How long does the spatial structure of an initial state influence the dynamics of a forest growth model ? A simulation study using the Capsis platform.

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ABSTRACT
Spatially explicit Individual Based Models are more and more often used in forest modelling, especially because they take into account the influence of the spatial structure on the dynamics. However, they are potentially very sensitive to the initial spatial structure used for a simulation, which can be problematic if the initial state is not known, or is simulated in an unrealistic way.

The aim of our paper is to study this sensitivity to initial spatial structure in the case of the Mountain model, an individual based model of irregular spruce stands implemented in the Capsis platform. In order to characterise the influence of the initial spatial structure on the dynamics of the model, we simulated different initial spatial structures and compared the results of long term simulations.

We showed that the initial spatial structure can highly influence the dynamics of the model, not only during the first cycle of the evolution, but also at very long term in the evolution of the next generations. We also illustrated how some disturbances, such as a periodic gap opening through storms, can modify both the long term dynamics of the stand and the duration of the influence of the initial spatial structure.

KEYWORDS
Forest, tree, growth model, simulation, Monte Carlo, Spruce, spatial structure, initial state

1. Introduction

Individual Based Models (IBM) are more and more often used in forest modelling (*e.g.* [Ek Monserud 1979] [Tomé Burkhart 1989]), especially for complex forest stands with mixed tree species or irregularity in size or age. Because they consider each tree individually, individual based models can take into account the high variability of such stands [Spellmann 1992]. This was impossible with simpler stand level models, based on mean properties at the stand level such as density or total basal area [Houllier *et al.* 1991]. Different forest growth simulators have been recently developed to integrate both stand level and individual based forest models (*e.g.* [Pretzsch *et al.* 2002] [de Coligny *et al.* 2004]), and can be used either as management tools or for research purposes.

Some of these IBM are moreover spatially explicit, which means that they also consider each tree location. With such models, it is possible to characterise the local neighbourhood around each tree through competition indices. Many different competition indices can be found in the literature, taking into account the number, size and location of neighbouring trees [Biging Dobbertin 1995]. One advantage of such models is that they take explicitly into account the influence of the spatial structure of an ecosystem on its dynamics. This relation between spatial structure and dynamics is considered as an important process in many ecosystems, and has been thoroughly studied (*e.g.* [Begon *et al.* 1990] [Dieckmann *et al.* 2000]). For instance in forest stands trees located in aggregates are supposed to grow less than isolated trees, because of the competition for light or nutrients. However, spatially explicit models also have the drawback of requiring very detailed initial states, including the location of all trees at the beginning of the simulation. Such data are very seldom available for real forests. Therefore, most of the time it is necessary to simulate a "virtual" initial state, i.e. a set of numbers representing the species, diameter, and location of simulated trees ([Pretzsch 1997] [Goreaud *et al.* 2004]).

Precisely because they take into account the influence of the spatial structure of a forest stand on its dynamics, spatially explicit individual based models are likely to be very sensitive to the initial spatial structure used in a simulation. In real forest ecosystems, the influence of the spatial structure on the dynamics is usually supposed to be a short term influence, because many stochastic events (either natural disturbances such as storms, or human sylvicultural actions such as thinning) can modify the spatial structure and thus the growing conditions (*e.g.* [Pontailler *et al.* 1997] [Wolf *et al.* 2003]). However, ecological models do not always include as much stochasticity, and can sometime show a long term sensitivity to the initial spatial structure ([Dubé *et al.* 2001] [Goreaud *et al.* 2002] [Ménard *et al.* 2002]). This problem is quite general and can be encountered in other types of models, for instance cellular automaton or grid based models [Dieckmann *et al.* 2000].

This high sensitivity of individual based models can become a real problem if the spatial structure of the initial state is not known, or is simulated in an unrealistic way, because in that case it can lead to unrealistic simulation results. Unfortunately, this is often the case. Most of the time, the initial state of a simulation is simulated very simply, using random, clumped or regular patterns. Only very few studies propose to really fit a model of spatial structure on real data, or to estimate the realism of the spatial structure simulated as initial states for forest growth models ([Rathbun Cressie 1994] [Batista Maguire 1998] [Prévosto *et al.* 2003] [Goreaud *et al.* 2004]). In order to avoid this problem, some authors prefer not to consider the first part of a simulation, supposing it can be unrealistic because of the dependence on the initial state. This method however makes the implicit hypotheses (i) that the dynamics of the model will converge toward an equilibrium state independently of the initial state, which may not be the case, and also (ii) that the transition period is not too long.

Therefore, we believe it is important, before using a spatially explicit individual based model, to study how much it is sensitive to the initial state, and more precisely to estimate how long this influence can affect its dynamics.

The aim of our paper is to study this sensitivity to initial spatial structure in the case of the Mountain model, an individual based model of irregular spruce stands [Courbaud *et al.* 2001]. This model (detailed in section 2.1) is implemented in the Capsis platform (section 2.2), which facilitates the simulation work [de Coligny *et al.* 2004].

In order to characterise the influence of the initial spatial structure on the dynamics of the model, we simulated different initial spatial structures (section 2.3), and compared the results of the corresponding long term simulations. We hypothesised that significant differences will occur as long as the initial state has some influence on the dynamics. However, as our model is stochastic, we could not simply compare the evolution curves between two simulations. We therefore used Monte Carlo simulations to represent the variability of the results (section 2.4). We first used a given initial state to assess the intrinsic variability of the model (section 3.1). Then we used a set of simulations with an initial spatial structure corresponding to our null hypothesis of Complete Spatial Randomness (section 3.2). Then, when using different initial spatial structures (section 3.3) we considered that any additional variability corresponds to the influence of the initial spatial structure on the dynamics.

We also wanted to test if potential disturbances, such as storms, could affect the duration of this influence of the initial spatial structure on the dynamics. We therefore handled two sets of simulations : A first one without any disturbance (section 3), and a second one corresponding to disturbed dynamics with periodic gap opening through storms (section 4).

We finally discuss the consequences of such sensitivity on the use of the model.

2. **Material & Method**

2.1. **The model "Mountain"**

"Mountain" is a spatially explicit, individual based model simulating the dynamics of irregular mountain spruce stands [Courbaud *et al.* 2001]. Figure 1 summarises the different processes included in Mountain. Each tree is represented by its spatial co-ordinates, height, diameter at breast height, crown base height and crown base diameter. Competition interactions are modelled through the calculation of the radiation intercepted by every tree in the stand taking into account the shading effect of its neighbours in three dimensions [Courbaud *et al.* 2003]. Each year, the model simulates the individual height and diameter increments corresponding to a vegetation season, as functions of the initial dimensions of the tree and the amount of radiation intercepted. Regeneration is simulated in openings by a probability of installation of new seedlings on every ground cell with irradiance higher than a given threshold. Seedling growth depends on the irradiance of their ground cell, until they reach a height of 1.30 m. They are then recruited as trees with all the related attributes. Mortality is modelled with two processes : a first probability of mortality depending on the radiation intercepted by a tree, simulating competition effects; and a second probability of mortality depending on tree height, simulating senescence and disturbance effects.

The Mountain model has been fitted and validated on data from two experimental plots in the French Alps [Courbaud 1997]. It is implemented in the Capsis platform, freely available on the Capsis Project homepage (http://capsis.free.fr).
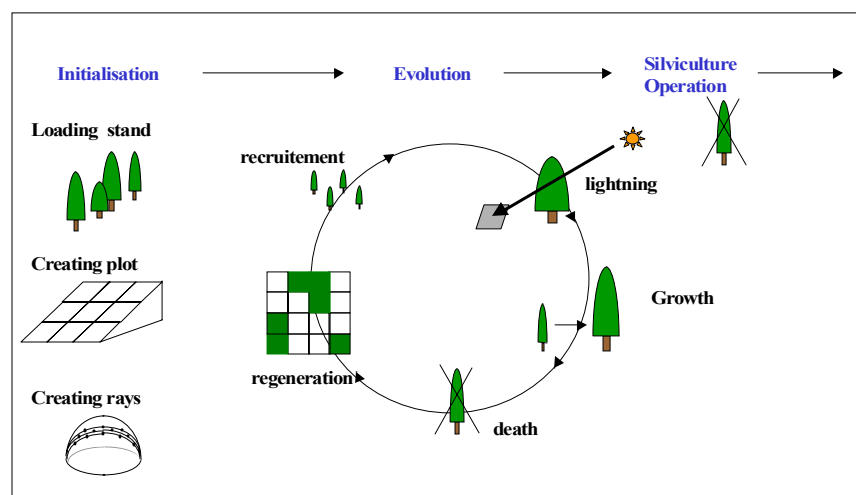
Figure 1 : The chain of processes successively simulated in the model mountain. The initialisation phase downloads or creates an initial stand, creates the ground cells and the light rays. During each vegetation season, the model first calculates radiation interception, then growth and mortality, and finally regeneration and recruitment. A scenario can alternate periods of growth and steps of silvicultural operations.

2.2. **The Capsis platform**

Capsis (Computer-Aided Projection for Strategies In Silviculture) is a generic forest simulator which has been developed by French researchers since 1994 ([Dreyfus Bonnet 1997] [de Coligny *et al*. 2004]). The objective of the Capsis project is to build a perennial, open and shared modelling platform (1) to contribute to the development and evaluation of models, (2) to share tools and methods, (3) to compare results of different models, (4) to transfer models to forest managers and (5) to serve as teaching material.

The version 4 of Capsis (figure 2) is generic enough to integrate very different kinds of models: stand models, distance independent or spatially explicit tree models, individual based or not, wood quality models, seed dispersal models, etc. It provides forest management tools to establish and compare different silvicultural scenarios. At the present time, Capsis hosts 25 models and 5 specific libraries which are all being co-developed by researchers and computer scientists. This shared forest modelling platform has already showed many advantages : allowing modellers to re-use sub-models and share specific tools and providing to foresters and students an easy-to-use software to compare different management strategies.
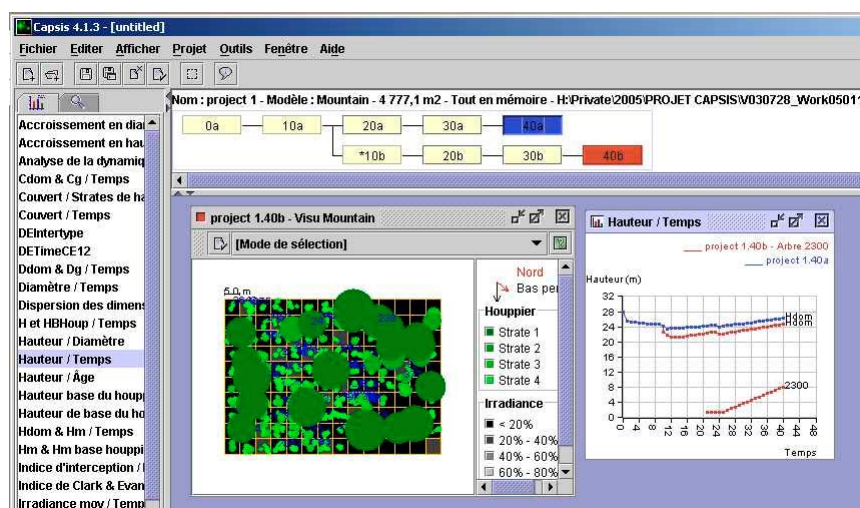

Figure 2 - A glance at Capsis4 : Project manager with two scenarios, a stand viewer, and a graphic.

In this paper, we simulated 1500 stand evolutions, each of them being quite long because of the computation of light rays trajectory for each trees (up to 5000 trees in a 1ha stand) at each time step. We therefore used the script pilot of Capsis to run the simulations on a cluster of 48 PCs, using approximately a total of 8300 h CPU time.

2.3. **Simulating different initial spatial structures**

In order to study the influence of the initial spatial structure on the dynamics of the model, we defined different initial states, composed of the same trees in terms of age and size, but with different spatial structures. We chose to consider a 1 ha young stand, composed of 5000 trees with the same 2cm diameter, and a mean height of 1.5m. Such a stand could correspond to a natural regeneration after a clear cutting. For all initial states we used exactly the same trees, and only modified their location. We used the classical point process formalism to simulate spatial patterns (*e.g.* [Diggle 1983] [Tomppo 1986] [Cressie 1993]), and the corresponding tools of the "spatial library" in Capsis [de Coligny *et al.* 2004].

We first ran a set of simulations with the same initial state (section 3.1), in order to characterise the variability corresponding to the intrinsic stochasticity of the model. For these simulations, we used one given realisation of a Poisson process as spatial pattern for the initial state. The locations of these trees correspond to the map in figure 3a.

We then used very classically as null hypothesis the Complete Spatial Randomness hypothesis (CSR), corresponding to the absence of constraint in the location of trees. This spatial structure is easily simulated by a Poisson process [Diggle 1983], for which the co-ordinates of each tree are random numbers. We have considered the variability resulting from this CSR initial states as a reference for our comparison work (c.f. section 3.2).

Finally, in order to simulate other very different spatial patterns, corresponding to highly variable spatial structure, we used a generalised Gibbs process with random values of the parameters, as defined in [Goreaud *et al.* 2002]. Gibbs point processes are classically used to simulate complex patterns [Diggle 1983]. The general principle of Gibbs processes is to define a pairwise cost function, whose values will lead either to aggregation, or to regularity, at various scales. When using it with random values of the parameters, we simulated very highly variable spatial structures, from aggregation to regularity, at different scales and intensity. Details of the algorithm can be found in [Goreaud *et al.* 2002]. Figure 3b and 3c illustrate two possible initial states, with the same trees, but very different spatial structures simulated with this Gibbs point process. When running a set of simulations with these highly different initial states, we have considered that the additional variability corresponds to the influence of the initial spatial structure on the dynamics.
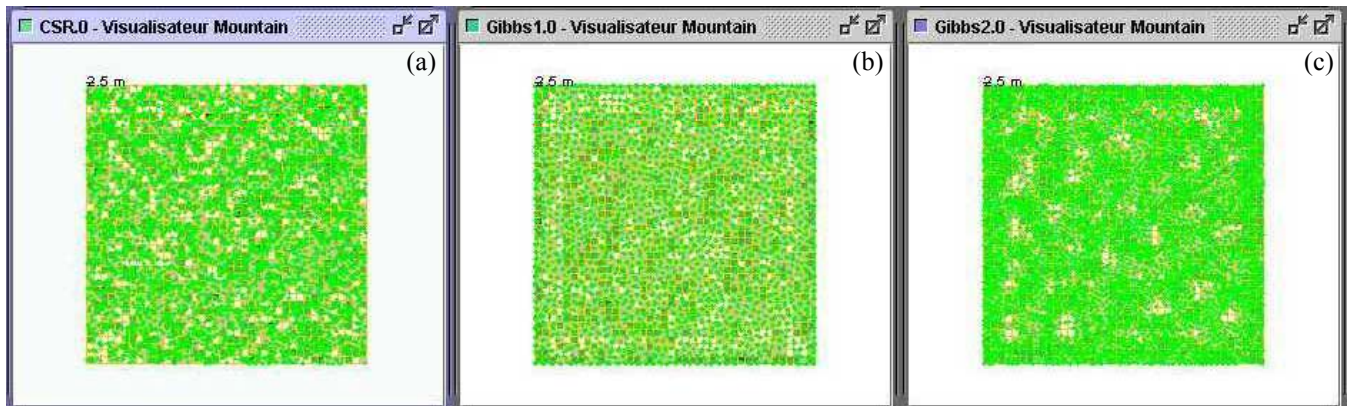

Figure 3 : Example of three initial states corresponding to the same trees, but to different spatial structure. (a) : Complete Spatial Randomness (CSR); (b) & (c) : Complex structures simulated with a Gibbs Process.

2.4. **Long term simulations**

Because we wanted to determine how long the spatial structure of the initial state can influence the dynamics of the Mountain model, we ran very long term simulations of 1000 years. The usual life time for trees is over 100 years, so a 1000 years period enables to simulate successive generations, and thus to let mortality and regeneration express themselves and modify the spatial structure of the stand. Note that such long term simulations are not realistic, and therefore must only be used to study the behaviour of a model [Shugart 1984], and not for predictive purposes.

We defined a few global variables to represent the dynamics of the stand, and followed their evolution during this 1000 years period. For each simulation, the model simulates the evolution of each tree, from its birth to its death. This corresponds to a huge amount of data. Therefore, we decided to focus on the evolution of some classical mean values at the stand level. In this paper, we have more precisely considered the evolution of : (i) N : the total number of trees in the stand; (ii) G : the total basal area, which is an indirect measure of the biomass of the ecosystem; (iii) Dg : the mean quadratic diameter, which characterises the mean evolution of each individual tree; and (iv) CE : the Clark & Evans index, which characterises the spatial structure of the stand (CE is a normalised measure of the distance to nearest neighbour : CE=1 for a random pattern, CE<1 for aggregation and CE>1 for regularity [Cressie 1993]).

For each set of parameters, we used 100 Monte Carlo simulations to represent the variability of the results. Indeed, the Mountain model is intrinsically stochastic, especially because the mortality and regeneration sub-models are probability models. For a given set of parameters and a given initial state, each simulation will lead to different choices of dying trees or regeneration locations, and thus to somehow different evolutions of the stand. Moreover, as the distribution of these curves does not follow a Gaussian distribution, it was not possible to use only the mean and standard deviation. In this simulation study, we thus obtained 100 different evolution curves for each variable of the stand, and we characterised the variability of these results by considering the max and min values of the simulated variables for each time step (see 3.3).

The different values for the parameters we used for these simulations are detailed in Table 1. They mostly correspond to the values obtained when fitting the model on two experimental plots in the French Alps [Courbaud 1997]. We used the same values of the parameters for all simulations, except for the parameters concerning disturbances. In the first set of simulation (section 3), those parameters were set to 0 so that no disturbance occur. Then, in section 4 we considered different values to assess the impact of disturbances on the dynamics.

Table 1 : Values of the main parameters of the simulations.

Main parameters	corresponding to :	value
Crown :		
treeLeafAreaDensity	Leaf area density	$0.8 \ m^2/m^3$
maxCrownRadius	Maximum crown radius	5 m
Growth :		
growthHmax	Maximum height	40 m
growthdHmax	Maximum height increment	45 cm/year
growthRH2	Height radiation threshold : over this value, height growth is maximum	40 %
growthDmax	Maximum diameter	90 cm
growthdDmax	Maximum diameter increment	8 mm/year
growthRD2	Diameter radiation threshold : over this value, diameter growth is maximum	80 %
Regeneration :		
seedlingStep	Time between two seeding events	10 years
limitEnergyInf	Sapling minimum radiation : under this value, no regeneration can occur	20 %
saplingPotHeightIncrement	Sapling maximum height increment	25 cm/year
recruitDensity	Sapling density	0.2 sap./m²
Mortality :		
deathPmax	Death maximum probability (for a tree with a null diameter increment)	0.5
deathLimitdD	Minimum diameter increment : under this value there is a risk of mortality	0.75 mm/year
Disturbances :		
gapRadius	Gap radius	0, 5, 10, 20 m
disturbanceStep	Gap frequency : number of years between 2 successive gap openings	5 or 10 years

3. Influence of the spatial structure on the undisturbed dynamics

In this first step of our study, we characterised the influence of the initial spatial structure of a simulation on the undisturbed dynamics of the stand modelled by the Mountain model. We therefore set the values of the parameters so that no disturbance occurs (i.e. no natural phenomenon such as storm, and no human actions such as thinning).

3.1. **Taking into account the intrinsic stochasticity of the model**

We have first considered a set of 100 simulations corresponding to 1000 years evolution of a stand with this undisturbed model, using always the same initial state, corresponding to the random pattern presented in figure 3a. At the beginning of each simulation the stand was always the same, but then progressively the stochasticity of the model led to different evolutions. Figure 4 shows the curves corresponding to the evolution of 4 global variables, that illustrate the evolution of the stand for these 100 simulations : the total number of trees, the total basal area, the mean quadratic diameter, and Clark & Evans index (see 2.4).
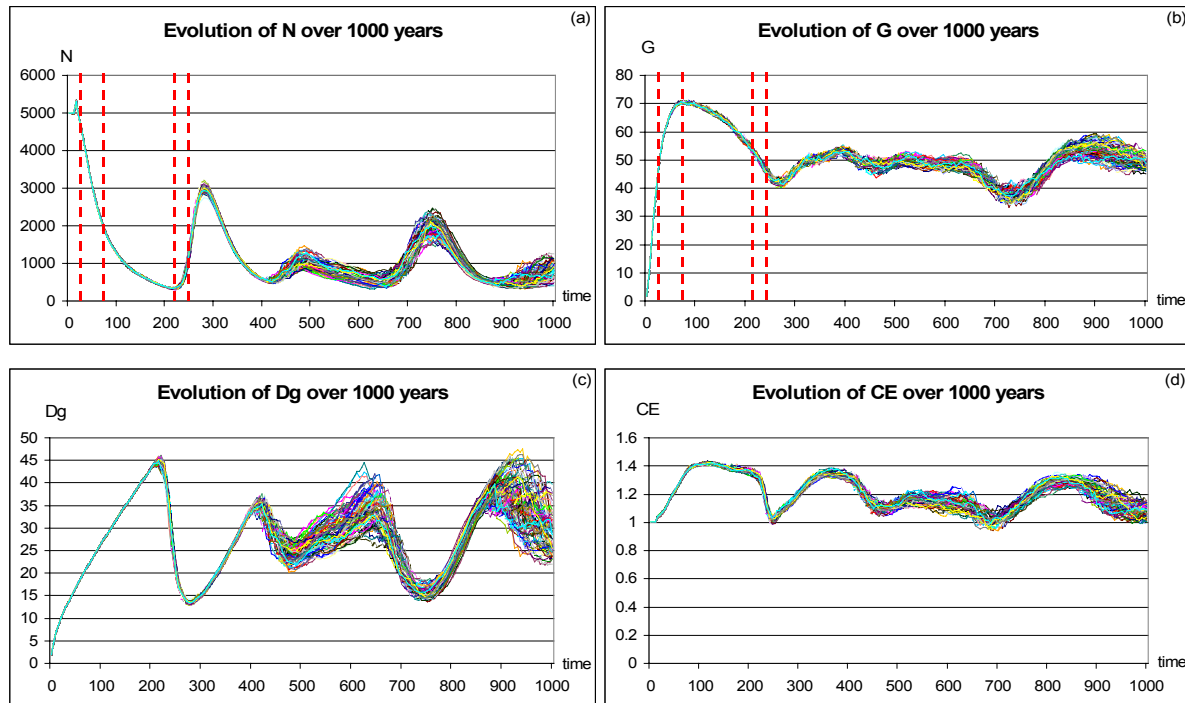
Figure 4 : Curves of 1000 years evolution for 100 simulations with the same initial state. (a) Number of trees in the stand, (b) total basal area, (c) mean quadratic diameter, (d) Clark & Evans index.

We can first notice that the simulations followed a rather cyclic evolution pattern, with a cycle of approximately 250 years. This cyclic evolution seems to correspond to 4 successive generations of trees, following more or less a regular stand dynamics. However, the third cycle does not seem to be very clearly defined. The first cycle is really characteristic to this regular stand dynamic, which is not surprising as our initial state corresponded to a very young and regular stand. However, we have also obtained similar cyclic evolution patterns with other initial states, and especially with initial states corresponding to real irregular experimental plots. Therefore, we believe that this cyclic evolution pattern characterises a potentially frequent behaviour of the model.

In the first cycle, we can identify the 4 main phases of forest dynamics [Oliver Larson 1996] : First the initiation phase (up to 30 years), corresponding to a progressive closure of the canopy with a fast increase of G (and fluctuations of N) ; then the stem exclusion phase (up to 75 years), with a fast decrease of N through competition and mortality (called self-thinning) but still an increase of G through the growth of surviving trees ; third the senescence phase (up to 220 years), with a decrease of both N and G, corresponding to the death of old and big trees ; and finally the renewal phase (up to 250 years) with a massive regeneration inducing an increase of N, whereas the death of the last old trees leads to a decrease of G. [Dubé *et al*. 2001], simulating northern hardwood forest succession over 1000 years, also obtained cyclic behaviour around 200-250 years.

There is however also a variability around this mean pattern, which is the result of the stochasticity of the model. This variability increases with time (which is quite usual with stochastic models) : at the beginning of the evolution the various simulated stands remained very similar, but then progressively the stochasticity of the model led to different evolutions. This is especially the case at the end of each cycle, when the regeneration process, which is highly stochastic, expressed itself on a wide area. As we used here always the same initial state, we have considered that this variability in the evolution curves really corresponds to the intrinsic stochasticity of the model, i.e. the use of random numbers when simulating mortality and regeneration.

3.2. **Null hypothesis of Complete Spatial Randomness**

The usual null hypothesis when studying the influence of spatial structure on the dynamics of ecosystems is the hypothesis of Complete Spatial Randomness [Cressie 1993]. This null hypothesis is more complex than a given initial state with a precise location of individuals, as we used in (3.1). Indeed, this null hypothesis corresponds to one given point process (the Poisson process), and thus to an infinite number of potential realisations. In each realisation, that can be used as an initial state, the locations of trees are different, but all realisations correspond to the CSR spatial structure. This stochasticity in the location of trees for a given spatial structure can bring an additional variability in the simulation results. Therefore, when using the model with the null hypothesis of CSR, the global variability of the results is composed of both the intrinsic variability of the model and the variability induced by the stochasticity of the CSR initial state.

In order to characterise this variability, corresponding to our null hypothesis, we have considered another set of 100 simulations corresponding to 1000 years evolution (with the undisturbed model) of a stand whose initial states all follow a completely random initial spatial structure simulated by a Poisson process. Figure 5 shows the curves corresponding to the evolution of the same 4 global variables than previously (the total number of trees, the total basal area, the mean quadratic diameter, and Clark & Evans index) for these 100 simulations.
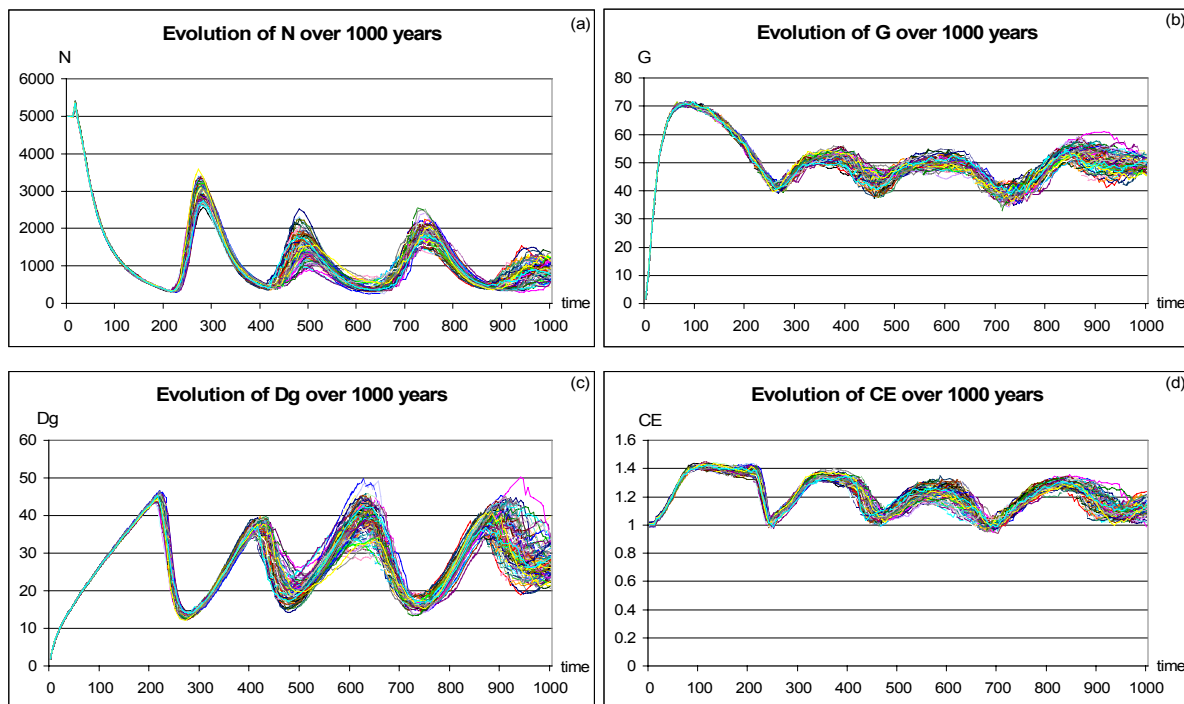
Figure 5 : Curves of 1000 years evolution for 100 simulations with a CSR initial spatial structure. (a) Number of trees in the stand, (b) total basal area, (c) mean quadratic diameter, (d) Clark & Evans index.

The results of these simulations are quite similar to those obtained previously, except for two details. First, as we expected, the evolution curves corresponding to our null hypothesis have a slightly higher variability, especially during the first cycle. This is due to the additional stochasticity induced by the different locations of trees in each initial state. Second, the evolution curve have a much clearer periodicity : each cycle is more precisely defined than when using the same initial state (cf. 3.1). We therefore hypothesised that this cyclic evolution was indeed characteristic of the dynamics of a stand with a CSR initial structure, and that the unclear third cycle obtained in (3.1) was only a specificity of the precise locations of trees used in the initial pattern. This difference illustrates the interest of using the CSR spatial structure as null hypothesis instead of a given initial state.

We therefore considered this variability, obtained with our CSR null hypothesis initial state, as a reference for our comparison work.

3.3. **Long term dynamics with a highly variable initial spatial structure**

We have then considered another set of 100 simulations, still corresponding to 1000 years evolution of a stand with the undisturbed model, but this time with very different initial states, corresponding to the same trees (in terms of size and age),

but to highly variable spatial structures simulated by a Gibbs process (c.f. 2.3). Figure 6 shows the curves corresponding to the evolution of the same 4 global variables (the total number of trees, the total basal area, the mean quadratic diameter, and Clark & Evans index) for these 100 simulations.

These results confirm that the initial spatial structure can highly influence the dynamics of the model. Indeed, these simulations followed the same overall evolution pattern than the previous ones corresponding to our null hypothesis (c.f. 3.2), but with a much higher variability around this global pattern. This high variability means that the differences in the spatial structure of the initial state have led to evolutions significantly different from those obtained under our null hypothesis. It seems to be especially true in the first cycle of the evolution, probably because the different initial spatial structures had already led to different competition contexts, and thus to some variability in the evolution of the global variables of the stand, whereas the simulations beginning with a CSR initial state had a very small variability of the competition context.
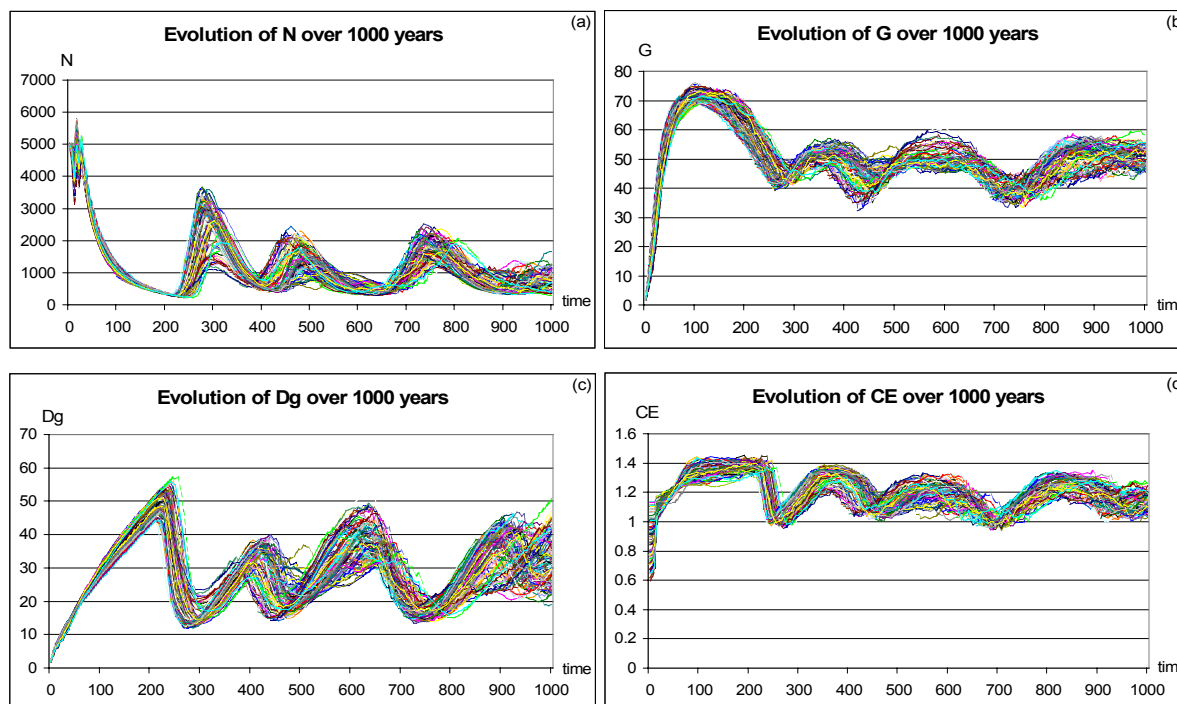

Figure 6 : Curves of 1000 years evolution for 100 simulations with a highly variable initial spatial structure simulated by a Gibbs process. (a) Number of trees in the stand, (b) total basal area, (c) mean quadratic diameter, (d) Clark & Evans index.

In order to clarify this phenomenon, we focused on the simulations corresponding to the most extreme initial states. Using the initial values of the Clark & Evans index, which characterises the spatial structure of the stand, we chose the 5 most aggregated (smallest values of CE) and the 5 most regular (highest values of CE) initial states, and compared their simulated evolution (figure 7). We obtained very different behaviours up to 1000 years, which confirms that the initial spatial structure can influence the dynamics of the model on a very long term.

We also noticed a very interesting phenomenon of alternative modification of the relative location of these curves. Thus, at the beginning of the first cycle, some trees of the most aggregated stands (blue) died rapidly, probably because the competition was too harsh in the centre of aggregates. Therefore, the total basal area became and stayed lower during the stem exclusion phase (until 75 years). Then, as the competition and the mortality increased, the mean and total basal area became lower in the most regular stands (green). We assume that, in aggregated stands the spatial structure had already led to an important differentiation, so that only small dominated trees died, whereas a lower differentiation in regular stands induced the death of bigger trees. Finally, the regeneration was larger in formerly regular stands, probably because more light was available everywhere in the stand. During the next cycles, the relative location of the curves swapped, which could be the result of an inversion in the spatial structure of the successive stands, as suggested by the Clark & Evans index. The precise interpretation of this phenomenon would however require to identify the different cohorts in the stand.
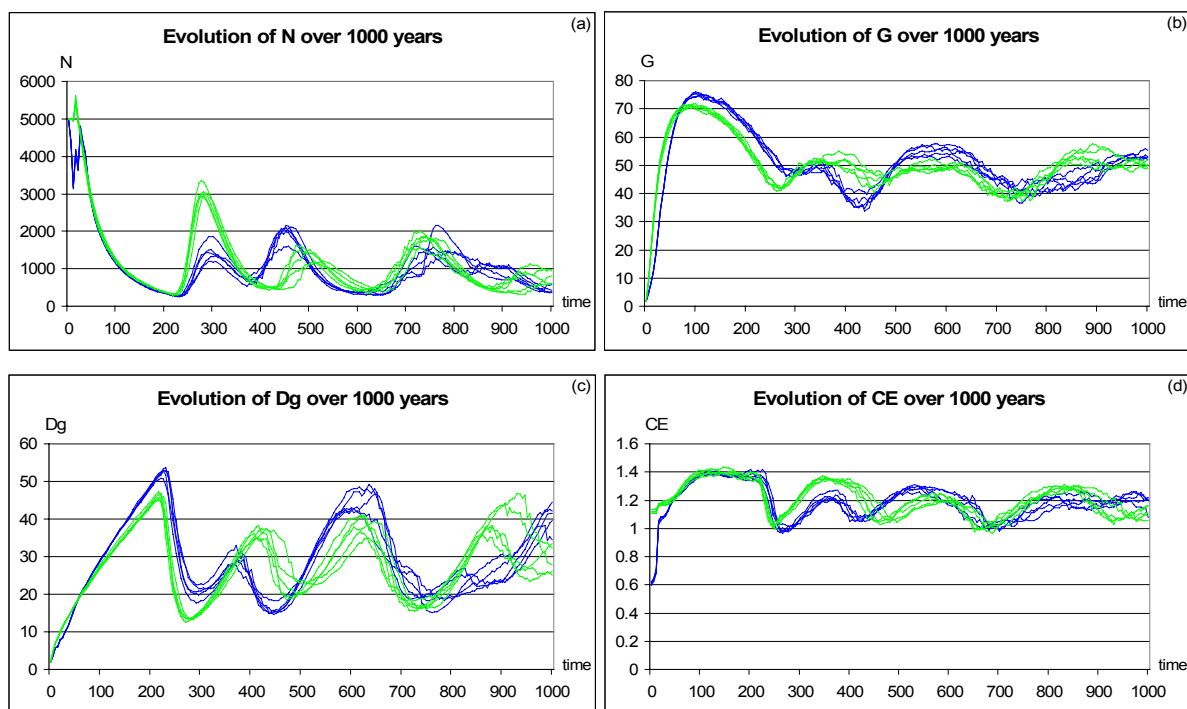
Figure 7 : Curves of 1000 years evolution for the 5 most aggregated (blue) and the 5 most regular (green) initial states. (a) Number of trees in the stand, (b) total basal area, (c) mean quadratic diameter, (d) Clark & Evans index.

3.4. **Quantifying the influence of the initial spatial structure**

In order to measure more precisely this increase of variability, we have used a very simple and classical Monte Carlo approach, comparing the min and max values of the different variables for both sets of simulations, corresponding either to our null hypothesis of CSR, or to highly variable spatial structure (figure 8). In fact, min and max values of a set of N simulations can be used to estimate a confidence interval corresponding to a significance level alpha of $1/(N+1)$. Unfortunately, this estimator is not very robust, and can lead to imprecise estimates of the confidence intervals. More precise estimates of the confidence intervals can be obtained by using order statistics (see for instance [Cressie 1993]), but this requires more simulations. In this paper, we chose to simply use min and max values to characterise the variability of the model, and we assumed that large differences of these min and max values are the result of a significant influence of the initial spatial structure on the dynamics.

First, when looking at the first cycle of the simulation (until 250 years), we can notice that there are very large differences of the variability of the results at all time step and for all variables. This corresponds to the direct effect of the differences in the initial spatial structures, who have led to different competition contexts for the trees of the first generation. We can thus conclude that the dynamics of the stand modelled in Mountain, mainly based on the competition for light, has not compensated for these different initial spatial structures.

Then, when looking at the next cycles, we can still point out some large differences of the variability of the results at some periods, even after a very long evolution (for instance 800 years). This means that the initial spatial structure can have a very long term influence on the dynamics of the model, even on the successive generations. We will discuss the implications of this result in section 5. We can also notice that this difference of the variability is larger at certain specific phases of the dynamics, and can differ from one variable to another. This is probably due to the fact that the stochasticity is mainly the result of the regeneration process, and that the impact of the regeneration is not similar for the different variables. For instance, a huge regeneration modifies the number of trees immediately, but as the new trees are small it does not modify the total basal area much.

In real forest stand, the spatial structure is usually not considered to have such a long term influence on the dynamics, and we therefore supposed it to be an artefact of the model. Indeed, real stand encounter many disturbances, and we can hypothesise that such stochastic events can shorten the influence of the spatial structure on the dynamics. This is what we have tested with the additional simulations presented in chapter 4.
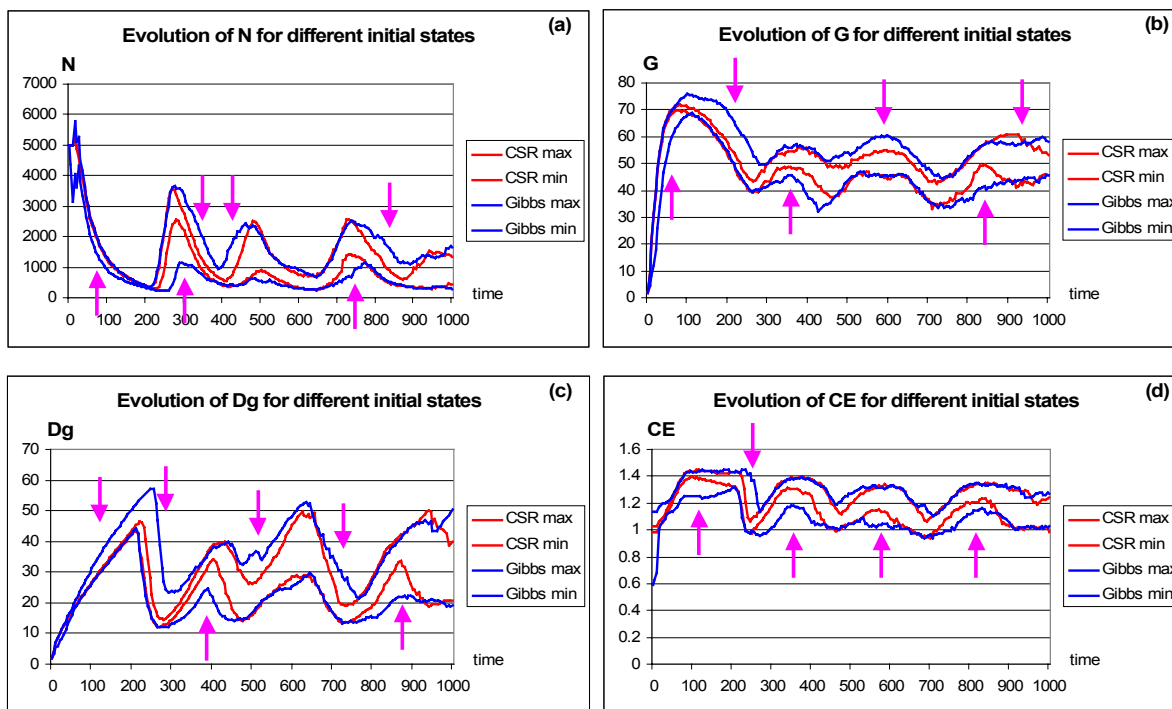
Figure 8 : Min and max values of the evolution curves for 100 simulations from a CSR initial spatial structure (red), and 100 simulations from a highly variable initial spatial structure (blue). Purple arrows point out the large differences of the variability. (a) Total number of trees in the stand; (b) total basal area; (c) mean quadratic diameter; (d) Clark & Evans index.

4. **Taking disturbances into account**

In this second step of our study, we characterised the influence of the spatial structure of the initial state of a simulation when the dynamics of the stand, modelled by the Mountain model, is periodically disturbed by storms. We therefore set the values of the parameters so that storms occurred, at different rhythms (every 5 or 10 years), leading to gap openings of different radius (5, 10 or 20 m).

We have first considered a disturbance corresponding to the opening of a 10m radius gap every 5 years, which is already a strong disturbance. We ran a new set of 100 simulations, corresponding to 1000 years evolution of a stand with very different initial states, with the Mountain model including this specific periodic disturbance. Figure 9 shows the curves corresponding to the evolution of the same 4 global variables (the total number of trees, the total basal area, the mean quadratic diameter, and Clark & Evans index) for these 100 simulations.

The simulation of this disturbance has completely modified the shape and the variability of the evolution curves. The different variables of the stand did not have cyclic evolution any more. The first 250 years still correspond roughly to the beginning of the first cycle simulated by the undisturbed model (see section 3), but then the disturbances have modified the stand sufficiently to avoid a new cyclic evolution of the stand, so that the variables converged toward equilibrium values, with small stochastic variations.

The variability of the curves is also smaller, and we have compared it to the corresponding variability when simulating the disturbed model with an initial state following CSR (figure 10). We can notice that the variability of the simulations with highly different initial spatial structures is slightly higher, but only during the 250 first years. We can therefore conclude that the disturbances have lowered the sensitivity of the model to the initial spatial structure, so that the influence of this spatial structure lasts less than 250 years in the disturbed model.

In order to characterise the sensitivity of the model to these disturbances, we have run other sets of simulations, corresponding to other values of the disturbance parameters : gap radius of 5, 10 or 20 m for 1 opening every 5 or 10 years. Table 2 presents the global behaviour of the simulations with these parameters. These results show that only large and frequent openings were able to modify the cyclic dynamics of the stand. We can conclude that small openings did not modify the spatial structure of the stand enough to influence its dynamics.
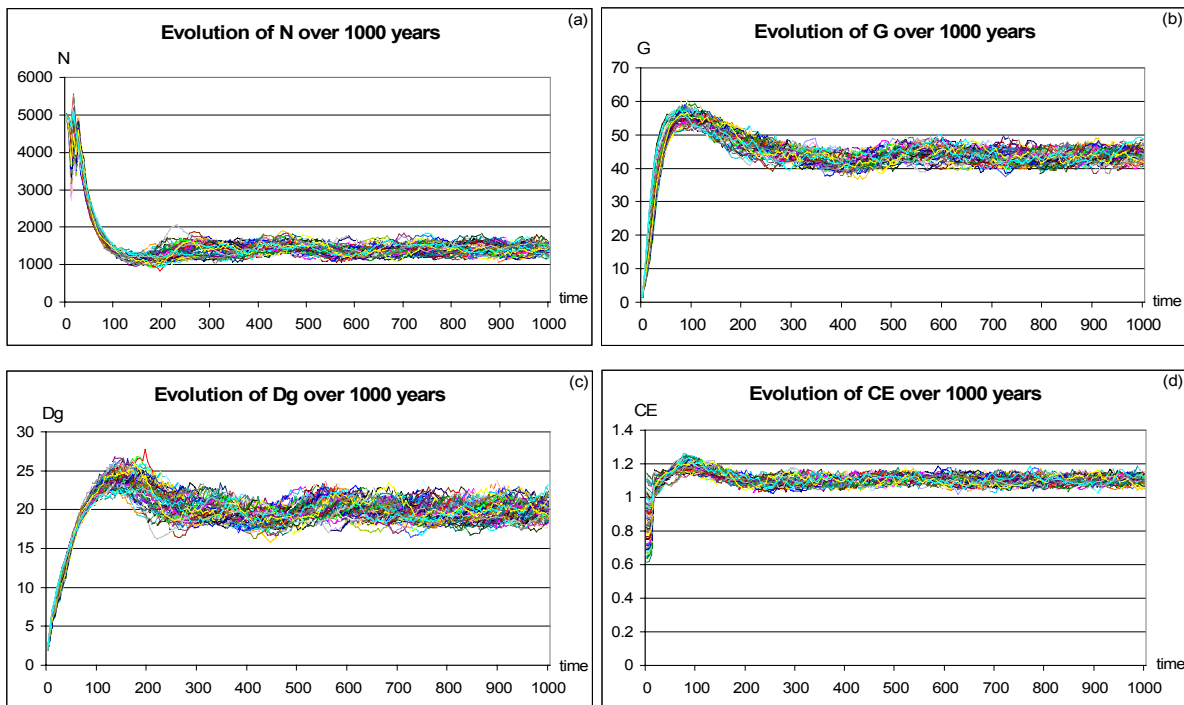
Figure 9 : Curves of 1000 years evolution for 100 simulations with a highly variable initial spatial structure simulated by a Gibbs process, and periodic openings of 10m radius gaps every 5 years. (a) Number of trees in the stand, (b) total basal area, (c) mean quadratic diameter, (d) Clark & Evans index.
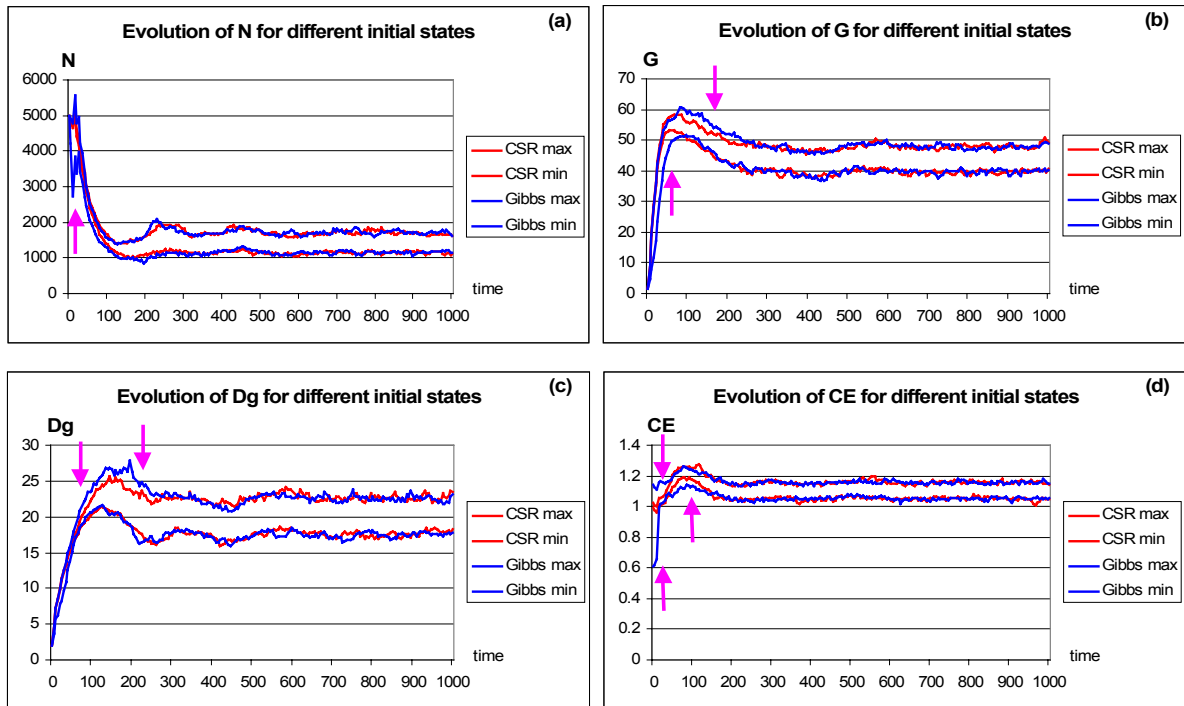

Figure 10 : Min and max values of the evolution curves for 100 simulations from a CSR initial spatial structure (red), and 100 simulations from a highly variable initial spatial structure (blue), with periodic openings of 10m radius gaps every 5 years. (a) Total number of trees in the stand; (b) total basal area; (c) mean quadratic diameter; (d) Clark & Evans index.

Table 2 : Global behaviour of the simulations for various disturbance parameters.

	Gap radius = 5m	Gap radius = 10m	Gap radius = 20m
1 opening every 5 years	cyclic evolution pattern	**convergence**	**fast convergence**
1 opening every 10 years	cyclic evolution pattern	cyclic evolution pattern	cyclic evolution pattern
without openings	cyclic evolution pattern		

5. **Discussion**

The long term sensitivity of forest models to the initial spatial structure has not been much studied and rises many questions ([Dubé *et al.* 2001] [Ménard *et al.* 2002]). In this paper, we have characterised this sensitivity for the Mountain model. We have shown that the initial spatial structure highly influences the dynamics of the undisturbed model, not only during the whole first cycle of the evolution (corresponding to the first generation), but also at a very long term at some periods in the evolution of the next generations. Such a very long term sensitivity is usually not expected in stochastic models, especially because the stochastic sub models (regeneration and mortality) highly modify the spatial structure and growing conditions of the stand. In our case, this long term sensitivity may come from the fact that the three biological processes of growth, mortality and regeneration are based on the same computation of available light, itself depending on the spatial structure of the stand. This potentially very long term sensitivity is an additional argument for not using long term simulation for prediction purposes

The importance of disturbances on the dynamics of forest stands has been more and more studied recently (*e.g.* [Pontailler *et al.* 1997] [Wolf *et al.* 2003] [Cordonnier 2004]). In this paper, we have illustrated how the addition of some disturbances in the model (such as a periodic gap opening through storms) can modify both the long term dynamics of the stand and the duration of the influence of the initial spatial structure. These results are consistent with those obtained by [Dubé *et al.* 2001], and [Ménard *et al.* 2002] with another forest model. We have also shown that small disturbances are not always sufficient to modify the dynamics of the stand or to lower the influence of the initial state. A finer exploration will be necessary to determine precisely the threshold values of these parameters.

These results confirm that long term simulations can be very interesting to study the behaviour of a model, but must not be used for predictions. Long term simulations of forest models are usually considered as not realistic at all, for different reasons. Firstly, forest stands growth models are usually fitted and validated on very short time periods (classically from 5 to 20 years). Their extrapolation on longer periods is not validated and can lead to errors accumulation. Secondly, the environmental conditions that are supposed to be constant in the model are likely to change during a long period [Dhôte Hervé 2000]. Thirdly, mortality and regeneration are very complex processes, that are still not well understood and not very precisely modelled. Other processes, such as different sorts of natural disturbances and human actions can not be planned on such a long period. In this paper, we pointed out the potential very long term sensitivity of forest models, that appears to be another argument for non using long term simulation in prediction purposes.

The potential sensitivity of forest growth models to the spatial structure of the initial state also questions the relevance of using simulated or virtual initial states, even for short term simulations. Indeed, if the model is sensitive to the spatial structure of the initial state, using an unrealistic initial spatial structure will lead to unrealistic results of the simulation. Unfortunately, the simulation of initial states for individual based models is usually very simply done, and very few authors evaluate the realism of these simulated initial stands ([Rathbun Cressie 1994] [Batista Maguire 1998] [Prévosto *et al*. 2003] [Goreaud *et al.* 2004]). Our results therefore confirm the need to improve the realism of the simulation of initial states for individual based models.

This study also points out the importance of disturbances, regeneration and mortality processes on both the simulated dynamics and the sensitivity of the model. These three stochastic processes are still not as well understood as growth, and thus the corresponding sub-models are often very simple. However, recent studies have illustrated their importance in the dynamics of a forest ecosystem. We therefore believe that a specific effort on the development of these sub-models, and on their integration in forest dynamics models could bring real improvement in the quality of the simulations, especially if we want to use simulations on longer periods.

Finally, our results rise some interesting questions on the long term dynamics of forest stands. Of course in this paper we obtained only some insights on the behaviour of the model, and not on the real forest ecosystem, as it is always the case with simulation studies [Pavé 1994]. This is all especially true because the model we studied has not been validated on its ability

to simulate long term dynamics, and such a very long term validation will probably remain impossible because it would require very long time measurements. It would however be very interesting to test on real stands the main qualitative results of the simulations, and especially the potentially long term influence of the initial spatial structure, and the role of disturbances in lowering this influence. Indeed, the influence of the spatial structure is usually considered as a short term process, precisely because many stochastic processes can modify the structure and the dynamics of a stand. However, this phenomenon has been rarely studied, and could have major implications on forest management. The combined use of real measures and simulation may facilitate the research work in this field.

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