similar to the ones used in the pioneer recruitment stage.

2.4.4. Clearing formation

Finally, ‘Forest’ zones can revert to ‘Herbs’ (see definition above) through small-scale disturbances (treefall gap formation). This is analogous to many gap model approaches (see, e.g. Vanclay, 1995). The gap formation is a complex phenomenon, involving the death of a large tree (that depends on the tree age) and the effect of the crown fall (whatever the age of the plot). In a first approximation, it can then be considered that the basic probability of gap formation is uniform across space and does not depend on vegetation age (see, e.g. Riera and Alexandre, 1988).

2.5. Fires

We could model fire propagation stochastically by two methods: an iterative propagation algorithm (like the one used by Hargrove et al., 2000), where at each iteration the fire front is updated, and a cluster-search algorithm (Hoshen and Kopelman, 1976, used in Chave, 2000), where connected clusters of fire-sensitive cells are first constructed, and then ignited. The cluster algorithm is faster (the time of execution is proportional to $n \ln(n)$ for the Hoshen-Kopelman algorithm and to $n^{3/2}$ for the iterative one, where n is the total number of cells) but it cannot easily incorporate wind and slope effects and it ignores the possibility for a cell to be attained by a fire front more than once. We here thus used the iterative propagation algorithm, and considered three burning states: intact, burning and burnt cells. The number of fires per year can be either fixed or be distributed according to a Poisson distribution. Intact cells chosen randomly among the savanna cells become starting points for fire.

At each time sweep, a fire spreads from the burning foci onto their four nearest neighbours, with a rate that depends upon the vegetation type in these neighbours. Every burning cell is turned into burnt cells at the next stage. The algorithm ends when there are no more burning sites. Then, burnt cells regenerate in ‘Herbs’ (Fig. 1).

A wind factor (intensity and direction) can be taken into account: the burning probability of the neighbours depends on wind direction and intensity relative to the burning sites. Climate has a homogeneous influence on the burning probability. Differences between early and late dry season fires are taken into ac-

count by modulating this parameter; although we do not do it here, it would be more realistic to store the time elapsed since the last burning episode to determine whether trees—young and adult pioneers—are destroyed or not (Moorcroft et al., 2001).

3. Model validation

3.1. Comparison with a real biogeographical study

In this section, FORSAT emergent behaviour is confronted with the processes identified by biogeographical studies. We have based our comparison on the site studied by Youta Happi (1998) in Cameroon. We use a realistic local seed dispersal model with the seed shadows represented by a Gaussian curve. The other parameters are summarised in Table 1.

3.1.1. Progression of forest

From field studies, it appears that the progression of forest does not always consist of a regular advance of the forest edge. In particular, forest progression is faster between narrow savanna fingers, which causes the edge to smoothen. Moreover, clusters can appear in savanna and be connected to the main forest when the edge reaches them. The first stage of the connection is a vegetation bridge between the cluster and the edge (see Fig. 2a and b).

Fig. 3 shows snapshots of simulations using the parameters summarised in Table 1. The initial configuration consists of two gulfs of savanna in a linear forest

Table 1
Parameters for simulations described in the section ‘Comparison with a real biogeographical study’

State	Transition to the next state	Burning probability
‘Herbs’	Global: $p_0^{h \rightarrow yp} = 0.02$ Local: Gaussian seed shadows $f(x) = 0.1 \exp(-x^2/10)$ up to 10 cells near ‘Adult Pioneers’ and ‘Forest’ cells	1
‘Young Pioneers’	Global: $p_0^{yp \rightarrow ap} = 0.2$	0.55
‘Adult Pioneers’	Local: $f(x) = 0.2$, up to 1 cell near ‘Forest’ cells	0.2
‘Forest’	Global: $p_0^{f \rightarrow h} = 0.005$ <i>5 fires every other year</i>	0.005 <i>Climate factor: 1.0</i>

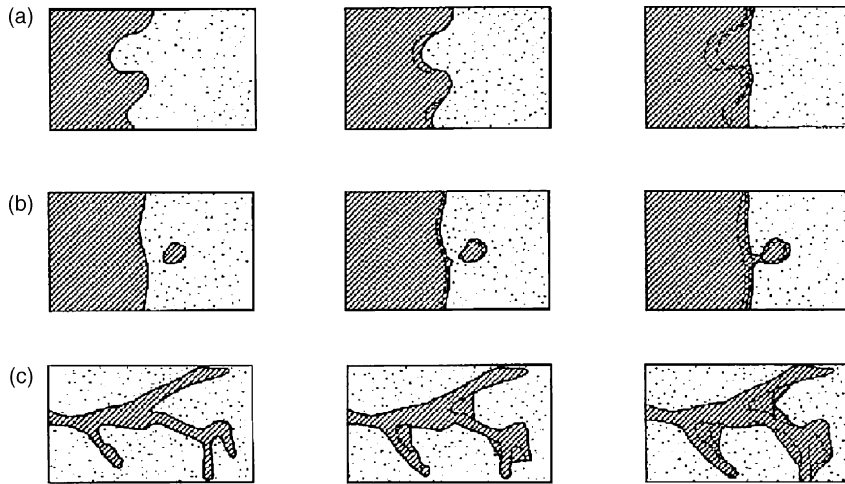


Fig. 2. Observation-based diagram of (a) savanna gulfs, (b) incorporation of cluster and (c) growing of gallery forest (from Youta Happi, 1998).

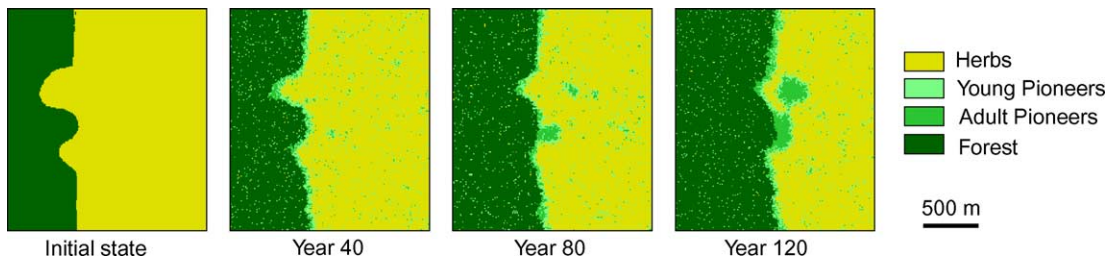


Fig. 3. Evolution of forest–savanna ecotone for parameters summarised in Table 1, with filling of the savanna gulfs, formation and growing of clusters, and their incorporation to the forest domain by the apparition of a ‘vegetation bridge’.

edge. The simulation shows the filling of these gulfs and the formation and incorporation of a forest cluster. These processes are similar to the observations made by Youta Happi (1998).

3.1.2. Colonisation of savanna from a gallery forest
 A gallery forest grows by extension of its extremities and afforestation of savanna gulfs. The simulated maps in Fig. 4 are very similar to the observations

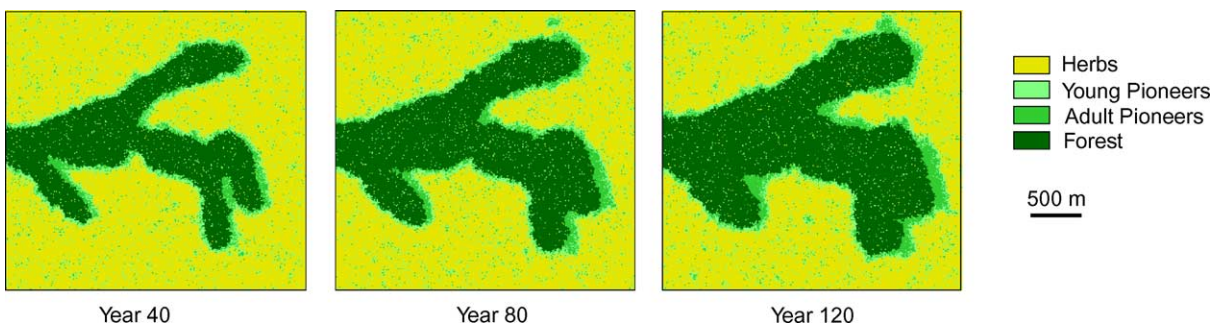


Fig. 4. Simulated evolution of a gallery forest for parameters summarised in Table 1, with the progression of the heads and the filling of the gulfs.

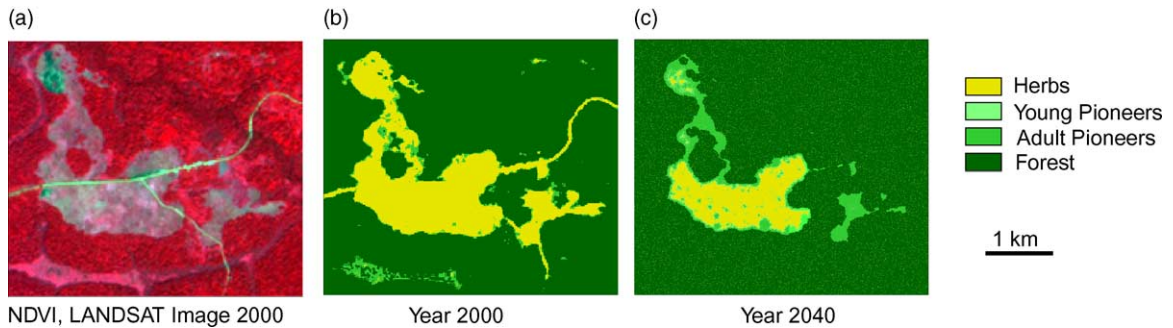


Fig. 5. Tentative application of the model to Kandara savanna (Cameroon): (a) LANDSAT image 1999; (b) translation in FORSAT variables; (c) after 50 years.

(Fig. 2c): the smallest gulfs are quickly afforested, while larger ones are gradually encroached.

3.2. Tentative application to real data

Here, we illustrate the compatibility of FORSAT with remote sensing data. Fig. 5a depicts a LANDSAT image of an included savanna at Kandara, East Cameroon, which has been used as an entry for the FORSAT model (Fig. 5b). This zone has been studied for some 20 years (e.g. in Youta Happi, 1998; Vincens et al., 2000; Guillet et al., 2001), and it has been shown that forest is expanding. Pioneer trees mostly belong to the genus *Albizia* (Mimosaceae) which is mainly located along the forest edge and in clusters in savannas. We have modelled the dispersal of its wind-dispersed seeds by the superposition of a homogeneous background and a Gaussian curve in delimited region around each disperser. Fig. 5c depicts the simulated map after 50 simulated years. Of course, as we did not parameterise our model with real field data (dispersal characteristics, fire frequencies), this map does not really reflect an expected situation but illustrates well FORSAT compatibility with common satellite images and the future use of the model.

4. Qualitative model emergent behaviour

Here we describe the phenomenological behaviour of the model, and see under which assumptions it is able to reproduce, at least qualitatively, the transgression from savanna to forest. Two problems need to be distinguished: what happens in the savanna zone, and what happens at the front between them. In the for-

est zone, the model behaves as a classic gap model (Botkin et al., 1972) and, as such, it does not deserve particular comment. Important processes take place at the forest edge and in savanna.

4.1. Trees in savanna

We first consider a mean field approximation of the model. The mean-field approximation neglects spatial correlation and heterogeneity, hence, it provides a qualitative clue to understand the emergent behaviour of the model. Let us consider the simplified three-state system (savanna, pioneer forest and burning cell), represented by the cell density of each state n_s , n_p , n_b . Let the rate of appearance of a pioneer forest cell in a savanna be $a \times n_s$. Any of the four pioneer cells that neighbour a burning site is assumed to ignite with probability b . Because we neglect spatial correlation, the probability for a given cell to be next to zero burning cell is $(1 - n_b)^4$ and therefore, the probability for it to be next to at least one burning cell is $1 - (1 - n_b)^4$. Then, the burning rate of the pioneer cells is $bn_p[1 - (1 - n_b)^4]$. Under this assumption, the evolution equation of the density of pioneer cells is

$$\frac{dn_p}{dt} = an_s + bn_p[1 - (1 - n_b)^4] \quad (6)$$

Similarly, the burning rate of the savanna cells is $n_s[1 - (1 - n_b)^4]$ (savanna cells ignite with probability 1), and the recovery rate of a burnt cell into the savanna stage 1 over the course of a year. The equation of evolution of the density of savanna cells is

$$\frac{dn_s}{dt} = n_b - an_s - n_s[1 - (1 - n_b)^4] \quad (7)$$

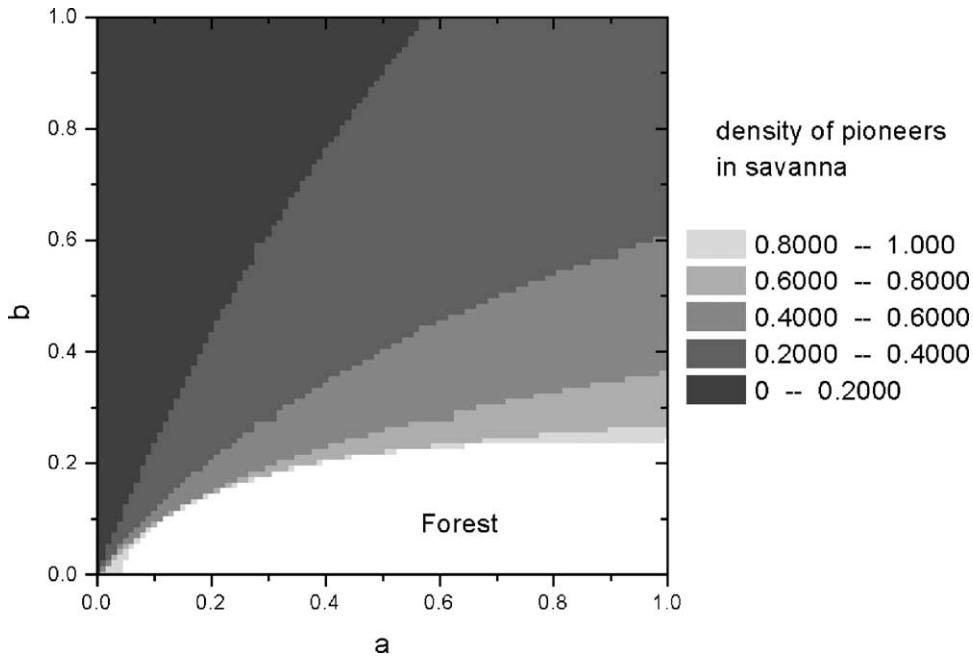


Fig. 6. Equilibrium density of pioneers in savanna in the mean field theory, when the two parameters a (rate of creation of pioneers) and b (probability of burning of pioneers) vary. In the (small b , large a) zone, the savanna is totally invaded, while in the other one, the equilibrium state is composed of some pioneers in savanna. The transition between the two zones is very sharp.

Finally, the total number of cells is constant:

$$n_s + n_p + n_b = 1 \quad (8)$$

When solving this system of differential equations, an equilibrium is reached for all values of the parameters a and b . Fig. 6 shows the plot of the fraction of space occupied by cells of savanna at equilibrium, as a function of a and b . The (a, b) space is divided into two regions, one with small b and large a for which the whole space is occupied by pioneers ($n_p = 1$) and another (small a , large b), where savanna and pioneers coexist. To interpret this result, we relate the rate of appearance of pioneers to climate and soil fertility (the more humid or fertile the climate, the greater is a), and the probability of burning b to the amount and intensity of fires, which in turn is a proxy of human activity. A region can be maintained under savanna despite favourable climatic conditions for dense forests. However, it is more and more difficult to maintain savanna as humidity increases. The qualitative concept of environmental pressure can then be defined as the combined effects of fire frequency and soil and climate conditions. The environmental pressure increases

when fire frequency increases, and the influence of soil or climate factors decreases. In the mean field model, a high environmental pressure is a stabilising factor for the savanna phase.

This result also holds for the spatially explicit model, but with the full model, it is possible to consider the spatial arrangement of ‘Adult Pioneers’ cells in savanna. As we want to study the phenomenology of the model, we consider the basic hypotheses summarised in Table 2: fire frequency, soil fertility or climate factors are varied while everything else is held constant. Seedling recruitment is a superposition of a homogeneous component and of a Von Neumann neighbouring (i.e. four nearest cells) dependence (later on, more realistic seed shadows will be considered—see Section 4.4).

As we saw in the mean field approximation, there is a threshold along the environmental axes. On the forest favourable side of this threshold (low fire frequency/high soil and climate factors), the landscape is invaded by pioneers. Far above this threshold, the zone is rapidly invaded: ‘Adult Pioneers’ cells occupy nearly the whole space (cf. Fig. 7), while close to the

Table 2

Parameters for simulations described in the sections ‘Trees in savanna’ and ‘Dynamics of the forest edge’

State	Transition to the next state	Burning probability
‘Herbs’	Global: $p_0^{h \rightarrow yp} = 0.1$ Local: Gaussian seed shadows $f(x) = 0.1$ up to 1 cell near ‘Adult Pioneers’ and ‘Forest’ cells	1
‘Young Pioneers’	Global: $p_0^{yp \rightarrow ap} = 0.2$	0.5
‘Adult Pioneers’	Local: $f(x) = 0.1$, up to 1 cell near ‘Forest’ cells	0.2
‘Forest’	Global: $p_0^{f \rightarrow h} = 0.005$	0.005
Wind: no	5 fires each year with fire	

Climate factor, soil fertility factor and fire frequency vary.

threshold, forest clusters grow within the savanna and coalesce until total invasion (cf. Table 2 and Fig. 8). On the other side (savanna favourable) of the threshold (high fire frequency/low soil and climate factors), equilibrium is reached for some density of the ‘Adult

Pioneers’ cells (Fig. 9): the density of ‘Adult Pioneers’ cells can be very low when deep below the threshold. For the parameters reported in Table 2 and annual fire events, these cells have a mean lifespan of 0.75 year (92% are less than 3 years old). Near the threshold, the proportion of green cells (all vegetation cells except ‘Herbs’ ones) and that of ‘Adult Pioneers’ increase (Fig. 10) and clusters appear. The threshold does not correspond to the same values in densities than in the mean-field approximation. For fire frequency of 1 year out of 3, the mean cluster size is 3.14 cells. Cells inside clusters tend to be protected from fire by borderline cells: the mean lifespan of these cells is 8.9 years and 40% of them are more than 8 years old.

4.2. Dynamics of the forest edge

Here, we describe the processes that take place at the forest edge under conditions preventing stable savanna/forest coexistence. The parameters of the simulation are still those of Table 2.

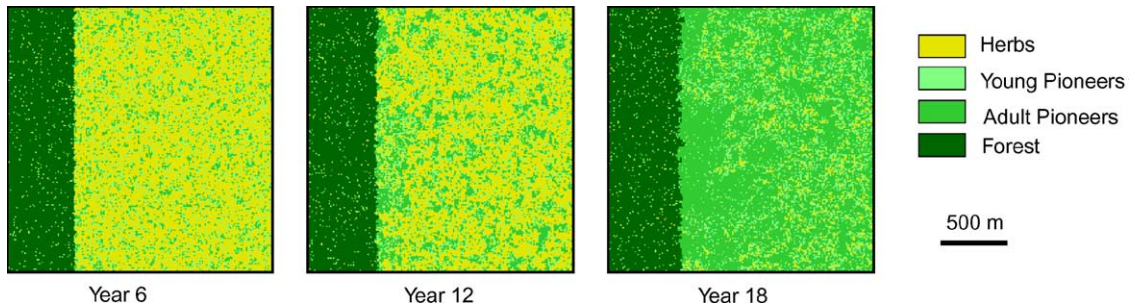


Fig. 7. Fast encroachment of savanna (from left to right, situation after 6, 12 and 18 simulated years). The initial map is composed of a forest zone on the left-hand side and a savanna zone on the right-hand side. The parameters are summarised Table 2, climate and soil factors are set to 1 and fire occurs 1 year out of 6.

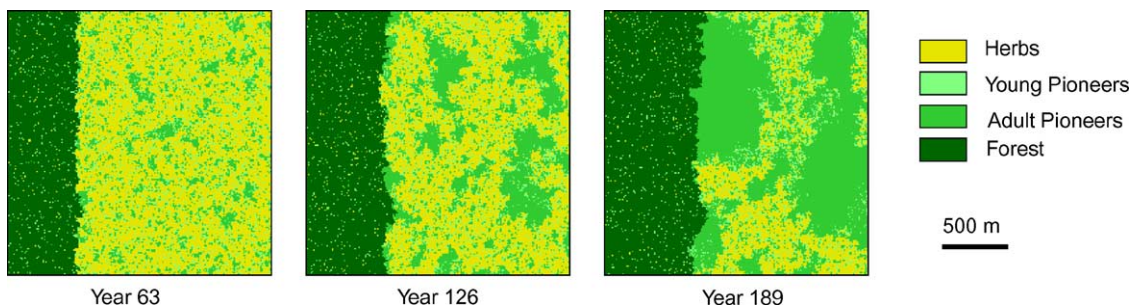


Fig. 8. Coalescence of clusters in savanna (from left to right, situation after 63, 126 and 189 simulated years). Initial map and parameters as for Fig. 7 except for fire frequency: 2 years out of 7.

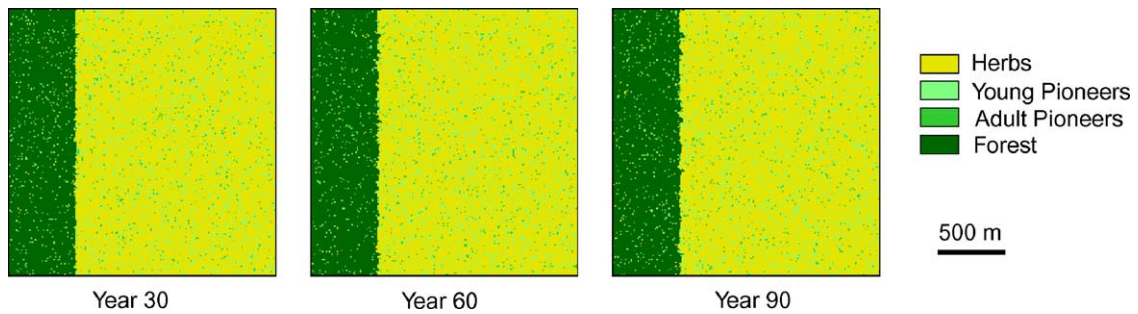


Fig. 9. Progression of forest edge (from left to right, situation after 30, 60 and 90 simulated years). Initial map and parameters as for Fig. 7 except for fire frequency: 1 year out of 2.

We consider two characteristics of the front: the mean position and the standard deviation, which measures the length scale of the front irregularity (roughness). Fig. 11a depicts the evolution in time of the mean position of the front. After a transient period, the mean position moves at constant speed. In Fig. 12, this mean velocity is plotted against climate, soil fertility, and fire frequency factors. The velocity increases when fire frequency decreases or when soil and climate factors increase. For this particular set of parameters, a high fire frequency induces a regression of the forest edge. It is not a generic pattern: for other sets of parameters, even yearly fires do not prevent the encroachment of forest on savanna.

Edge roughness always increases with time (Fig. 11b) but quite slowly. An increase of this magnitude would be impossible to detect in field studies.

4.3. Soil heterogeneity: termite mounds

Termite mounds are common in forest and savanna landscapes that once were under dryer climatic conditions (with densities of the order of 1–10 per hectare). They form fertile patches where forest pioneer species establish preferentially (Youta Happi, 1998; Dangerfield et al., 1998). To investigate their effects on forest transgression, we modelled them by zones of 10 m × 10 m with fertility factors equal to 3, dispatched randomly with a density of 2–5 per hectare. It appears that the introduction of termite mounds can lead to an increase of the woody cover in savanna or even help the transgression change from a simple edge progression to a progression of forest by advanced positions, as illustrated by Fig. 13.

4.4. Cluster formation in relation with seed shadows

To investigate the difference in the transgression resulting from the difference of pioneer tree seed shadows, especially in the edge progression and the clump formation, near seed shadows of Eq. (3) are varied between a very peaked form to a very flat form, the mean being kept constant:

$$f(r) = \alpha \left[0.25 \exp\left(-\frac{r^2}{4}\right) \right] + (1-\alpha)0.03(1-0.1r),$$

$$(r < 10, 0 \leq \alpha \leq 1) \quad (9)$$

Fig. 14 depicts the shapes of this near seed shadows for different values of α : the curve flattens when the parameter α decreases from 1 to 0. For values in between, it can vary continuously from one form to the other; this can cover the typical dispersion ranges of the different mechanisms (barochory, zoochory, anemochory). In this numerical experiment, homogeneous far seed dispersal is turned off. In savanna, peaked seed shadows favour the apparition of clumps, as shown in Fig. 15, which depicts the probability that a single ‘Adult Pioneers’ cell gives rise to a cluster. However, the rate of progression of a forest edge increases as the seed shadows flatten. That means that clumps appear less often with flat seed shadows but, once established, grow faster.

5. Discussion

5.1. Modelling techniques

The issue we consider in this article is the dynamics of the boundaries between humid tropical forests

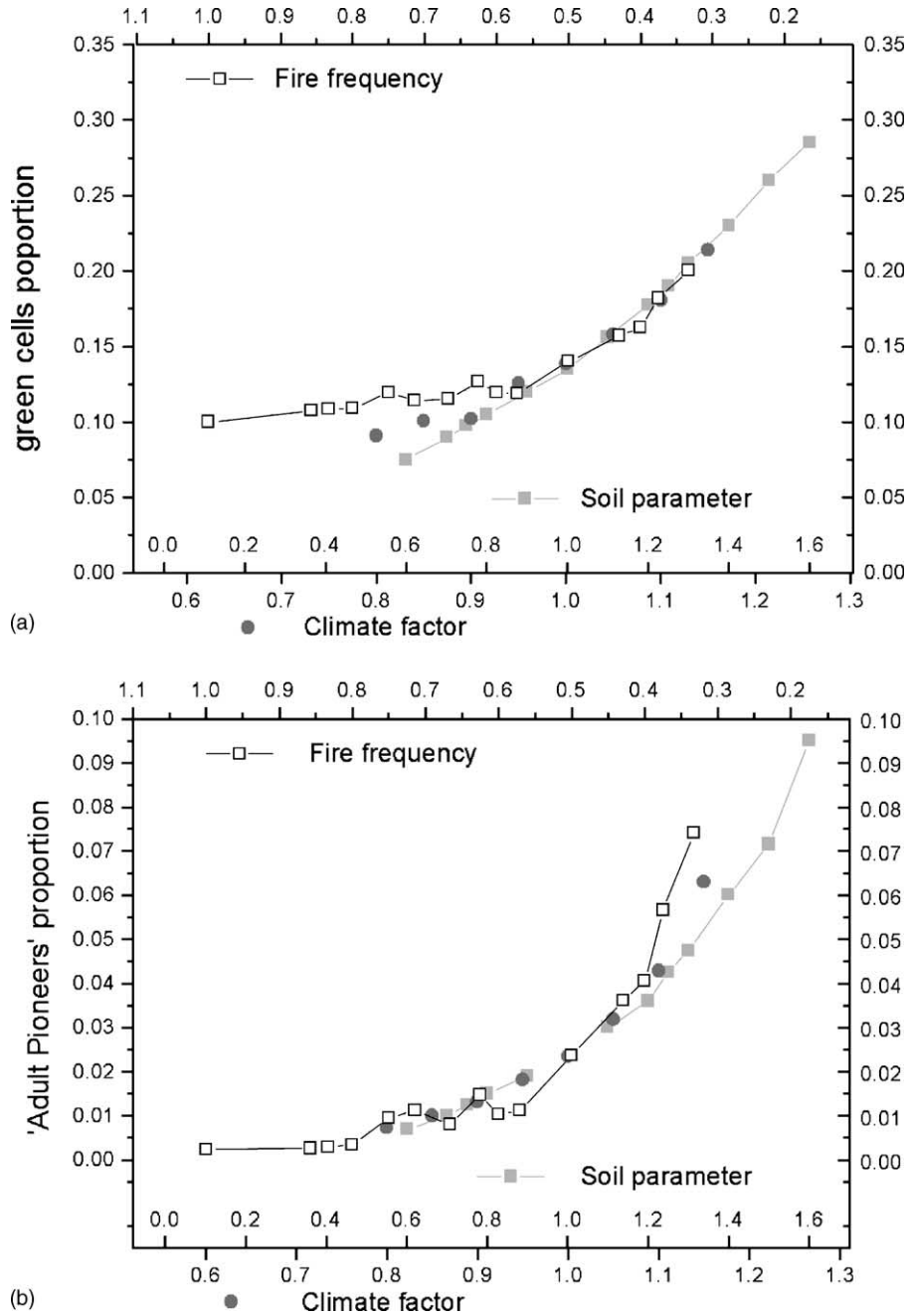


Fig. 10. (a) Evolution of the density of the green cells ('Young Pioneers' + 'Adult Pioneers' cells) when soil parameter, climate factor and fire frequency vary. (b) Evolution of the density of the 'Adult Pioneers' cells. Other parameters summarised in Table 2.

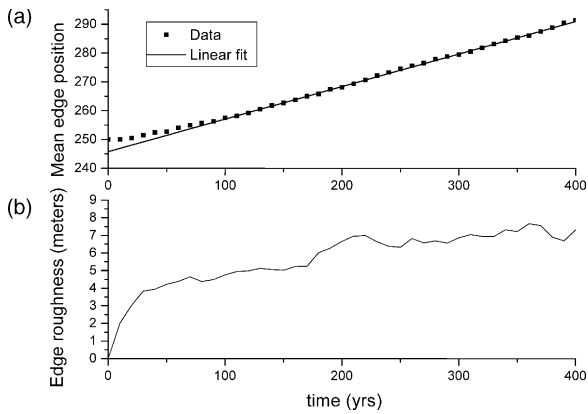


Fig. 11. Evolution of edge (a) mean position and (b) roughness through time for parameters of Table 2 with fire every other year and a climate factor equal to 1.05.

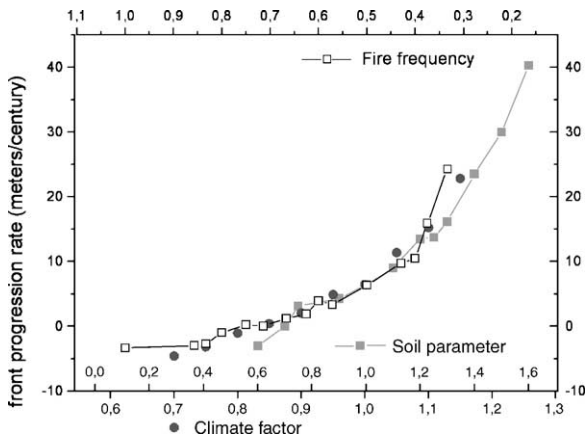


Fig. 12. Compared evolution of front progression when soil parameter, climate factor and fire frequency vary (other parameters summarised in Table 2).

and adjacent savannas. Comparison with the results of forest–savanna models in drier climatic conditions is not directly relevant (e.g. dry tropical forest savanna mosaic in the USA, see Loehle et al., 1996; Bachelet et al., 2000; Peters, 2002): a specific difference is the fact that water distribution in the ground is not critical in humid forest–savanna mosaics. Nevertheless, in the next paragraph, we will list the differences between the various approaches.

Previous approaches consist either (i) in a thorough process-based description of the system at the plant level (Menaut et al., 1990; Peters, 2002) or at the vegetation class level (Bachelet et al., 2000) or (ii) in considering that the dynamics of the ecological system can be represented by a general dynamical system studied separately (e.g. percolation in Loehle et al., 1996). This second kind of model gives clues to interpret the dynamics on a general scope, as it deals with general concepts and phenomena while the first type of approaches are of great value when they can be precisely parameterised for realistic simulations of local dynamics.

We built the FORSAT model along a third philosophy lying at an intermediate level on the scale ranging from abstract generality to applied realistic studies. We have identified the major processes involved in the invasion of savannas by forest, in particular seed dispersal, savanna fire, and the main environmental variables that influence them (climate, soil fertility, fire frequency). We have searched the best compromise between realism and efficiency to model them and have constructed a simple model that reproduces field observations of the savanna-forest transgression. Our approach permits an easier ex-

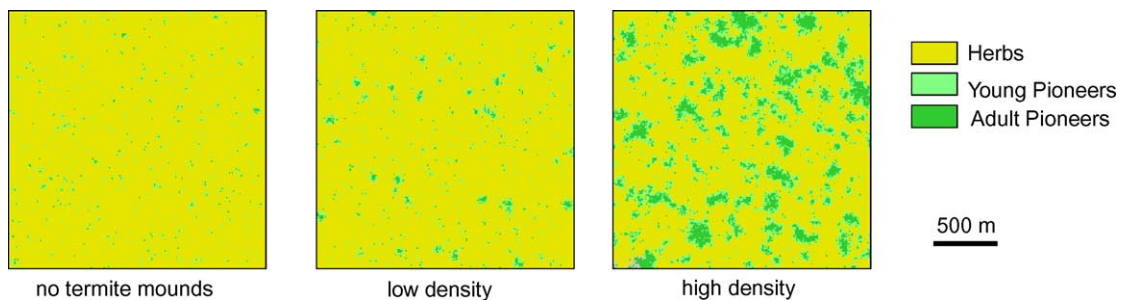


Fig. 13. Comparison between three runs without (left) and with low- (middle) and high- (right) density termite mounds after 50 simulated years: termite mounds can either simply modify the equilibrium ‘Adult Pioneers’ density in savanna (middle) or can help pass over the threshold and allow progression by cluster coalescence (right).

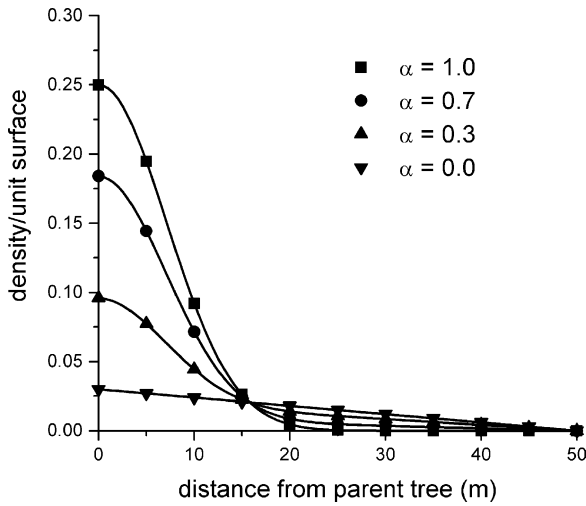


Fig. 14. Near seed shadows from Eq. (9) for different values of the parameter α : 1.0, 0.7, 0.03 and 0. The mean probability of apparition of a ‘Young Pioneers’ cell around a parent cell is the same for every curve. For values of α near 1, ‘Young Pioneers’ cells preferentially appear next to the parent cell, while for lower values, the probability is more regularly distributed in the neighbourhood (up to 10 pixels—50 m—from the parent cell).

ploration of the relative influence of the different phenomena.

5.2. Interest of the FORSAT model

The FORSAT model brings together the knowledge about the main processes occurring at the humid forest savanna boundary in a simple model. There is satisfactory agreement between the model emergent

behaviour and observations. When tuning the parameters, the model qualitatively reproduces the behaviour observed in nature:

1. linear progression (or regression) of forest edge without formation of clumps in savanna (de Foresta, 1990);
2. positive balance between initiation and disappearance of clumps (Gautier, 1989);
3. afforestation of a whole zone (Eden and McGregor, 1992; Adjanohoun, 1964; Louppe et al., 1995 for the description of the same zone).

From a quantitative point of view, typical values of edge transgression rates are compatible with literature rates: up to some hundreds meters by century (Youta Happi, 1998).

The three parameters have a similar impact on the transgression, with a sharp threshold between the forest edge progression scenario and the cluster formation one. It is clear that soil fertility and fire frequency are local parameters, whereas a climate change would affect a larger region. However, on the scale we consider, a change in the fire frequency or in climate would result in the same kind of transition between the two scenarios. Following Li (2002), it is possible to consider these dynamics in the phase transition framework, with two phases in presence. ‘Forest’ and ‘Adult Pioneers’ cells represent forest cells and ‘Young Pioneers’ and ‘Herbs’ represent savanna phase. Then, the emergent behaviour of FORSAT indicate a phase transition between forest and savanna, controlled by fire frequency, soil or climate. When exploring the FORSAT emergent behaviour, we have focused on whether the savanna

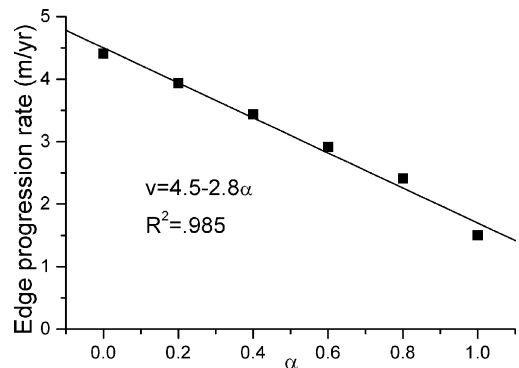
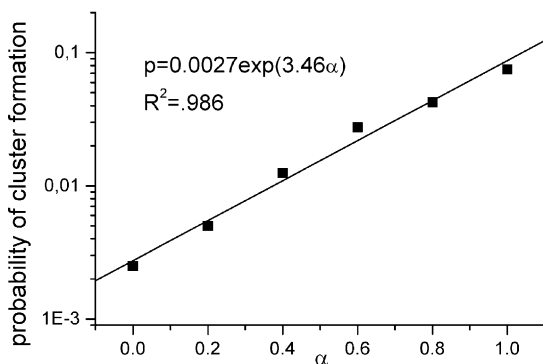


Fig. 15. Probability of cluster formation from a single ‘Adult Pioneers’ pixel source (left) and rate of edge progression (right) for different near seed shadows ($\alpha = 0$: flat seed shadows, $\alpha = 1$: peaked seed shadows).

phase is stable or not, that is whether (re)forestation was possible or not, and disregarded the savannisation process. It is actually reasonable as the fragmentation of forests proceeds from other mechanisms than savanna fires, especially repeated clearings. However, the FORSAT model can be applied to answer the question of the stability of derived savannas.

The dynamics of phase transitions characterised by: (i) the evolution of the boundary between the two phases (the ecotone) and (ii) the nucleation of one phase in the other (apparition of clusters of forest in savanna). At the forest edge, two processes take place: a tendency to smoothen the interface, with a time scale of several years, and an increase of the roughness through time, with a time scale of several decades. Secondly, the spatial aggregation of pioneer forest species is induced by the combined effect of seed dispersal and fire. There are more pioneer seedlings near established trees (because of local seed sources, as well as enhanced zoochorous and anemochorous sources due to the presence of the tree itself—see, e.g. Carrière et al., 2002), and these seedlings protect trees from fire. At frequent fire regimes, there is a maximal cluster size that can be attained; this leads to relatively small clusters scattered in the savanna. When the fire regime is less important, it cannot prevent the growth of clusters and their coalescence. Finally, seed dispersal and recruitment of pioneer trees are fundamental aspects of the transgression of forest over savannas. Seed dispersal curves relate the probability of successful dispersal events to the distance from the parent trees. These curves depend on the species (especially on the seed structure and the recruitment probability) and strongly influence the way the transgression takes place. The formation of clumps around seed trees established in savanna is dependent on the importance of the dispersion of seeds on short distances. The probability of this formation increases with the sharpness of the peak near source. However, the establishment of solitary trees requires long distance dispersal events. What is more, when established, the edge progression over savannas is faster for pioneers with flat seed shadows. This suggests a difference between two pioneer strategies: a clump strategy for pioneers whose seed shadows is leptokurtic (with a sharp peak near the source and a long tail that allows seedlings to settle far from the parent tree) and an edge progression strategy when pioneer seed shadows decreases slowly

around the source (platykurtic seed shadows). Observations in littoral Congo confort this view (de Namur et al., in preparation). There, groves in savanna are originated by pioneers with the ability to travel far and settle in savanna, whereas the edge is dominated by wind dispersed pioneers.

5.3. Interpreting the data with FORSAT

The FORSAT model emphasises the critical role of human action. An interesting question indeed is the existence of long lasting forest–savanna mosaics, implying the coexistence of the two phases although each phase is—without human influence—stable for given climatic conditions (humid for forests, dry for savannas), and tends to eliminate the other. It is true that the mechanisms of progression of the two phases are not symmetrical (Hopkins, 1992): forest progression is a complex dynamical phenomenon (settling of pioneer light-demanding forest trees on the edge and in savanna, progression of the edge, settling of woodland clumps in savanna, filling of isolated savannas), while the dynamics of savannas installation is simpler—they just fill the space no longer covered by forest. Still, in the absence of man, one phase would invade the entire space depending upon the climatic conditions. Our model helps to understand that men can stabilise the mosaic in humid climatic conditions by maintaining open spaces (clearing and burning), while in dry conditions, its role will be to accelerate deforestation (which is what is happening in sub-sahelian regions).

A correlation can be established with field experiments to explain why current measured transgression rates can be so much weaker than those inferred from paleo-environmental reconstruction. One scenario is that gallery forests constituted microrefuges of dry epochs, from which the dense forest could have expanded. Once favourable environmental conditions are met, dense forest clusters would have formed in savanna, and been progressively included in the forest zone, creating included savannas that would in turn be rapidly filled. With the increase of human pressure (fires), the system switched to the other regime of a slow linear progression scenario that has been observed in most present studies (Guillet et al., 2001).

Paleo-environmental patterns of forest–savanna dynamics can be interpreted within this framework. In western Africa, the dry episode at ca. 3000 bp led

to deforestation and allowed southward migration of Bantu people (see, e.g. Schwartz, 1992), but the man-induced pressure was weaker than it is now and when more humid conditions were restored, the system was able to cross the threshold leading to fast re-afforestation; modern exploitation and increased population has slowed down the forest transgression, and led to a nearly stable coexistence/invasion state.

The FORSAT model can also help to understand the discrepancies between present transgression rates. In a region ecologically homogeneous (in particular where the same species are involved in the transgression), the differences arise because of heterogeneity in soil conditions and/or in the fire frequencies. When considering different ecoregions, the pioneer species are then determinant and their differences should not be disregarded.

The model is being applied to two trial study sites in the zone of Bertoua (Cameroon) and Pointe Noire (Congo). Once these parameterisations are completed, we are planning to conduct an ensemble of synchronic studies (comparison of the model result to field studies) and diachronic studies (studies of paleo-environmental dynamics, compared to field studies to discover in what extent human action has changed through time). The FORSAT model will also be used as a tool to understand and interpret larger-scale data: in a forest–savanna mosaic, detailed data are available only for specific zones. When parameterised with this limited data, it may allow generalisation to a regional scale.

6. Conclusion

We have developed a simple model of FORSAT in human populated environments that is compatible with data sources on vegetation, and especially with remote sensing data. The main processes involved in the transgression (succession cycle, fire) were modelled using probabilistic rules and observed patterns were successfully reproduced (progression of the forest edge, expansion from a gallery forest, effect of soil heterogeneity). Our study emphasises that climate and fire frequency have a similar influence on a local scale. Our results support the hypothesis of forest microrefuges of riparian zones and give hints to understand the differences between transgression rates presently mea-

sured and those inferred from paleo-environmental reconstruction.

Acknowledgements

This work is part of the ECOFIT program. We warmly thank L. Couranc C. de Namur, A. Vincens and J. Youta Happi for interesting and useful discussion, as well as Louise H. Emmons who also helped to make the English more acceptable.

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