

Quantifying gap dynamics at the patch mosaic level using a spatially-explicit model of a northern hardwood forest ecosystem

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Abstract

Small-scale disturbances that create canopy gaps play a key role in regulating successional pathways in temperate forests. SORTIE, a spatially-explicit, individual-based model, allows the modelling of temperate forest succession by means of gap dynamics. The aim of this paper is to evaluate, using a spatio-temporal sensitivity analysis, the spatial cohesiveness of gaps generated by SORTIE. Northern hardwood forest succession, based on local interactions of three shade tolerant and three shade intolerant species, was simulated over 1000 years. To investigate the effects of initial conditions, two seedling densities (low and high) and two spatial configurations of new seedlings (random and aggregated) were replicated five times. Statistical analyses were then performed to detect the presence of significant global spatio-temporal gap structures. These analyses were followed by a more detailed characterisation of the spatio-temporal behaviour of the model using three different spatial statistics (spatial join-count, nearest neighbour and gap size) at each time step. The cohesive temporal periodicity of these statistics was assessed using phase coherence (PC) analysis. Results exhibit consistent global spatial dynamics, with subtle differences between replicates and between initial conditions. PC analysis reveals the presence of important cyclic behaviour around 200–250 years. Finally, our results provide useful insights about the intrinsic factors regulating long-term spatial gap dynamics, as well as the effects of shade tolerance on the immediate responses of tree species to disturbance in temperate forests. © 2001 Elsevier Science B.V. All rights reserved.

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1. Introduction

The importance of local small-scale disturbances for global forest dynamics is a well-recognised concept in ecology (Bormann and Likens,

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1979; Pickett and White, 1985; Payette et al., 1990). Gaps increase light levels and change local environmental conditions, with significant impacts on tree interactions. Gaps are necessary for almost all tree species to attain canopy status (Canham, 1988, 1989; Pouslon and Platt, 1989) by means of a myriad of different strategies. Gaps also play a major role in species coexistence by creating local ecological niches for specific species (Denslow, 1980). They constitute an important source of entry sites of new genotypes and new taxa (Silvertown and Smith, 1988), and may enhance the resistance of some species to herbivory (Coley, 1993). Overall, local disturbances play an important role as the driving forces of community change (Withmore, 1989; Payette et al., 1990). Consequently, our ability to model local disturbance regimes may have a direct impact on our understanding of successional dynamics (Vitousek and White, 1981), and on the quality of management activities (Lorimer, 1989).

This importance of small-scale disturbances led many researchers to carefully study gap dynamics to better understand the underlying processes at a local scale (e.g. Brokaw, 1985; Runkle, 1985; Canham, 1989; Lieberman et al., 1989). Gap dynamics can be studied at two distinct but interrelated levels of organisation, the disturbance level and the patch mosaic level (or stand level). Traditional empirical field studies brought many valuable insights about gap replacement processes and gap resource heterogeneity. However, few studies emphasise the emergent gap spatial dynamics (i.e. the spatio-temporal organisation exhibited by many gap patches) produced at the stand level in relation to local disturbance dynamics. Yet, such patterns are considered to be directly related to species composition in the subsequent forest cycles (Withmore, 1989). Studies documenting the spatial structure of gap dynamics at the stand level are rare because necessary field data are very difficult to collect. Time series covering entire successional sequences are rarely available in the field, and spatial gap surveys are very labour intensive. Paleoecological studies have been proposed as one solution to the lack of suitable, direct observations of time series. Payette et al. (1990) focused on the mapping of disturbances

due to canopy gaps in a 25 ha study area using expansion/contraction patterns extracted from paleo-dendrochronological data.

Ecologists have also emphasised the use of distributed dynamic simulation models in order to generate new hypothesis and to improve their understanding of gap and population dynamics through time (Botkin et al., 1972; Shugart and West, 1977; Leemans and Prentice, 1989; Bossel and Krieger, 1991, 1994). However, most of these models make use of arbitrary areal units having little if any ecological correspondence with real-world canopy gaps at an aggregated semantic level. In the last decade, these models have been refined in the form of true spatially-explicit models of forest dynamics (Urban, 1990; Urban et al., 1991; Cosalanti and Grime, 1993; Green, 1994; Wissel, 1994; Coquillard and Hill, 1997). This new generation of models now emphasises the potential of simulating the complexity of natural dynamic systems by taking into account the local spatial interactions of their physical components. This shift in ecological models has been partially driven by the arrival of the object-oriented paradigm in computer science, recent developments in theoretical ecology and the emergence of complex systems theory from which theoretical dynamic systems like cellular automata have been shown to produce complex global behaviour while being very simple in their internal structure (Wolfram, 1984; Langton, 1990; Green, 1992; Bradbury and Green, 1996). Because they focus on real physical entities, individual-based models such as SORTIE (Pacala et al., 1993, 1996) are becoming a very popular class of spatially-explicit models. However, despite their apparent potential, there are problems associated with these models. First, they usually produce an immense amount of raw output that makes them barely tractable (Judson, 1994). Second, while these models are based on the premise that spatial processes are of major importance (Pacala and Deutschman, 1995; Deutschman et al., 1997), the interpretation of the results is still mostly based on the analysis of time series illustrating the behaviour of *non-spatial* descriptors.

The objective of this paper is to study the spatio-temporal structure of stand level gap dy-

namics in a northern hardwood forest taking into account the way different species 'perceive' small-scale disturbances according to their own shade tolerance characteristics. For the purpose of this study, we are using the spatially-explicit, individual-based model SORTIE. Specifically, our aim is (1) to evaluate the spatio-temporal sensitivity of the model to initial conditions (initial seedling density and spatial arrangement), and (2) to characterise the stand level spatio-temporal pattern associated with gap dynamics emerging from local tree interactions.

We are specifically interested in whether gap dynamics predicted by the model exhibits a cohesive and consistent global, spatio temporal behaviour across different initial conditions. We also hypothesise that the model will exhibit a long-term, temporal convergence towards a similar emergent dynamics in relation to different initial conditions. This temporal convergence should be revealed in the trend of the predicted time series, as well as in its periodicity.

2. Materials and methods

2.1. The model

SORTIE (Pacala et al., 1993, 1996) is a model built using an object-oriented architecture. It attempts to reproduce the global behaviour of stands of northern hardwood forests by explicitly modelling the life cycle of each tree, as well as the local interactions between them. Individual growth, mortality and seedling dispersal are modelled according to each species individual's size and light availability. Competition between individuals is approximated by modelling the shading effect of each individual's neighbours. The model has been developed and calibrated using a large set of empirical observations taken in a northern hardwood forest of Connecticut, USA (Canham et al., 1994; Pacala et al., 1994; Ribbens et al., 1994; Kobe et al., 1995) and has proven to successfully reproduce and forecast non-spatial global descriptors of forest dynamics (such as basal-area), as well as community composition and spatial distribution of individuals through

succession (Pacala et al., 1996). Some studies have been conducted to assess the sensitivity of this model to internal parameters in order to characterise and quantify with accuracy the key elements behind emergent dynamics (Deutschman et al., 1997, 1999).

Among the nine species incorporated in the SORTIE model, we selected a subsample of six species for the purpose of the present study. These species are classified into two groups, shade tolerant species (*Fagus grandifolia*, *Tsuga canadensis* and *Acer saccharum*), and shade intolerant species (*Quercus rubra*, *Acer rubrum* and *Fraxinus americana*). A description of the ecology of these species and of the experimental stand conditions associated with SORTIE can be found in Pacala et al. (1993). Simulations were performed using a toroidal lattice of 120 × 120 m over 1000 years, with a time step of five years. A central 100 × 100 m sub-region was subsequently extracted for analytical purposes to reduce edge effect.

The overall experimental design is composed of four main parts and is illustrated on Fig. 1. Part A refers to the simulation process and describes the four initial conditions. Part B represents the way small-scale disturbances were extracted from the simulated datasets. Part C illustrates the spatial analyses performed at each time step to quantify emergent spatial structures. Finally, part D refers to the temporal analysis performed in order to monitor the spatial dynamics of the system.

2.2. Initiating the simulations

In order to perform a sensitivity analysis of the model, four sets of initial conditions were defined based on initial seedling density (low and high) and spatial configuration (random and aggregated). The former is modelled by varying the proportion of seedlings produced by each species under consideration, keeping the overall number of seedlings constant. For the latter, seedling dispersion was initially random. Then to obtain an aggregated spatial seedling structure, the entire simulation area was disturbed with a total clearcut after 250 years of simulation. By doing so, only the remaining in situ seedling population was incorporated in the model as an initial condi-

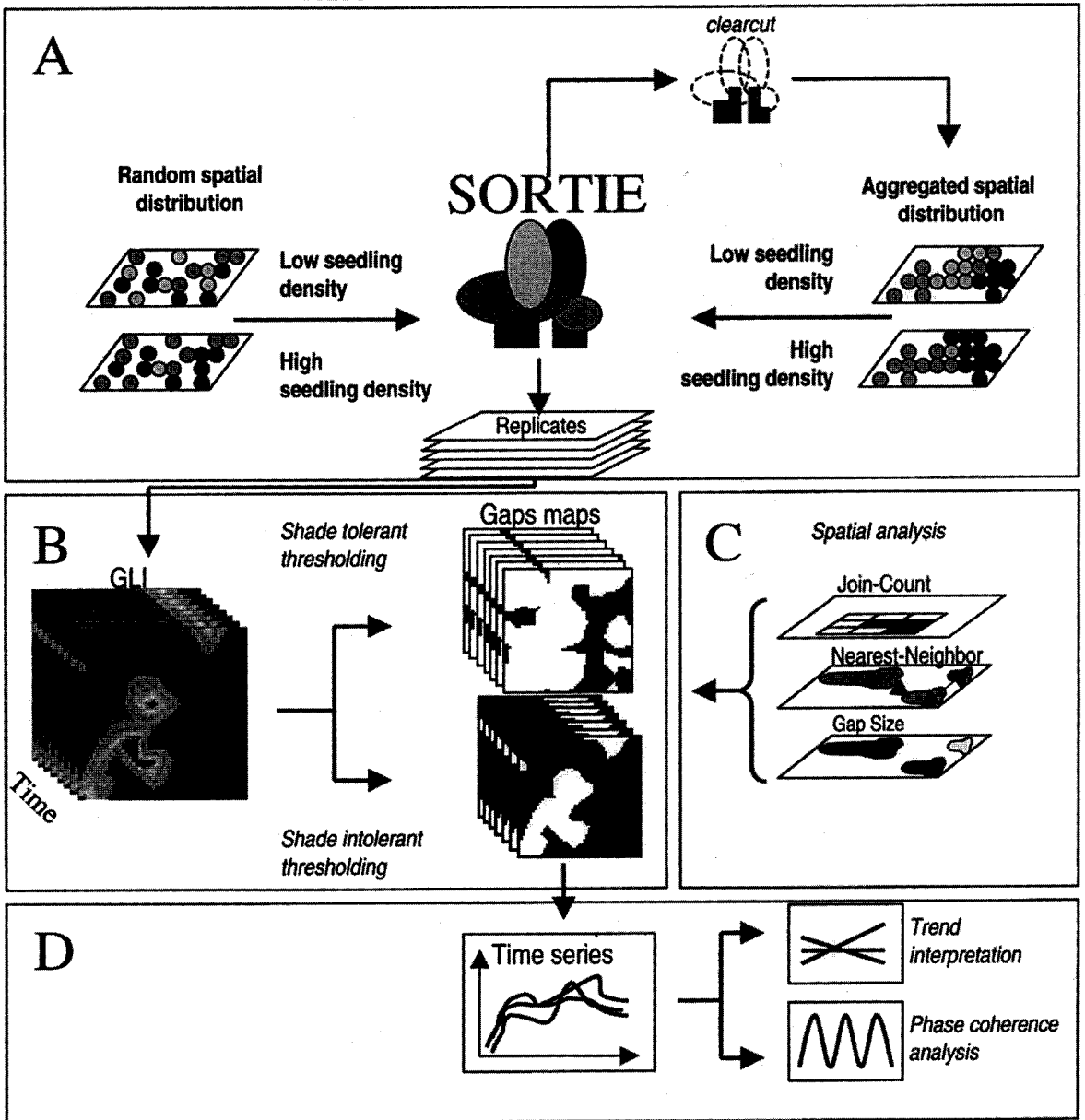


Fig. 1. Chart illustrating the simulation and analytical processes.

tion assuming that its spatial arrangement reflected a more 'natural pattern' than with the random distribution. In order to perform statistical analysis, we generated a set of five replicates for each of the initial conditions under consideration.

2.3. Quantifying light

SORTIE estimates incident radiation that reaches the top of the centre of the crown of each individual seedling, sapling, and adult tree in the modelled stand. Incident radiation is quantified

using the *Gap Light Index* (GLI, Canham et al., 1990), which ranges from 0 to 100 in units of percent of full sunlight. For our purposes, we modified SORTIE to also produce a set of raster layers where each cell contains GLI at various heights from the ground. GLI quantifies the percentage of incident photosynthetically active radiation (PAR) transmitted through the canopy to any horizontal and vertical spatial location in the understory over the period of the growing season. The GLI is formalised in Canham et al. (1990) as:

$$\text{GLI} = [(T_d P_d) + (T_b P_b)] 100.0 \quad (1)$$

where, P_d and P_b represent the proportion of diffuse and beam radiation that reaches the top of the canopy over the course of the growing season, and where T_d and T_b represent the proportion of diffuse and beam radiation that are transmitted through the canopy to a point in the understory. A value of GLI near 0 suggests the absence of any clear, detectable gap in the canopy while a value of 100 reveals the presence of a fully open site. The sensitivity of the model to this measure has been investigated by Deutschman et al. (1999). This study demonstrated that cohesive emergent population dynamics are produced by SORTIE even when using a coarser approximation of the fine-scale light heterogeneity in the model. While these results are based on circumstantial evidences, they strongly suggest an appreciable behavioral stability of SORTIE to the light modelling approach which reinforces the use of the GLI in the present study. For our purposes, this measure has been computed in its original fine-scale formulation (Pacala et al., 1993) at 1 m from the ground surface for the entire simulated area, for every time step.

2.4. To be a gap or not to be a gap?

A major challenge arises when relating light regimes to small-scale disturbances, the gap definition itself. It is more than likely that the way we define a gap will have a direct impact on its analysis at the stand level. Should a gap be defined as something discrete or as a fuzzy entity? Traditionally, a canopy gap is defined geometrically by the space generated by the death of one

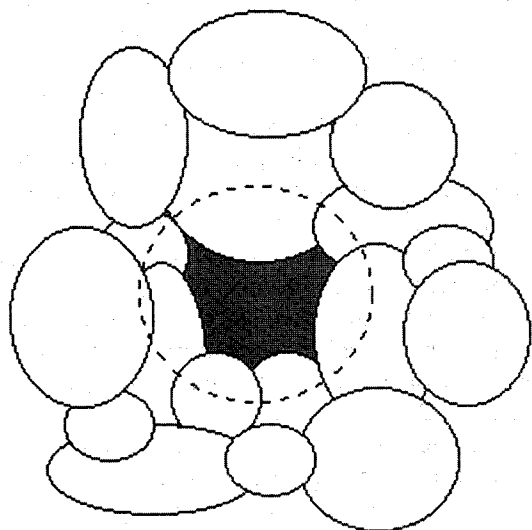
or a few canopy trees (or even by the loss of major branches from canopy trees). In order to relate this geometric conception of a gap to light, and considering that solar radiation may reach beyond the vertical projection of a conventional canopy gap, Runkle (1982) proposed the expanded (or extended) gap concept (EGC). Poulson and Platt (1989) also defined a canopy gap for eastern hardwood forests as a locally elevated light level, but this definition remains too simple and does not bring enough information to be operational.

Runkle (1982) expanded gap was originally defined as the vertically-projected area associated to the canopy hole created by the removal of the crown of a dead individual, extended to the bases of the individual trees that border the gap. Fig. 2 shows these two definitions of a gap. The grey areas represent the extent of the actual gap in the canopy. The dotted circles represent the extent of the crown of the tree that initiated the gap. In the first case, the gap extent is restricted to the area that was occupied by the dead tree crown. In the second case, the expanded gap incorporates the influence of the canopy opening on the light regime beneath the crowns of the immediately neighbouring trees.

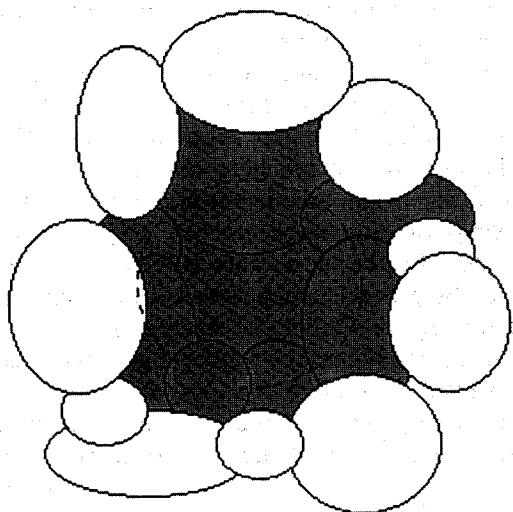
Using the GLI, Canham et al. (1990) demonstrated the presence of significant spatial heterogeneity in spatial gap organisation. They also showed that the influence of a canopy gap can 'extend considerable distances beyond the projected outline of the gap' (Canham et al., 1990). It is likely that this influence may also exceed the first-order neighbour distance and may influence saplings of different species in a species-specific manner. Furthermore, this influence will be affected by processes such as vertical gap filling and lateral gap reinvasion (Lorimer, 1989).

In this study, we use a generalised and species-dependent version of the *expanded gap concept*. This concept embeds the combined influence of direct beam radiation and sky diffuse radiation on the light regime reaching the understory, using GLI. This *species expanded gap concept* (SEGC) is defined by the portions of space in which light levels are suitable for the establishment and growth of particular species. We have focused on

light in our operational definition of SEGC because of the empirical evidence suggesting that light was the key limiting resource in the definition of seedlings habitats at the sites where SORTIE was parameterised (e.g. Pacala et al., 1994). In principle, the concept could also incorporate the effects of canopy gaps on spatial variation in



A



B

Fig. 2. Traditional ways to define a gap in ecology (grey areas). (A) canopy gap concept; (B) expanded gap concept.

Table 1

Different levels of seedlings density defined for each species in the process of generating the two density scenarios of initial conditions^a

Species Names	Low density (%)	High density (%)
<i>F. grandifolia</i>	11	6
<i>A. saccharum</i>	11	6
<i>T. canadensis</i>	11	6
<i>A. rubrum</i>	22	28
<i>F. americanus</i>	22	28
<i>Q. rubra</i>	22	28

^a Low and high density means, respectively, a lower and a higher representation of shade intolerant species in the set of initial conditions.

Table 2

GLI threshold values extracted for each species under consideration (Kobe et al., 1995)

Species	Group	GLI threshold
<i>F. grandifolia</i>	Shade tolerant	0.100
<i>A. saccharum</i>	Shade tolerant	0.625
<i>T. canadensis</i>	Shade tolerant	0.135
<i>A. rubrum</i>	Shade intolerant	1.860
<i>F. americanus</i>	Shade intolerant	2.430
<i>Q. rubra</i>	Shade intolerant	2.640

soil resource availability (Belsky and Canham, 1994) (Table 1).

In practice, we have defined species-specific, expanded gaps on the basis of empirical relationships between sapling mortality rates and incident light levels (GLI, Kobe et al., 1995). These relationships provide an objective basis for defining shade tolerance by definition, shade tolerant species have higher rates of survival at low light levels than intolerant species (Kobe et al., 1995; Kobe, 1996; Kobe and Coates, 1997). For each species, the relationships in Kobe et al. (1995) were used to determine the minimum light level that would result in a threshold mortality rate of 10% over 5 years (Table 2; Fig. 3). Hence, very small openings in the canopy can create functional gaps for shade tolerant species, while the same opening would not serve as an effective gap for less tolerant species. The threshold is based on field experience, but is ultimately arbitrary, and must be seen as an experimental exercise. Using

these thresholds, the GLI data for the raster layer output generated by SORTIE were reclassified to produce species-specific gap maps at each time step.

Fig. 1 (Part B) shows a portion of the GLI image produced at a specific time step during a simulation. On the same figure we can observe two binary images generated by applying two of the predefined GLI thresholds to the original GLI values. These images, further referred to as 'gap maps' in the text, both reflect the actual spatial distribution of canopy openings, but each map differs according to the shade tolerance of the target tree species. The important idea is that the dataset used in the present study is derived from a quantitative and continuous underlying representation of the light distribution that has been transformed to a binary representation corresponding to the presence/absence of a gap.

Compiling the series of binary gap maps extracted at each time step, we generated a spatio-temporal dataset that represents species-specific gap distributions through space and time, for each of the initial conditions simulated. Such spatio-temporal dataset allowed the detection of specific spatio-temporal gap events (appearance/disappearance, expansion/contraction, etc.) across the simulation space.

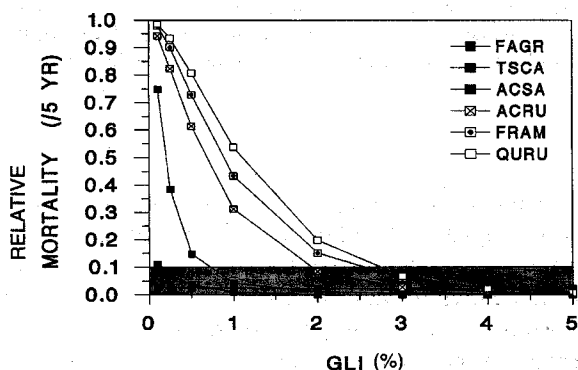


Fig. 3. Definition of the species-dependent GLI threshold (Kobe et al., 1995). *F. grandifolia*, ACSA, *A. saccharum*; ACRU, *A. rubrum*; QURU, *Q. rubra*; TSCA, *T. canadensis*; FRAM, *Fraxinus americanus*.

2.5. Characterising spatio-temporal gap dynamics

The first step in our spatio-temporal analysis of the gap dynamics was to test for the presence of an overall significant spatio-temporal structure over the entire successional sequence (as illustrated in Fig. 4). We performed a global spatio-temporal join-count analysis over each dataset, considering the temporal dimension as a third spatial dimension (H_0 = no significant spatio-temporal structure, $\alpha = 0.05$). This statistic is a 3D generalisation of spatial join-count statistics (Cliff and Ord, 1981; Fortin, 1999), a surface pattern method used to characterise the autocorrelation of qualitative/categorical data (in this study, the presence/absence of a gap). This method uses an isotropic neighbourhood and quantifies the gap/gap, gap/non-gap and non-gap/non-gap spatial links, allowing the characterisation of the dataset in terms of random, uniform or clustered spatial arrangement through the discretised simulation space.

In order to describe the details of the simulated gap dynamics, three spatial analyses were performed at each time step for each initial condition. These three statistics were chosen to highlight complementary information describing the spatial properties of the gap patterns generated by the model. First, the spatial join-count statistics were calculated for each time step to obtain a general picture of the spatial autocorrelation of the gap maps through time.

Second, nearest neighbour statistics were computed using the distance from one gap edge to the nearest gap in order to monitor the global expansion/contraction of the gap pattern at each time step. Finally, we computed the mean gap size, using the number of raster cells per gap, for each time step. This measure is often related to gap heterogeneity and used as a descriptor of gap dynamics (Payette et al., 1990; Coley, 1993; Gray and Spies, 1996); it was integrated in the present study for comparative purposes.

The values of these three statistics were plotted against time to produce time series. The periodicity of the temporal signal was analysed using the phase coherence (PC) approach (Lindström et al., 1997). This technique measures the periodicity of

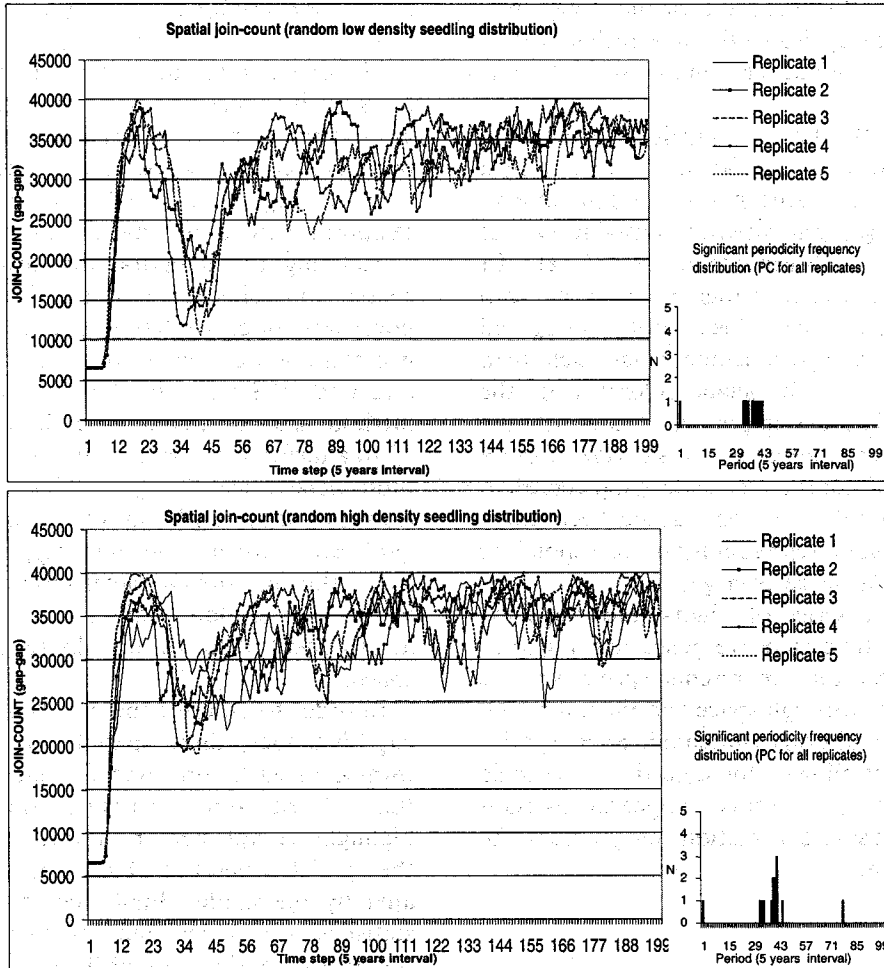


Fig. 4. *Q. rubra*, join-count time series representing the gap-gap spatial relationship. The histogram in the lower right corner illustrates the results of the PC analysis applied on the corresponding five replicates, for each initial condition. The Y axis of the histogram corresponds to the number of times a significant periodicity has been detected by the PC analysis among the five replicates for the corresponding time step period (plotted on the X axis).

a temporal signal by examining the deviation of data points from their zero-mean values (computed from a set of vectors including the time series values sampled at a specific period) for a period p to a period $p + n$. The main advantage of PC analysis over temporal autocorrelation analysis lies in its efficiency at detecting 'true periodicity' (i.e. good ability to detect periodicity in simple mathematical functions known to exhibit mathematical cyclical properties on the Poincaré

planes) while dealing with short and noisy time series signals. Another salient advantage of PC analysis is that it doesn't assume a linear correlation behaviour among the data. In addition, it does not assume the presence of white noise processes in the time series, as it is the case with other indices from the family of autocorrelation statistics. All the PC values were compared for statistical significance with 1000 permutations of the time series with an α threshold of 0.05.

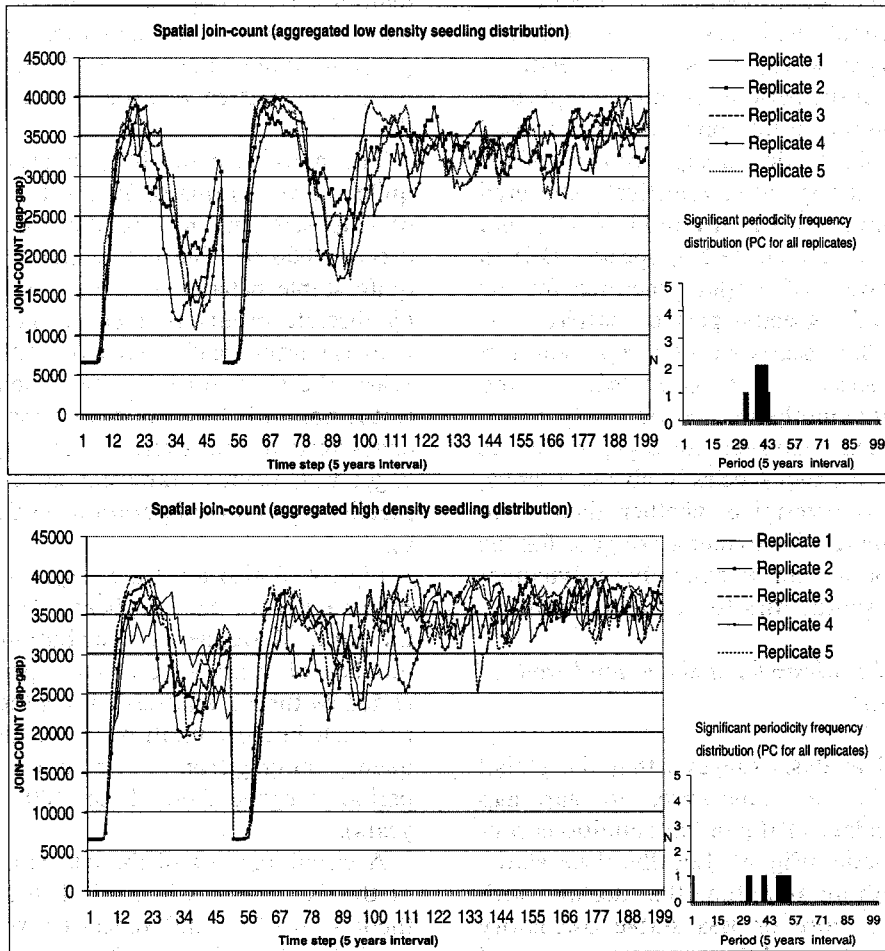


Fig. 4. (Continued)

3. Results

The global spatio-temporal join-count statistics reveal significant, spatio-temporal structures in all simulations ($\alpha = 0.05$). The comparison between initial conditions for this statistic is shown in Table 3 for each species. According to these results, we reject the null hypothesis and conclude that there are significant differences in the effective, global, spatio-temporal gap pattern for all of the species under consideration and for all of the different initial conditions.

More detailed spatial analysis was performed in order to capture the gap structure generated by

Table 3

Kruskal–Wallis results showing global comparison for the spatio-temporal join-count statistic between the four initial conditions

Species	Kruskal–Wallis	P(KW)
<i>A. saccharum</i>	15.11	0.002
<i>A. rubrum</i>	14.17	0.002
<i>Q. rubra</i>	14.01	0.002
<i>F. americanus</i>	14.01	0.002
<i>F. grandifolia</i>	12.25	0.006
<i>T. canadensis</i>	13.71	0.003

the model. Each of the three statistics, used in the context of this analysis, is described by reference to the variability observed in the global trend, the local trend and in the periodicity among replicates and between initial conditions. While we used different thresholds to define gaps for each of the six species, the species were effectively clustered into shade tolerant (GLI threshold < 1%) and intolerant (GLI threshold > 1%) species. Due to the massive amount of output generated for the analysis of each species-specific pattern, we present below the results of one representative shade tolerant species — *F. grandifolia* — and one representative intolerant species — *Q. rubra*. While we expected spatio-temporal gap dynamics to vary between the two species in absolute terms, our goal was to determine whether there were similarities in the relative dynamics of gaps for the two species groups, and whether those dynamics showed similar sensitivities to initial conditions.

3.1. Gap spatial analysis for a shade intolerant species (*Q. rubra*)

A first visual analysis suggests that the global trend of the join-count time series (for gap–gap links) is independent of the initial conditions simulated by the model (Fig. 4). Locally, these statistics oscillate with an amplitude that declines with time towards a more or less stable oscillatory state. The initial conditions with aggregated seedling distribution exhibit an evolution after the disturbance at the 50th time step (250 years) that is similar to the random runs, regardless of the density of seedlings initially incorporated into the model. Nonetheless, it appears that the aggregated, high density initial condition is associated to rapid stabilisation of the system compared with the aggregated low density scenario.

Distances between nearest gaps for the shade intolerant species ranged from 0 to 80 m, depending on the replicate and the initial condition observed¹, with a mean of approximately 15 m. The long-term trend in nearest neighbour statistics was quite stable (Fig. 5). At a very fine

temporal sampling, all replicates exhibit a pronounced saw-toothed signature. At coarser temporal sampling, the signal produces a smoother oscillating pattern regardless of initial conditions (Fig. 5).

The amplitude of the gap size time series is quite variable, ranging from 0 to 8000 m²(²) (Fig. 6). Gap sizes in most of the time series do not exceed 1000 m. The global trend also exhibits a quite stable behaviour that is locally punctuated by discrete events that cause mean gap size to increase dramatically. After the disturbance at 250 years, the time series reveals a behaviour similar to the period before the disturbance. The signal is characterised, however, by reduced amplitudes, suggesting again a stabilising effect of aggregated seedling spatial configuration on the system (Fig. 6).

Figs. 4–6 also illustrate a synthetic view of the PC analysis for each replicate. These results take the form of frequency distributions showing the number of times a significant periodicity is detected by the PC analysis among the five replicates for each initial condition. In ordinate is the frequency ranging from 0 to 5, and in abscissa is the period ranging from 1 to 100 timesteps (500 years).

A visual analysis of the frequency distributions of the PC analyses in Figs. 4–6 provides a synthetic view of the differences between the oscillating behaviour of the replicates for a given initial condition and for the three different spatial statistics. There is no initial condition for which the same periodicity is expressed by all of the replicates. We suggest that differences in periodicity between replicates are likely to be related to a delayed response of each replicate towards a similar (but not in phase) oscillatory pattern, rather than to truly different temporal trajectories. This interpretation is supported by the fact that results show peaks of high frequency as well as an important clustering effect for the majority of the distributions around 200–250 years (40–50 time steps). Between initial conditions, this clustering effect is quite pronounced and consistent for the join-

¹ A distance of 0 illustrates the presence of a single gap patch in the simulation area.

² A size of 0 illustrates the fact that there is no species expanded gap in the simulation area.

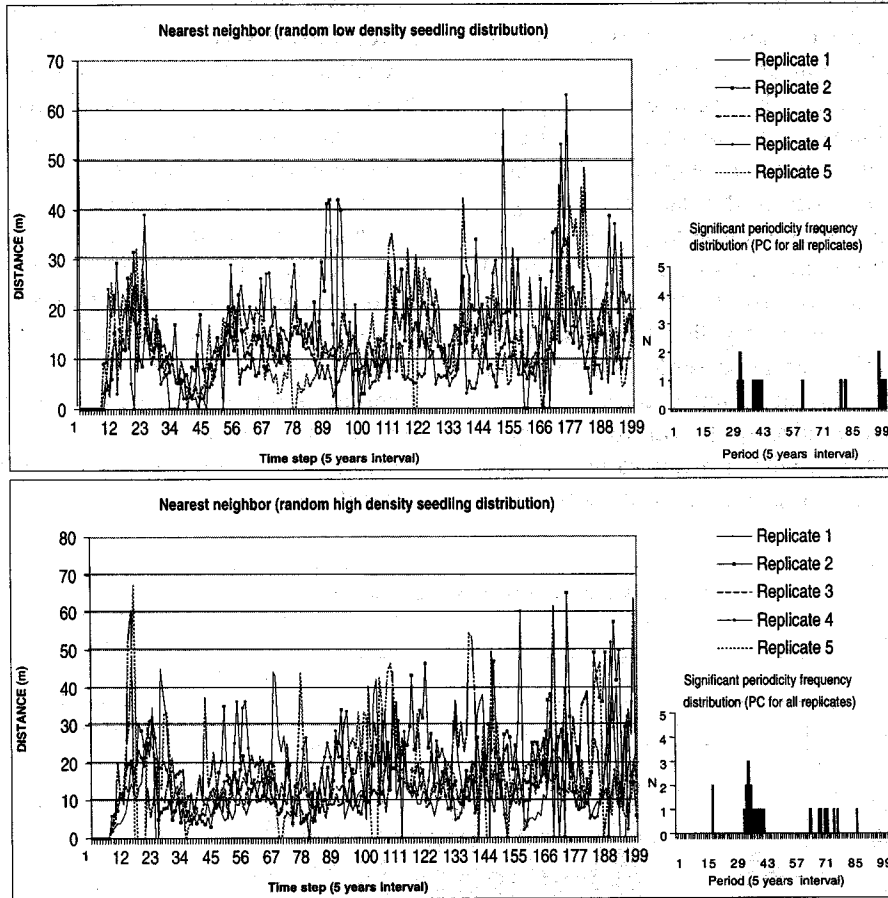


Fig. 5. *Q. rubra*, nearest neighbour time series representing the average distance between discrete gap objects (distance computed from the gap borders). The histogram in the lower right corner illustrates the results of the PC analysis applied on the corresponding five replicates, for each initial condition. The Y axis of the histogram corresponds to the number of times a significant periodicity has been detected by the PC analysis among the five replicates for the corresponding time step period (plotted on the X axis).

count analysis and the gap size analysis. This recurrent, temporal autocorrelation across replicates and initial conditions indicates the presence of a potentially important periodicity in gap formation of 200–250 years.

3.2. Gap spatial analysis for a shade tolerant species (*F. grandifolia*)

The join-count analysis of the shade tolerant species *F. grandifolia* (Fig. 7) exhibits temporal trends that are consistent between replicates and for each initial condition. These series describe a

global trend that increases with time, and with increasing amplitudes in the local oscillating pattern (Fig. 7). This behaviour is strikingly different from the trends exhibited by the join-count analysis of *Q. rubra*, the shade intolerant species (Fig. 4). The initial conditions with aggregated initial seedling distribution show an important peak after the disturbance event that differs from the early behaviour of the undisturbed simulations, regardless of initial seedling density. These results are effectively the opposite of the patterns seen for the intolerant species, suggesting that gap dynamics experienced by shade tolerant and intolerant species are qualitatively different.

Distances between nearest gap patches for the shade tolerant species range from 0 to 20 m, depending on the replicate and the initial condition observed (Fig. 8). The average inter-gap distance is approximately 5 m, which is one third of the average distance between gaps for the shade intolerant group. As it is the case for inter-gap distances for the shade intolerant species, the long-term trend is relatively stable. The temporal signal is characterised by a pronounced saw-toothed behaviour at a very fine temporal sampling, but oscillations at a coarser level are weaker than they are for the intolerant species.

Mean gap size is also quite variable, ranging from 800 to 8000 m², with a mean value oscillating around 5000 m² (Fig. 9). The time series also

exhibits a pronounced high-frequency oscillation. After disturbance at 250 years, the time series reveals a local behaviour different from the period before the disturbance. Specifically, the time series does not reach the same stable sill as it does at the beginning of the simulation. Nonetheless, the behaviour of the signal eventually tends to converge on dynamics similar to those observed with the two sets of random initial conditions. This suggests that the spatial extent of seedlings habitats as illustrated by the gap size statistics would be more dynamic on a short-term basis for shade tolerant dominated stands compared with shade intolerant dominated stands without, however, showing a strong sensitivity to this factor in long-term dynamics.

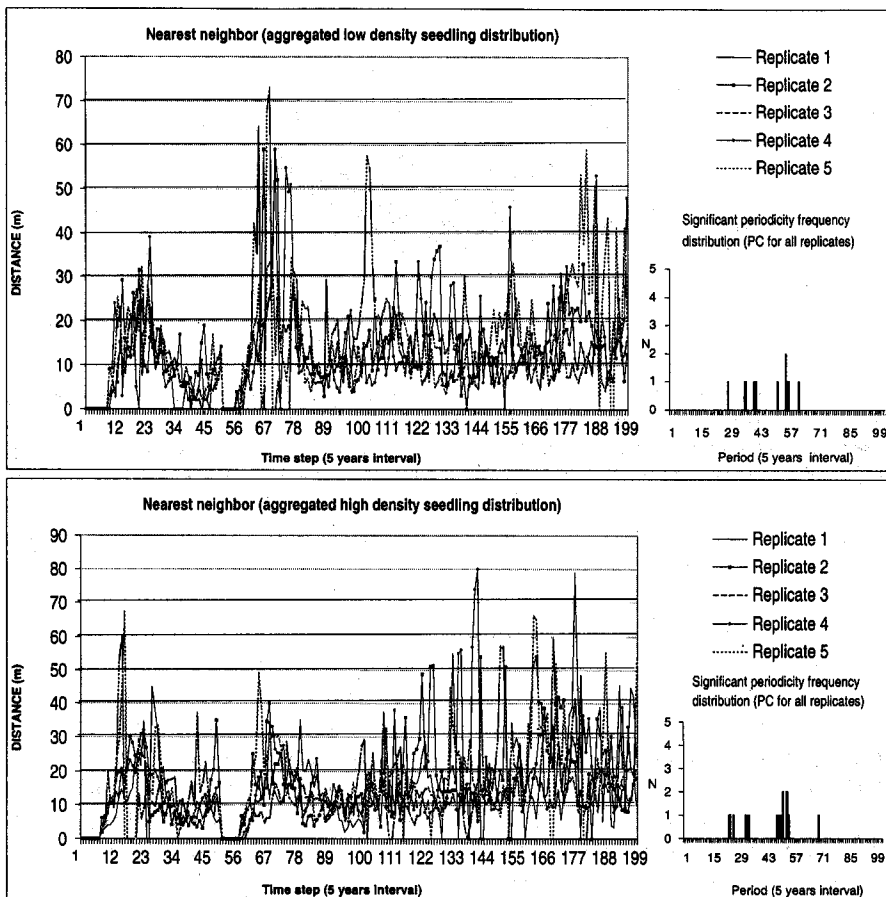


Fig. 5. (Continued)

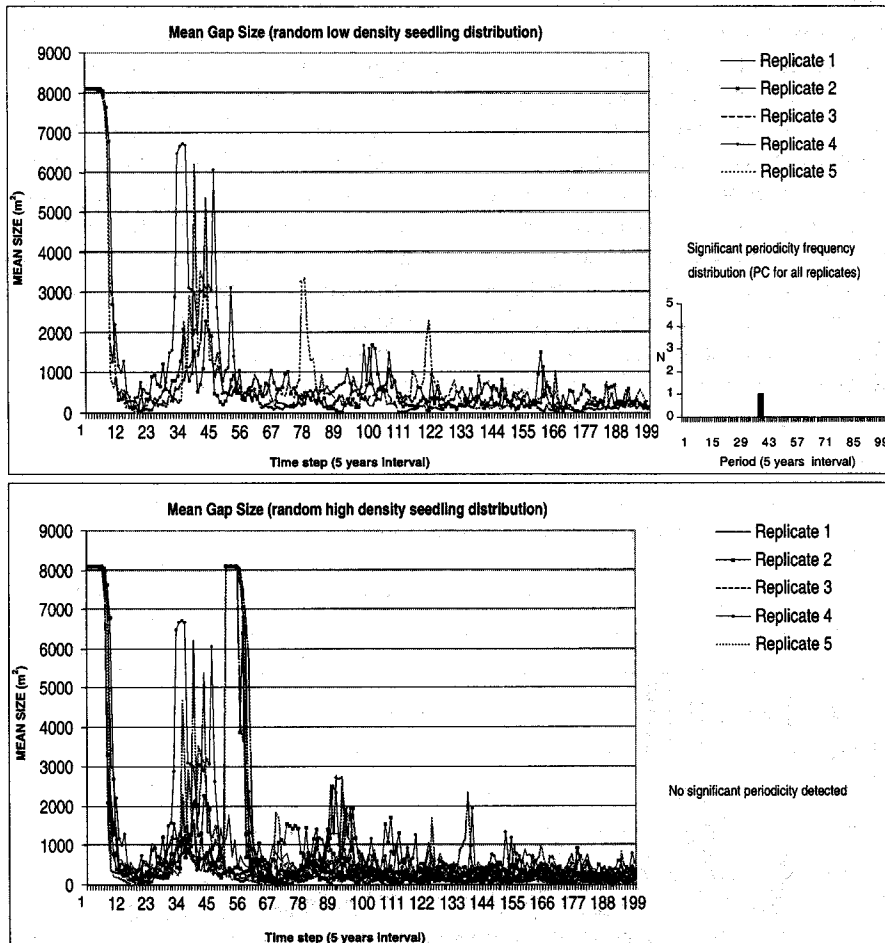


Fig. 6. *Q. rubra*, mean gap size time series. The histogram in the lower right corner illustrates the results of the PC analysis applied on the corresponding five replicates, for each initial condition. The Y axis of the histogram corresponds to the number of times a significant periodicity has been detected by the PC analysis among the five replicates for the corresponding time step period (plotted on the X axis).

As for the shade intolerant species, the PC analyses of the three spatial statistics reveal that similar initial conditions can produce different oscillatory patterns. Overall, our results suggest a clustering in the periodicity of gap dynamics of around 200–250 years, remarkably similar to the periodicity observed for *Q. rubra* in the earlier section. In contrast to the results for the shade intolerant species, significant periodicities in gap dynamics for the shade tolerant species are present in fewer replicates in only 3 of the 4 sets of initial conditions (Figs. 7–9).

4. Discussion and conclusion

4.1. Spatio-temporal sensitivity of the model to initial conditions

One of our first observations is that SORTIE exhibits a significantly cohesive global spatio-temporal behaviour. It is likely that the global differences observed between initial conditions are related to the inclusion of a disturbance in half of the simulations rather than solely due to strong sensitivity to initial conditions. This interpretation

is supported by the analysis of the global trends of the time series that show consistency between initial conditions despite the fact that they present many subtle local differences in replicate behaviour. Such local differences might be related to the sensitivity of the model to its own internal parameters (e.g. the pseudo-random number generator). If the disturbance simulated in order to spatially structure the seedling configuration influences the short-term behaviour of the time series, the results seem to be quite convergent in a long-term perspective. The aggregation effect of significant gap periodicity around 200–250 years, revealed by the frequency

distributions of the PC analysis, reinforces this view of a long-term stability of the gap behaviour. It suggests a coherent behaviour between replicates for a single initial condition despite a more sensitive response to initial conditions.

On the other hand, for a same initial condition, a change in the shade tolerance level used to define gaps is associated with a change in the amount of variability observed between different replicates. Variability increases as the level of shade tolerance increases (as an example, see Fig. 9 between 305 and 600 years). From a dynamical perspective, we also observe that different seedling

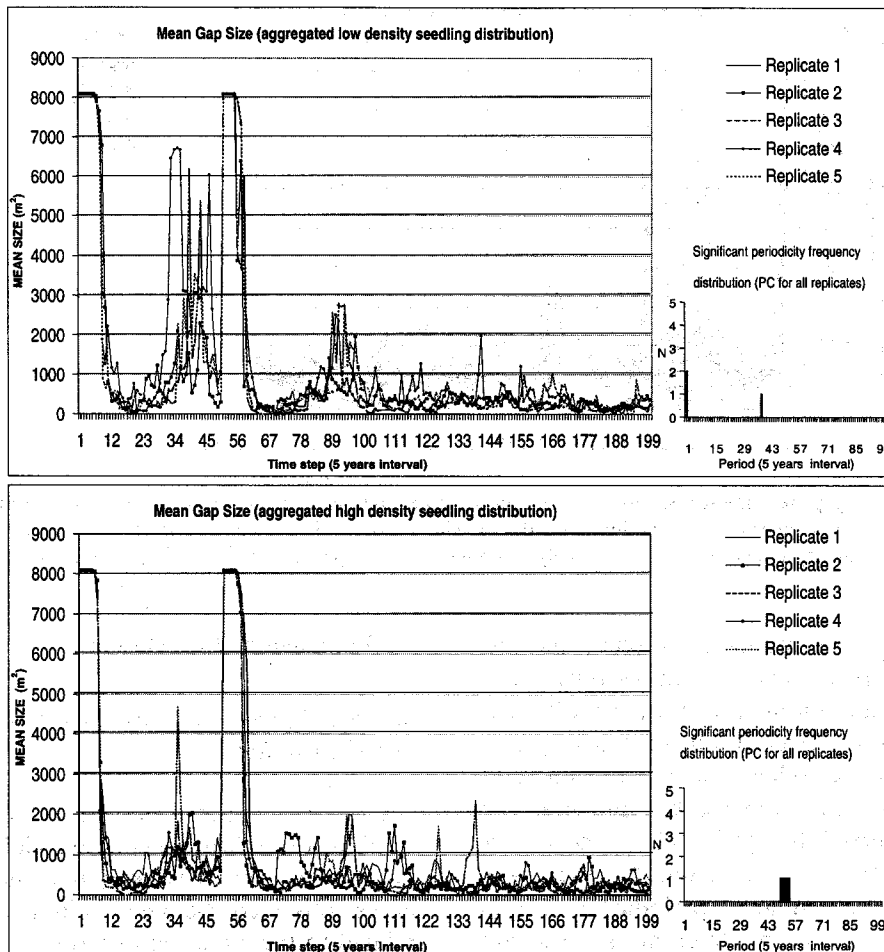


Fig. 6. (Continued)

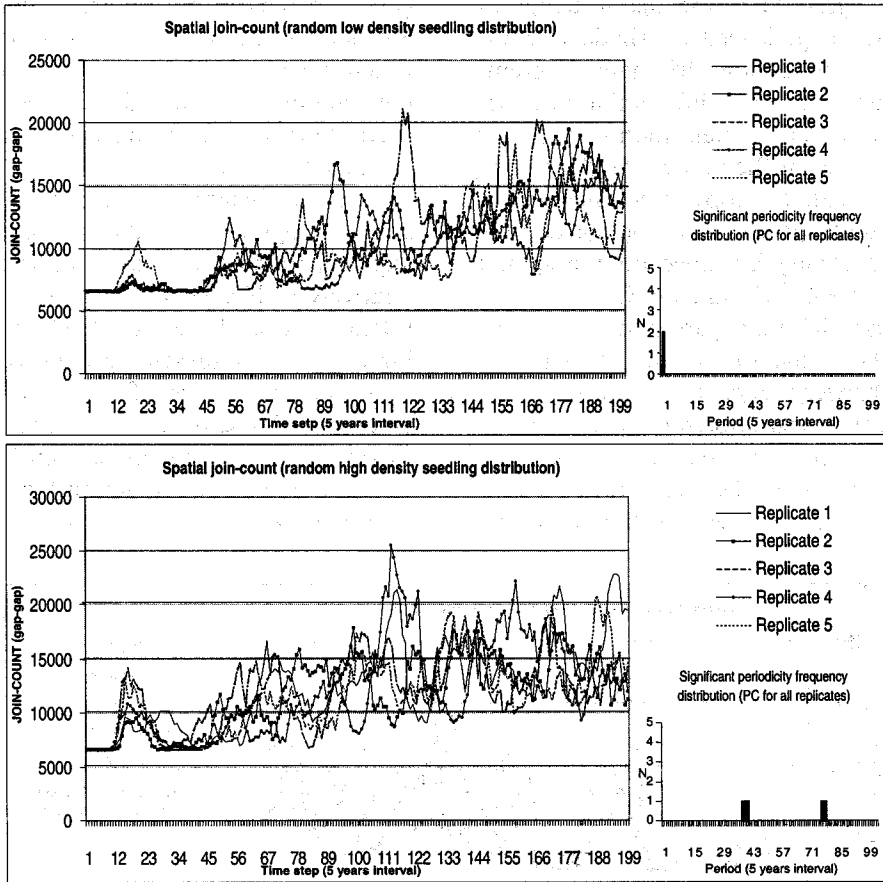


Fig. 7. *F. grandifolia*, spatial join-count time series representing the gap-gap spatial relationship. The histogram in the lower right corner illustrates the results of the PC analysis applied on the corresponding five replicates, for each initial condition. The Y axis of the histogram corresponds to the number of times a significant periodicity has been detected by the PC analysis among the five replicates for the corresponding time step period (plotted on the X axis).

distributions can induce differential transient dynamics among replicates but a similar long-term dynamics as observed with random initial seedling distributed simulations. Results also suggest that the magnitude and the direction of this effect might also depend on the selected GLI level for a specific simulation. The time series suggests that structuring the seed spatial organisation may contribute to stabilise or, at the opposite, to enhance the oscillations in specific phases of the system according to different GLI thresholds. An example of this stabilisation effect is provided by the mean gap size of the shade intolerant species (Fig. 6) between 50 and 120 time steps for the aggre-

gated scenario as compared with 0–70 time steps for the random distribution.

4.2. Ecological implications

Our results lead us to the presumably obvious but often neglected conclusion that consideration of spatial dynamics is of vital importance in characterising spatially-explicit models. For example, SORTIE produces spatio-temporally cohesive gaps constituted from aggregated pixels, not scattered ones, which is consistent with the patch dynamics resulting in a spatial mosaic signature (Pickett and White, 1985). The spatio-temporal

analysis also suggests that the spatio-temporal dynamics of gaps experienced by shade tolerant versus intolerant species are strikingly different. GLI thresholding first has a differential structuring effect on the spatial configuration of gaps for each species included in the model. As these gaps define areas of potential canopy recruitment (Canham, 1989) for each species, their configuration is likely to have a strong influence on the spatial arrangement of species within stands.

How do these different gap patterns evolve through time? Our analysis of gap size patterns and distances between gaps reveal clear differences for tolerant versus intolerant species. First, shade intolerant species generally experience *small, distant gaps*, while the shade tolerant species experience *large, close gaps*. In this sense, the

gaps experienced by the shade intolerant species are closer to the size and configuration of conventional gaps defined by the vertical projection of the canopy opening. Gaps experienced by the shade tolerant species are better described by the expanded gap definition.

From a dynamical perspective, the gap size analysis suggests that the temporal dynamics of gaps experienced by shade intolerant species are relatively stable, while the gaps perceived by the tolerant species have a relatively unstable oscillating behaviour representing high frequency *expansion and contraction* of the gap pattern in the landscape. These observations reflect the fact that expanded gaps are more sensitive to subtle changes in available radiation than are more conventional gaps.

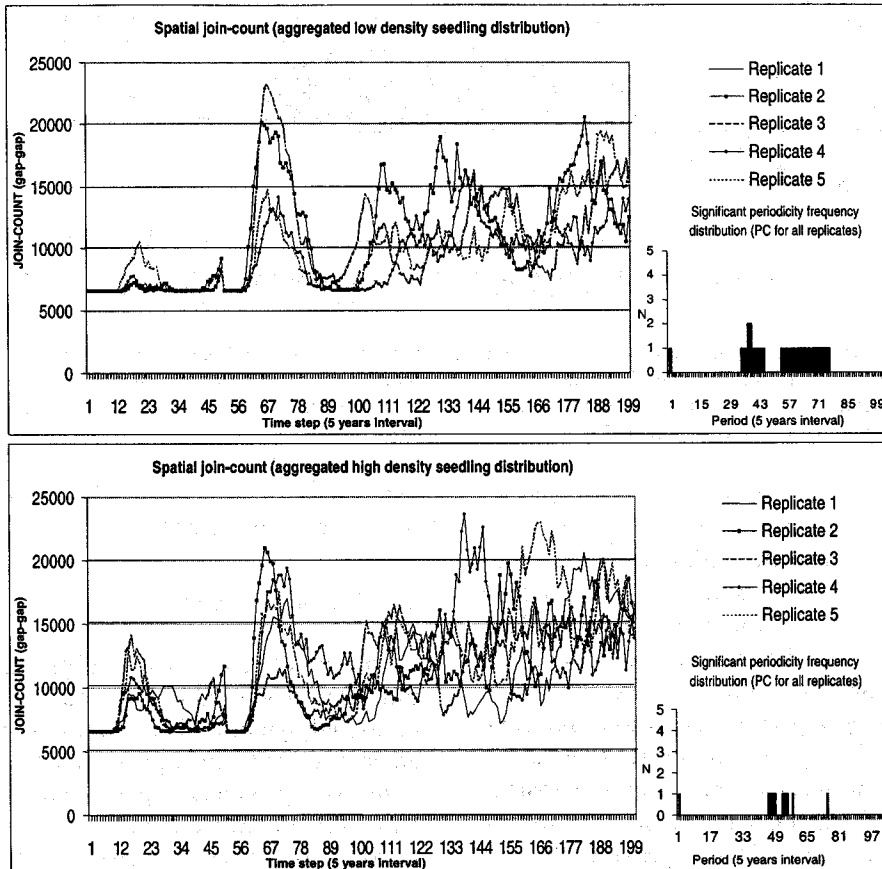


Fig. 7. (Continued)

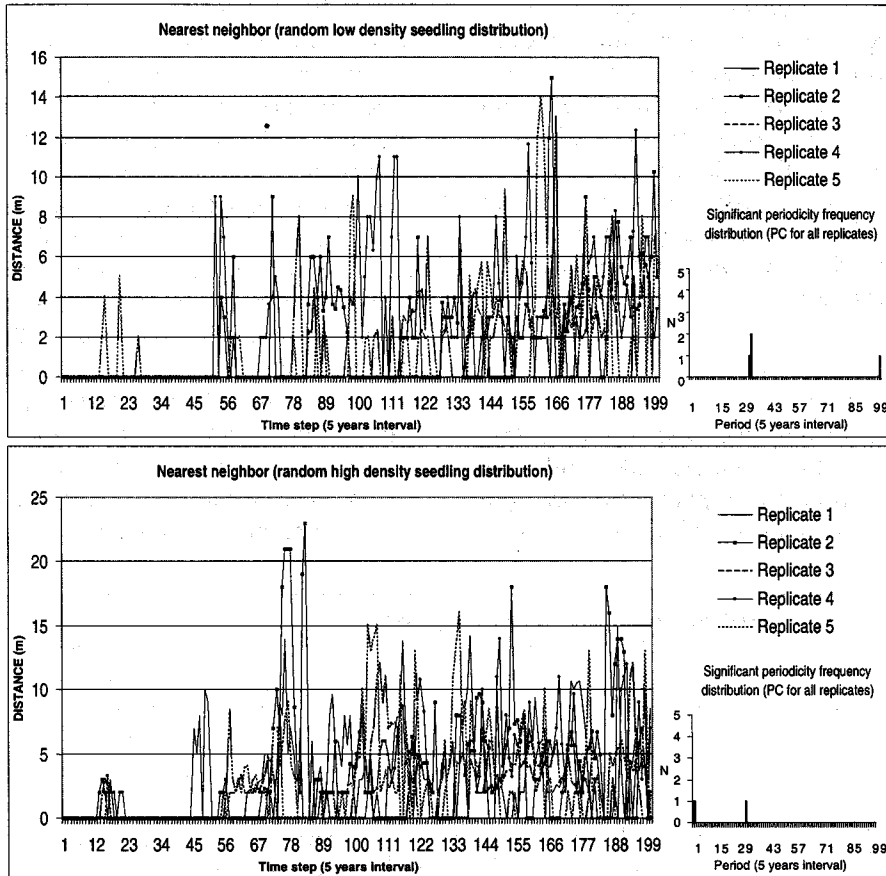


Fig. 8. *F. grandifolia*, nearest neighbour time series representing the average distance between discrete gap objects (distance computed from the gap borders). The histogram in the lower right corner illustrates the results of the PC analysis applied on the corresponding five replicates, for each initial condition. The Y axis of the histogram corresponds to the number of times a significant periodicity has been detected by the PC analysis among the five replicates for the corresponding time step period (plotted on the X axis).

Consequently, a shade tolerant species is likely to experience opportunities for seedling establishment and ultimate canopy recruitment that follow a sort of ‘flash flood’ dynamics, where the proportion of the habitat suitable to colonisation oscillates from very high to very low in a relatively small period of time. We suggest that this process may have significant consequences for species interactions, by constituting a very dynamic, spatial constraint on critical phases in tree life histories. Our results are consistent with the suppression-release dynamics of shade tolerant species documented by Canham

(1985, 1990) and subsequent studies (Merrens and Peart, 1992; Rebertus and Veblen, 1993; Orwig and Abrams, 1994; Cho and Boerner, 1995). Extensive research and model validation will be required to confirm the relationship between the model simulations and empirical observations of the temporal dynamics of canopy recruitment in both shade tolerant and intolerant species. Additional research will also be needed to address the much broader question of the effect of the observed spatial instability of gap dynamics on the nonequilibrium nature of succession and species coexistence.

Finally, the PC analysis of all the spatio-temporal datasets suggests that the dominant processes governing gap formation may be related to *mass event processes* that operate at a coarser temporal scale, and that can be complementary to documented, finer temporal scale events of 25–30 years (Payette et al., 1990). These results are consistent with the view that gaps produced by the death of old trees are one of the key components of gap dynamics.

4.3. Future research

This study is among the first attempts (see Acevedo et al., 1995) to understand stand level spatio-temporal patterns emerging from local gap dynamics predicted by an individual-based simu-

lation. We believe that the SEGCG has proven to be a flexible framework allowing a more accurate representation of the intimate relationship between species and light from an ecological perspective. This new interpretation of small-scale disturbances dynamics is now opening a whole new dimension of research opportunities.

In this study, we defined the GLI thresholds on the basis of an arbitrarily selected but realistic mortality rate. An interesting approach for future research would be to evaluate the potential of different light aggregation schemes using fuzzy sets theory to define membership functions to a gap/non-gap state for each spatial location, while still taking into account the relationship between species-specific mortality rates and the GLI. This operational approach is likely to provide more

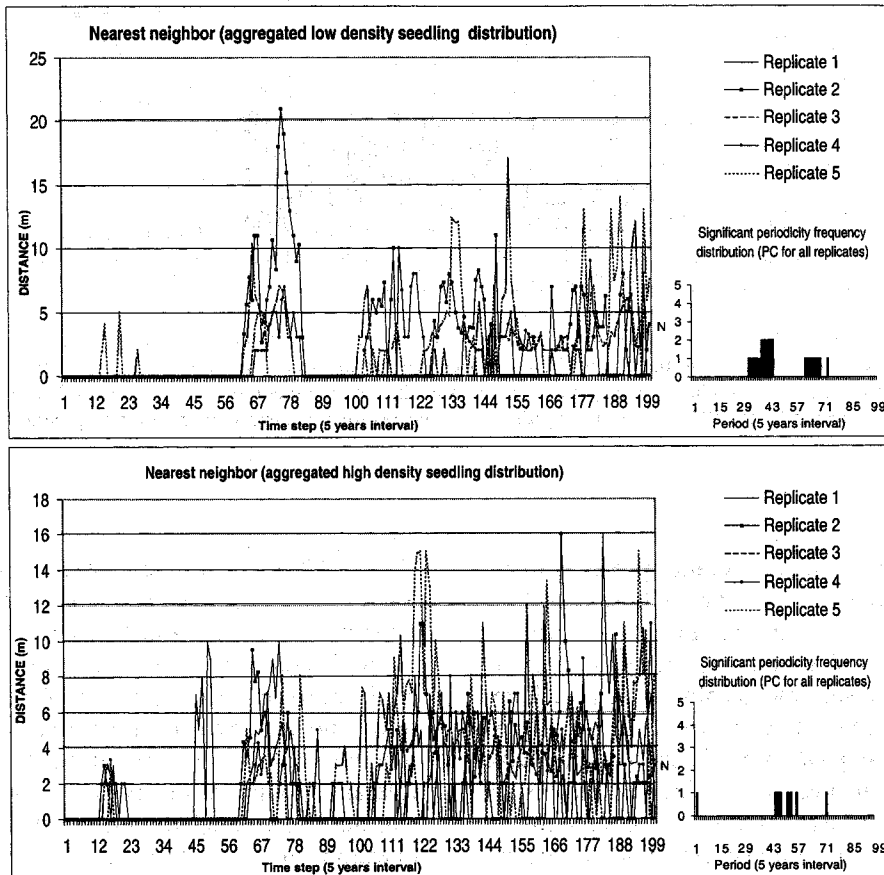


Fig. 8. (Continued)

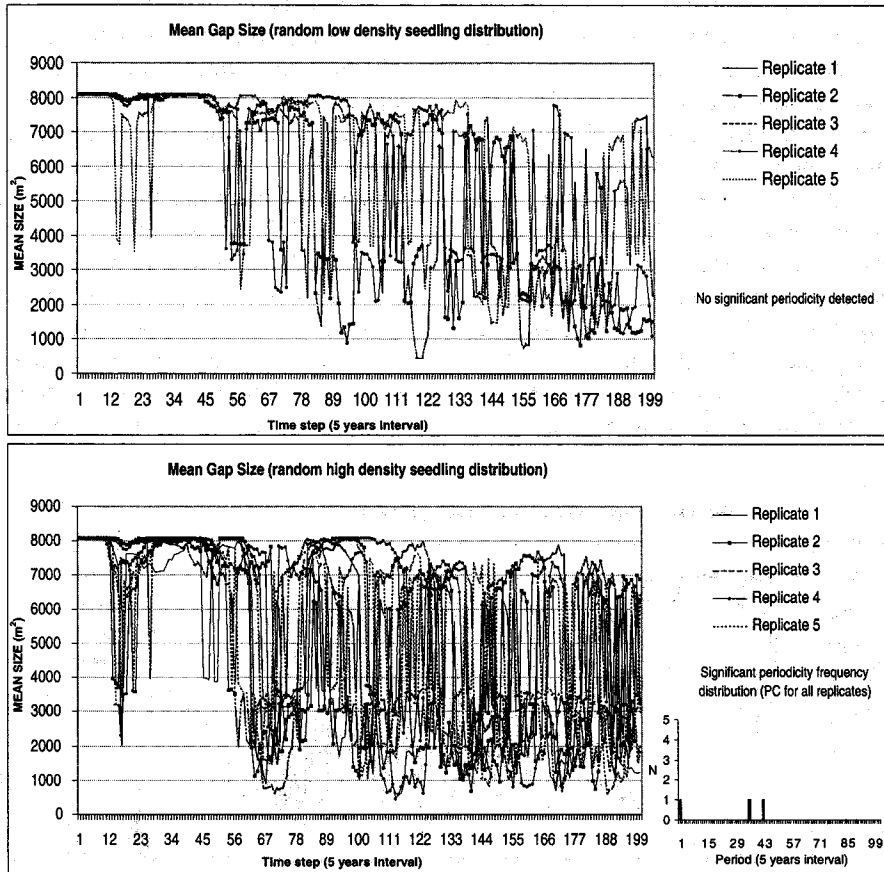


Fig. 9. *F. grandifolia*, mean gap size time series. The histogram in the lower right corner illustrates the results of the PC analysis applied on the corresponding five replicates, for each initial condition. The Y axis of the histogram corresponds to the number of times a significant periodicity has been detected by the PC analysis among the five replicates for the corresponding time step period (plotted on the X axis).

flexible rules in the definition of a *gap*. It is also important to recognise the need to evaluate the gap spatio-temporal dynamics for a more extensive set of species along the shade tolerance gradient. We expect this operation to enable the identification of species-specific behaviour characterising distinctive self-organised spatio-temporal patterns.

From a topological perspective, we recognise that gaps are dynamic entities that spatially interact with each other and that their borders are also dynamic. Relating gap spatial organisation to disturbance history may provide useful, new information about gap dynamics at the stand level.

This requires the development of a methodology to track ‘gap lineages’ through space and time. Here, the potential of object-oriented analysis and graph theory could be investigated.

Scale issues are also of vital importance in future research. At which spatial scales should simulations be conducted? What is the relationship between the spatial dimensions of the simulation space and the effects of the torus edge-wrapping method? Temporal scale is also likely to be important. In the past few years, researchers highlighted the fact that natural dynamical systems can exhibit very long transients over many thousands of years before reaching

their long-term dynamics (Hastings and Higgins, 1994). Over which temporal period should a forest be simulated in order to capture the essence of its dynamics? These questions are not usually addressed explicitly by modellers even if they are likely to promote incomplete and/or fallacious interpretations of the simulated dynamics by not being well-tuned at the scale at which the studied emergent pattern is really expressed. Time scale issue will be especially important in the process of further exploring the ecological meaning of the 200–250 years periodicity detected in this study.

Another interesting research path would be to explicitly refer to the spatio-temporal organisation

of seedlings habitats as a system of constraints acting on population dynamics and species dispersal into the succession framework. Field data suggest that some species regenerate better in gaps of specific age that were dominated by a specific species [e.g. beech regenerate better in old sugar maple gaps (Runkle, 1990)]. Other evidence shows that the ability of shade tolerant species to handle the period of light suppression between gap formation leads to very complex succession dynamics (Canham, 1989). We also suggest that emergent gap spatial patterns can influence population dynamics by defining a set of spatial constraints that influence species recruitment at the local level. It

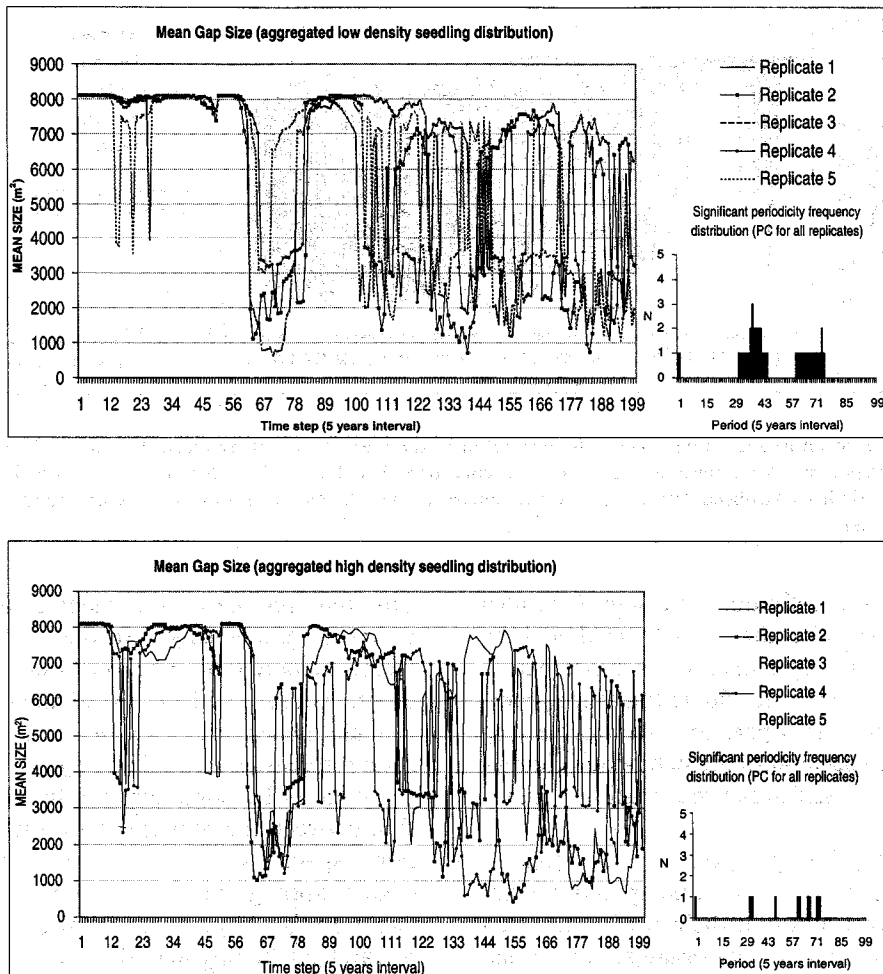


Fig. 9. (Continued)

would be interesting to relate the self-organised gap spatial heterogeneity to different modelling schemes of the GLI in order to link our results with those proposed by Deutschman et al. (1999).

Overall, it is clear that mechanistic interpretation relating gaps with individual trees at the stand level, new insights about local gap heterogeneity, and a better understanding of the cohesive emergent spatio-temporal properties of gap dynamics at the stand level, can replace the simplistic dichotomy between 'gap' and 'closed canopy' (Lieberman et al., 1989) conditions in forest ecology. The SEGC proposed in this study represents an important step in this direction.

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References

Acevedo, M.F., Urban, D.L., Ablan, M., 1995. Transition and gap models of forest dynamics. *Ecol. Appl.* 5, 1040–1055.

Belsky, A.J., Canham, C.D., 1994. Forest gaps and isolated savanna trees: an application of patch dynamics in two ecosystems. *BioScience* 44, 77–84.

Bormann, F.H., Likens, G.E., 1979. *Pattern and Process in a Forested Ecosystem*. Springer, New York, p. 253.

Bossel, H., Krieger, H., 1991. Simulation model of natural tropical forest dynamics. *Ecol. Modell.* 59, 37–71.

Bossel, H., Krieger, H., 1994. Simulation of multi-species tropical forest dynamics using a vertically and horizontally structured model. *Forest Ecol. Manag.* 69, 124–144.

Botkin, D.B., Janak, J.F., Wallis, J.R., 1972. Some ecological consequences of a computer model of forest growth. *J. Ecol.* 60, 849–873.

Bradbury, R.H., Green, D.G., 1996. In: Bossomaier, T.J., Green, D.G. (Eds.), *Are ecosystems complex systems?* In *Complex Systems*. Cambridge University Press, Cambridge.

Brokaw, N.V.L., 1985. Treefalls, regrowth, and community structure in tropical forests. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, pp. 53–68.

Canham, C.D., 1985. Suppression and release during canopy recruitment in *Acer saccharum*, vol. 112. *Bulletin of the Torrey Botanical Club*, pp. 134–145.

Canham, C.D., 1988. Growth and architecture of shade-tolerant trees: response to canopy gaps. *Ecology* 69, 786–795.

Canham, C.D., 1989. Different responses to gaps among shade-tolerant tree species. *Ecology* 70, 548–550.

Canham, C.D., 1990. Suppression and release during canopy recruitment in *Fagus grandifolia*. *Bull. Torrey Bot. Club* 117, 1–7.

Canham, C.D., Denslow, J.S., Platt, W.J., Runkle, J.R., Spies, T.A., White, P.S., 1990. Light regimes beneath closed canopies and tree-fall gaps in temperate and tropical forests. *Can. J. Forest Res.* 20, 620–631.

Cho, D.S., Boerner, R.E.J., 1995. Dendrochronological analysis of the canopy history of two Ohio old-growth forests. *Vegetation* 120, 173–183.

Cliff, A.D., Ord, J.K., 1981. *Spatial processes: Models and Applications*. Pion, London, p. 266.

Coley, P.D., 1993. Gap size and plant defenses. *Trends Ecol. Evol.* 8, 1–2.

Coquillard, P., Hill, D.R.C., 1997. Modélisation et simulation d'écosystèmes. In: *Des Modèles Déterministes Aux Simulations à Événements Discrets*. Masson, Paris, p. 273.

Cosalanti, R.L., Grime, J.P., 1993. Resource dynamics and vegetation processes: A deterministic model using two-dimensional cellular automata. *Funct. Ecol.* 7, 169–176.

Denslow, J.S., 1980. Gap partitioning among tropical rain-forest trees. *Biotropica* 12 (Supp.), 47–55.

Deutschman, D.H., Levin, S.A., Devine, C., Buttell, L.A., 1997. Scaling from trees to forests: analysis of a complex simulation model. *Science ONLINE*, <http://www.sciencemag.org/feature/data/deutschman/index.htm>.

Deutschman, D.H., Levin, S.A., Pacala, S.W., 1999. Error propagation in a forest succession model: the role of fine-scale heterogeneity in light. *Ecology* 80, 1927–1943.

Fortin, M.-J., 1999. Spatial statistics in landscape ecology. In: Klopatek, J.M., Gardner, R.H. (Eds.), *Landscape Ecological Analysis. Issues and Application*. Springer, Berlin, pp. 253–279.

Gray, A.N., Spies, T.A., 1996. Gap size, within gap position and canopy structure effects on conifer seedling establishment. *J. Ecol.* 84, 635–645.

Green, D.G., 1992. Emergent behaviour in biological systems. In: Green, D.G., Bossomaier, T.J. (Eds.), *Complex Systems From Biology to Computation*. IOS Press, Amsterdam, pp. 25–36.

Green, D.G., 1994. Connectivity and the evolution of biological systems. *J. Biol. Syst.* 2, 91–103.

Hastings, A., Higgins, K., 1994. Persistence of transients in spatially structured ecological models. *Science* 263, 1133–1136.

- Judson, O.P., 1994. The rise of the individual-based model in ecology. *Trends Ecol. Evol.* 9, 9–14.
- Kobe, R.K., 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. *Ecol. Monogr.* 66, 181–201.
- Kobe, R.K., Coates, K.D., 1997. Models of sapling mortality as a function of growth to characterise interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. *Can. J. Forest Res.* 27, 227–236.
- Kobe, R.K., Pacala, S.W., Silander, J.A. Jr., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. *Ecol. Appl.* 5, 517–532.
- Langton, C.G., 1990. Computation at the edge of chaos. Phase transients and emergent computation. *Phys. D* 42, 12–37.
- Leemans, R., Prentice, I.C., 1989. FORSKA, a general forest succession model. Institute of Ecological Botany, Uppsala.
- Lieberman, M., Lieberman, D., Peralta, R., 1989. Forests are not just swiss cheese: Canopy stereogeometry of non-gaps in tropical forests. *Ecology* 70, 550–552.
- Lindström, J., Kokko, H., Ranta, E., 1997. Detecting periodicity in short and noisy time series data. *Oikos* 78, 406–410.
- Lorimer, C.G., 1989. Relative effects of small and large disturbances on temperate hardwood forest structure. *Ecology* 70, 565–567.
- Merrrens, E.J., Peart, D.R., 1992. Effects of hurricane damage on individual growth and stand structure in a hardwood forest in New Hampshire, USA. *J. Ecol.* 80, 787–795.
- Orwig, D.A., Abrams, M.D., 1994. Contrasting radial growth and canopy recruitment patterns in *Liriodendron tulipifera* and *Nyssa sylvatica*: gap-obligate versus gap-facultative species. *Can. J. For. Res.* 24, 2141–2149.
- Pacala, S.W., Deutschman, D.H., 1995. Details that matter: The spatial distribution of individual trees maintains forest ecosystem function. *Oikos* 74, 357–365.
- Pacala, S.W., Canham, C.D., Silander, J.A. Jr., 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Can. J. Forest Res.* 23, 1980–1988.
- Pacala, S.W., Canham, C.D., Silander, J.A. Jr., Kobe, R.K., 1994. Sapling growth as a function of resources in a north temperate forest. *Can. J. Forest Res.* 24, 2172–2183.
- Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A. Jr., Kobe, R.K., Ribbens, E., 1996. Forest models defined by field measurements: II. Estimation, error analysis and dynamics. *Ecol. Monogr.* 66, 1–43.
- Payette, S., Filion, L., Delwaide, A., 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns, the Tantaré ecological reserve, Quebec. *Can. J. Forest Res.* 20, 1228–1241.
- Pickett, S.T.A., White, P.S. (Eds.), 1985. The ecology of natural disturbances and patch dynamics. Academic Press, New York.
- Poulsen, T.L., Platt, W.J., 1989. Gap light regimes influence canopy tree diversity. *Ecology* 70, 543–555.
- Ribbens, E., Silander, J.A., Pacala, S.W., 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75, 1794–1806.
- Runkle, J.R., 1982. Patterns of disturbance in some old growth mesic forests of eastern North America. *Ecology* 63, 1533–1546.
- Runkle, J.R., 1985. Disturbance regimes in temperate forests. In: Pickett, S.T.A., White, P.S. (Eds.), *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, Orlando, pp. 17–34.
- Runkle, J.R., 1990. Gap dynamics in an Ohio Acer-Fagus forest and speculations on the geography of disturbance. *Can. J. Forest Res.* 20, 632–641.
- Shugart, H.H., West, D.C., 1977. Development of an Appalachian deciduous forest succession model and its application to assessment of the impact of the chestnut blight. *J. Environ. Manag.* 5, 161–179.
- Silvertown, J., Smith, B., 1988. Gaps in the canopy: the missing dimension in vegetation dynamics. *Vegetation* 77, 57–1760.
- Urban, D.L., 1990. A versatile model to simulate forest pattern. In: *A User's guide to ZELIG 1.0*. University of Virginia, Department of Environmental Sciences, Charlottesville.
- Urban, D.L., Bonan, G.B., Smith, T.M., Shugart, H.H., 1991. Spatial applications of gap models. *Forest Ecol. Manag.* 42, 95–110.
- Vitousek, P.M., White, P.S., 1981. Process studies in succession. In: West, D.C., Shugart, H.H., Botkin, D.B. (Eds.), *Forest Succession, Concepts and Application*. Springer, New York, pp. 267–276.
- Wissel, C.H., 1994. A model for the mosaic-cycle concept. In: Remmert, H. (Ed.), *The Mosaic-Cycle Concept of Ecosystems*, Ecological studies 85. Springer, Berlin.
- Withmore, T.C., 1989. Canopy gaps and the two major groups of forest trees. *Ecology* 70, 536–538.
- Wolfram, S., 1984. Cellular automata as models of complexity. *Nature* 311, 419–424.