Université de Montréal

Caractérisation spatiale de l'impact périphérique des perturbations forestières de petite envergure par la modélisation

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Ce mémoire intitulé :

Caractérisation spatiale de l'impact périphérique des perturbations forestières de petite
envergure par la modélisation

présenté par

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Mémoire accepté le : ……………………..

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Les perturbations de petite envergure (PPE) est une expression récente englobant les trouées naturelles et les perturbations sylvicoles. Elles sont reconnues comme des éléments clés de la dynamique des forêts feuillues de l'Est de l'Amérique du Nord. Par conséquent, leurs comportements, leurs caractéristiques et leurs processus ont été largement étudiés dans les dernières décennies. Ces études ont initié une transformation dans la définition même des PPE. D'une conception physique associant l'aire d'une PPE à la projection verticale de l'ouverture dans la canopée, les chercheurs ont progressivement proposé une conception plus fonctionnelle et basée sur l'impact des PPE sur les ressources du milieu. Cependant, le moyen le plus direct d'appréhender l'étendue complète des PPE est d'examiner l'impact des PPE sur la croissance des arbres à leur périphérie. Cet examen étant presque impossible à réaliser sur le terrain dû aux limites spatio-temporelles des relevés forestiers, la modélisation forestière a été choisie comme alternative.

Le modèle de succession forestière SORTIE possède des caractéristiques adaptées aux études locales des dynamiques forestières. En effet, ce modèle stochastico-déterministe est basé sur les individus (arbres), possède des paramètres par espèce qui reposent sur d'importantes périodes d'échantillonnage et traite l'espace de manière continue. SORTIE innove car ces trois aspects sont rarement réunis dans un modèle.

L'objectif principal de ce mémoire est de caractériser l'étendue spatiale de l'impact périphérique de PPE de différentes tailles (500 à 2000 m²) sur la croissance des gaules. Cette caractérisation devant se faire avec le modèle SORTIE, une évaluation préalable du potentiel de ce modèle pour la réalisation d'études locales devenait nécessaire. C'est pourquoi une évaluation de la sensibilité des dynamiques spatiales locales du modèle aux conditions initiales de simulation et la vérification de l'impact de perturbations introduites sur la démographie des espèces ont préalablement été réalisées.

Pour ce faire, des simulations de 1000 ans ont été effectuées selon deux configurations spatiales initiales différentes (agrégée et aléatoire). Pour chaque simulation et à chaque itération, la structure spatiale locale des espèces a été quantifiée par la statistique du K de Ripley. Les résultats indiquent une sensibilité aux conditions initiales limitée aux trois premiers siècles et des structures spatiales locales par espèces très similaires entre

scénarios après cette période. D'autres simulations ont été effectuées dans lesquelles des PPE de différentes tailles (500 à 1100 m²) ont été introduites à deux moments différents (400 et 600 ans). Ces PPE ont un impact faible sur la densité des espèces et n'engendrent pas de comportements atypiques des espèces. Ces conclusions confirment le potentiel de SORTIE pour des études sur les PPE à cette échelle d'observation et servent de base à la réalisation de la seconde étape.

Pour quantifier l'impact en périphérie des PPE, dix simulations ont été réalisées dans lesquelles des PPE ont été introduites (500 à 2000 m²). À partir de fichiers extraits avant et après les perturbations, des épisodes d'essor (« release ») de gaules ont été déterminés et utilisés pour représenter l'impact des PPE. Les résultats indiquent que l'impact se propage bien au-delà des limites traditionnelles des PPE. Les épisodes se produisent en majorité dans les secteurs au nord des PPE et sont généralement très présents dans les premier 20 m en périphérie des PPE. De plus, de nouvelles superficies de PPE basées sur les fréquences des épisodes d'essor ont été calculées et comparées aux superficies associées aux conceptions traditionnelles. Les fortes différences observées entre ces superficies démontrent l'ampleur de l'impact périphérique des PPE et peuvent avoir d'importantes conséquences sur le travail des aménageurs forestiers et les travaux des écologistes.

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DÉDICACE

Aux personnes qui ont vécu cette citation avec moi.

« *The most exciting phrase to hear in science, the one that heralds the most discoveries, is not "Eureka!", but "That's funny…"* »

Isaac Asimov

CHAPITRE 1 : INTRODUCTION

1.1. PROBLÉMATIQUE

Les forêts sont des entités écologiques faisant preuve d'énormément de dynamisme sur des échelles spatio-temporelles très variées. Même si les arbres sont essentiellement immobiles, leurs dynamiques locales et globales à travers le temps ont des expressions spatiales très riches. Ce dynamisme est alimenté par le cycle de vie des arbres, la succession forestière et les perturbations de diverses origines. Depuis déjà longtemps, des chercheurs, que ce soit des biologistes, des ingénieurs forestiers ou des écologistes, étudient le fonctionnement, la morphologie, la composition et l'origine des espèces arborescentes et les processus qui façonnent la succession forestière. Cependant, ce n'est que depuis quelques décennies que des recherches sont effectuées concernant le rôle, les caractéristiques et les conséquences des perturbations. Bien qu'aucune définition n'obtienne de consensus, on peut retenir celle proposée par White et Pickett (1985) dans un ouvrage regroupant les principaux acteurs récents de la recherche sur les perturbations : « a disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment. » N'ayant visiblement aucune délimitation spatiale, plusieurs utilisent les termes perturbation de petite envergure (PPE) pour distinguer les perturbations originaires de la mort d'arbres (trouées) ou d'interventions sylvicoles localisées de celles causées par les feux de forêts, les coupes à blanc ou de violentes tempêtes, considérées de grande envergure.

Les PPE jouent un rôle clé dans la dynamique globale des forêts feuillues de l'Est de l'Amérique du Nord (Bormann and Likens, 1979; Brokaw, 1985; Payette *et al.* 1990). Cette importance leur a été attribuée à la lumière des résultats obtenus par plusieurs chercheurs au cours des années '80. Les PPE sont essentielles aux espèces arborescentes pour atteindre leur pleine maturité, c'est-à-dire la canopée (Canham, 1988; Poulson and Platt, 1989). Elles altèrent certaines conditions environnementales locales (Runkle, 1982), surtout le régime lumineux et, par le fait même, favorise l'hétérogénéité de la forêt (Denslow, 1985; Whitmore, 1989). Cette situation établit donc un lien direct entre les PPE et la composition spécifique des forêts (Runkle, 1985; Lorimer, 1989; Spies and Franklin, 1989). Cependant, même s'il y a unanimité sur l'importance des PPE, aucun consensus ne ressort au niveau de leur définition.

Les PPE ont longtemps été perçues comme des entités spatialement discrètes, c'est-à-dire limitées en taille à la projection verticale de l'ouverture dans la canopée (formalisée par Runkle, 1982 – trouée stricte). Pendant que cette perception « fromage suisse » (Lieberman *et al.* 1989) de la forêt perdait des adeptes dans la communauté scientifique, des chercheurs se sont mis à étudier l'étendue des PPE sous l'angle de leur impact sur les ressources du milieu, principalement la lumière. Leurs travaux ont permis l'émergence d'une conception plus fonctionnelle et continue des limites des PPE. Runkle (1982) a présenté le principe de la trouée étendue. Cette définition englobe la trouée stricte et y ajoute la zone s'étendant jusqu'à la base des arbres délimitant la trouée étant donnée que cette zone connaît aussi des régimes lumineux différents. Dubé *et al.* (2001) ont poussé cette idée un peu plus loin en définissant la « trouée étendue spécifique ». Sont inclus dans cette trouée tous les endroits où les régimes lumineux sont propices à la croissance des semis d'une espèce. Finalement, Payette *et al.* (1990), dans une étude des régimes de perturbations par la dendrochronologie, ont utilisé les patrons de croissance des arbres pour circonscrire l'étendue d'une PPE. Cette façon de faire permet de bien cerner l'impact des changements lumineux que génèrent les PPE sur leur véritable environnement physique, c'est-à-dire les arbres. Les recherches de terrain ne permettant que très difficilement l'examen spatio-temporel détaillé des comportements de croissance en périphérie des PPE et ce, en situation controlée, l'impact externe des PPE reste ainsi inexploré tant au niveau écologique que pour l'aménagement des forêts.

À travers la littérature consultée et présentée dans les deux articles de ce mémoire, il ressort d'importantes limites méthodologiques et analytiques liées à la manière traditionnelle d'approcher l'étude des PPE. En effet, ces recherches ont des dimensions spatio-temporelles limitées. Sur le plan spatial, un examen exhaustif de tous les arbres influencés par les PPE est très difficile et leur localisation précise nécessite des ressources expérimentales considérables. Sur le plan temporel, les processus forestiers évoluent lentement, même à l'échelle locale, en comparaison avec les carrières de recherche et la durée des subventions. Ces limites peuvent être contournées par l'utilisation de la modélisation forestière afin d'explorer des hypothèses qui, jumelées avec les études sur le terrain, permettraient d'améliorer la compréhension des PPE.

Au cours des dernières décennies, une des grandes préoccupations de certains chercheurs a donc été de concevoir, de créer et de tester des modèles (abstraction simplifiant le système réel étudié (Coquillard et Hill, 1997)) permettant de prévoir l'évolution d'indicateurs des écosystèmes forestiers et de mieux comprendre les

processus et phénomènes qui les structurent. Cependant, ce n'est que depuis tout récemment que la modélisation forestière peut être appliquée à la problématique des PPE, particulièrement à l'échelle locale. Les premiers modèles forestiers développés dans les années '70 étaient pour la plupart globaux et analytiques. La réalité forestière était décomposée en quelques variables qui étaient extrapolées dans le temps à l'aide d'équations différentielles ou de procédés stochastiques. À l'intérieur de ce processus, l'espace n'était que très peu approfondi et le temps était considéré comme réversible. Cette façon de procéder court-circuite l'évolution d'un système alors que c'est par cette évolution que se définit l'état final d'un système.

Sont ensuite apparus les modèles trouées-centrés (ou gap models), représentants de la catégorie des modèles de simulation distribués. Ceux-ci, tels que JABOWA (Botkin *et al.* 1972), FORET (Shugart and West, 1977), SILVA (Kercher and Axelrod, 1984) et FORSKA (Leemans and Prentice, 1989), incorporent enfin la dimension temporelle mais ont toujours des lacunes au niveau spatial. Ils segmentent l'espace en cellules de la taille de trouée ou de peuplement et ne considèrent que d'une manière très limitée les interactions entre celles-ci. Cette situation a pour effet de limiter l'horizon des comportements forestiers pouvant être modélisés. Cependant, à la décharge de ces modèles, il faut admettre que leur but premier était de prédire les compositions spécifiques et les surfaces terrières et non de favoriser l'émergence et la compréhension des dynamiques forestières. Pour parvenir à observer les comportements forestiers complexes par la modélisation, il a fallu attendre que les connaissances sur les écosystèmes s'approfondissent et que l'idée de complexité fasse son chemin.

La communauté scientifique s'entend maintenant pour dire que les systèmes vivants témoignent d'une complexité incroyable et un consensus ressort sur l'importance de cette complexité sur la dynamique des systèmes. C'est ce principe qui est à la base de la théorie des systèmes complexes. La complexité est une propriété des systèmes qui les rend irréductibles même lorsqu'on est en possession de l'entièreté de l'information à propos de ses composantes et de leurs interactions (Edmonds, 1998). De plus, on s'aperçoit que la complexité est générée par les relations, souvent très simples, qu'ont entre eux les composantes de base des écosystèmes (Itami, 1994; Wolfram, 1984). Étant donné qu'il faut désormais intégrer les interactions locales dans la modélisation, les dimensions spatiale et temporelle deviennent alors essentielles. L'espace est le seul véhicule par lequel les individus peuvent interagir et le temps, utilisé de manière explicite, permet aux interactions de transformer le système et de le dynamiser. Il devient alors

nécessaire d'utiliser la simulation (temps), un contexte spatial continu (espace) et une architecture de modélisation axée sur les individus (interactions). C'est ce contexte théorique qui a prédisposé le développement du modèle SORTIE, modèle utilisé dans ce mémoire et dont les caractéristiques et le fonctionnement sont présentés dans les chapitres 2 et 3.

1.2. OBJECTIFS

L'objectif principal de ce mémoire est de caractériser l'impact externe des perturbations de petite envergure par l'entremise du modèle de simulation forestière SORTIE. Plus spécifiquement, les épisodes d'essor des gaules avoisinants les PPE servent d'indicateurs de l'impact de PPE de différentes tailles (500, 1000, 1500 et 2000 m²). Cette caractérisation est le sujet du deuxième article de ce mémoire, c'est-à-dire le chapitre 3.

L'atteinte de cet objectif passe par l'accomplissement de travaux préliminaires portant sur le comportement du modèle dans ce nouveau contexte de recherche. En effet, le modèle n'ayant jamais été utilisé pour étudier localement des PPE, il s'avérait nécessaire de vérifier son potentiel d'utilisation. Cette vérification sert de base à l'exécution des travaux présentés dans le second article. Le premier article de ce mémoire (Chapitre 2) a pour objectif d'évaluer le potentiel de SORTIE pour l'analyse spatio-temporelle à l'échelle locale des PPE. Plus spécifiquement, sont examinés la sensibilité du modèle aux conditions initiales de simulation (configuration spatiale initiale) en ce qui a trait aux comportements démographique et spatial local des espèces modélisées et l'impact des PPE introduites sur les densités spécifiques des simulations.

CHAPITRE 2: EVALUATING THE POTENTIAL OF THE SORTIE FOREST SUCCESSION MODEL FOR SPATIO-TEMPORAL ANALYSIS OF SMALL-SCALE DISTURBANCES

2.1. ABSTRACT

Ecologists and forest managers both recognize the importance of detailed spatio-temporal knowledge on local small-scale disturbances (SSD) dynamics and impacts. However, a large proportion of the knowledge about SSD is based on temporally short data sets, and on non-spatial analysis. SORTIE, a stochastic and mechanistic spatially-explicit and individual-based forest succession model, is particularly well suited for simulating SSD and overcoming traditional field studies limitations. Our main goal is to investigate the potential of SORTIE for spatio-temporal analysis of SSD. More specifically, we intend to evaluate the model sensitivity to initial conditions, and to assess the impact of introduced minor disturbances on the species densities. We hypothesize that SORTIE will generate realistic species dynamics within the range of tested scenarios. We performed simulations over a period of 1000 years using two different initial spatial configurations (Random and Aggregated) and fifteen replicates. For each replicate we extracted, at each time step of five years, the species local spatial structure with the use of the Ripley's K statistic. The resulting time series periods and trends were compared between initial condition scenarios by performing phase coherence and regression analysis. In another set of simulations, SSD of different sizes (500, 800 and 1100 m²) were introduced at two distinct time steps (400 and 600 years). Species density time series were analyzed again in terms of periodicity and trend. Results indicate a sensitivity to initial conditions limited to the first 300 years, and a very similar species local spatial structure between the scenarios after that period. Also, statistical tests revealed that the species densities are not sensitive to single introduced SSD, for all SSD sizes and moments of disturbance. These conclusions suggest that SORTIE can be a valuable complementary tool to SSD field studies.

KEYWORDS : small-scale disturbance, SORTIE, forest modeling, gaps, silvicultural entities.

2.2. INTRODUCTION

A recurring conclusion in the recent literature on temperate forests is the key role of small-scale disturbances (SSD) in this ecosystem's global dynamics (Bormann and Likens, 1979; Brokaw, 1985; Runkle, 1985; Platt and Strong, 1989; Whitmore, 1989; Payette et al., 1990). Numerous field studies have been conducted to understand SSD, from which very important facts emerge. First, tree species need SSD in order to attain canopy maturity (Canham, 1988; Poulson and Platt, 1989). Second, SSD change local growth conditions (Runkle, 1982), mainly light regimes (Chazdon and Fletcher, 1984; Canham, 1988). Third, the variations in local environmental conditions generated by SSD increase forest heterogeneity (Denslow, 1985; Whitmore, 1989), which confer SSD a major role in forest species composition (Runkle, 1985; Lorimer, 1989; Spies and Franklin, 1989; Whitmore, 1989; Payette et al., 1990). However, as mentioned by Payette et al. (1990), a large proportion of the knowledge about SSD is based on temporally short data sets, and on non-spatial analysis. Consequently, there is a need for longer and more spatially explicit datasets, and for the analysis of SSD local spatio-temporal dynamics.

SSD can essentially be observed in two very different contexts: as forest natural gaps or as silvicultural entities. The former refers to canopy openings caused by the death of trees (Barden, 1989), originating from windstorm, thunderstorm light burst, insects, ice storms, and mainly natural death. They can vary in size from a few square meters to more than 1500 m², a large proportion of the size distribution being concentrated in the first 300 m² (Runkle and Yetter, 1987; Veblen, 1989; Lorimer, 1989; Brokaw and Schneider, 1989; Runkle, 1990; Runkle, 1991; Dahir and Lorimer, 1996). Silvicultural entities represent a management tool designed to help gap phase species regeneration (Gouvernement du Québec, 1997). In that context, SSD have a size extent similar to gaps: 500 m² to 1500 m² (Coates and Burton, 1997; Gouvernement du Québec, 1997). Forest managers apply SSD to enhance productivity (Coates and Burton, 1997) or the presence of old-growth forest features (Runkle, 1991). The importance of SSD studies is therefore justified by ecologists' desire to deepen their understanding of a key element of temperate deciduous forest dynamics, and by the managers' need for more spatially exhaustive and long-term assessment of their strategy impact.

In both situations however, field studies that locally investigate SSD are normally characterized by long and demanding data collecting periods, and by limited spatio-temporal dimensions. Actually, longitudinal field studies rarely surpass ten years (Runkle,

1982; Runkle and Yetter, 1987), and rarely explicitly consider the spatial dimension. A solution to counter these traditional limitations is to use forest modeling to simulate and study SSD.

Forest modeling has evolved mainly through two model categories in the last few decades: global models and gap models. The former refers to analytical (deterministic or stochastic) models (Coquillard and Hill, 1997) that do not explicitly consider space or time, while using differential equations (e.g.: MFPS - Moeur and Ek, 1981) or Markov chains (e.g.: Bellefleur, 1981; FINICS – El-Bayoumi *et al.*, 1983). The latter represents models that are almost all based, to some degree, on the JABOWA model (Botkin *et al.*, 1972). These models (e.g.: FORET – Shugart and West, 1977; SILVA – Kercher and Axelrod, 1984; FORSKA - Leemans and Prentice, 1989) discretize space by using spatial cells corresponding approximately to the size of a stand or a gap. The role and position of individual trees, the true key players in forest dynamics, are not considered, thus affecting aspects of growth, recruitment and competition. Recent models (e.g.: FORDYN - Luan *et al.*, 1996; FORMOSAIC - Liu and Ashton, 1998; LANDIS - He *et al.*, 1999) have all benefited from those early models but some still do not consider the tree as the basic simulation unit in grasping forest dynamics. With these limitations, it is impossible to focus on more local and recognized vital elements of forest successional dynamics (Vitousek and White, 1981).

As the science of complexity emerged (Wolfram, 1984; Kay *et al.*, 1999), linking time, non-linearity and space for the study of collections of [interacting] "units that are endowed with the potential to evolve in time" (Coveney and Highfield, 1995), models had to be reajusted consequently. A new generation of models was developed to take into account the complexity of forested ecosystems (continuous space, local interactions, individual-based (Judson, 1994)). SORTIE, the model used in this study, adopts this new approach.

SORTIE (Pacala *et al.* 1993; 1996), a stochastic and mechanistic spatially-explicit and individual-based temperate forest succession model, is particularly well suited for simulating SSD. Its spatial characteristics and its simple design, added to its reliance on considerable empirical data, makes it very popular for forest modelers. SORTIE models the development of forests affected by small intrinsic naturally-created gaps. It has been proven to consistently and realistically mimic the dynamics of such undisturbed forests (Pacala *et al.*, 1996). Using external software, it is possible to create and incorporate into

SORTIE simulations any kind of SSD (severity, size, location and shape). We can therefore conduct research concerning SSD growth impact on neighboring trees, impact on light regimes or other related issues.

In this study, our main goal is to investigate the potential of SORTIE for spatio-temporal analysis of SSD. More specifically, we intend to evaluate the model sensitivity to initial conditions, and to assess the impact of introduced minor disturbances on the species densities. We hypothesize that SORTIE will generate realistic species dynamics within the range of tested scenarios, and will therefore represent a valuable tool for more exhaustive investigations on SSD spatio-temporal dynamics. However, a non-verification of our hypothesis would not mean that SORTIE is unusable for SSD local studies. But in that case, the confidence in the results would be reduced and additional verifications would have to be made, therefore limiting the use of SORTIE by ecologists and forest managers.

According to complexity theory and to post-normal science (Kay et al., 1999; Tognetti, 1999), ecosystems have to be described and studied through their response envelopes, i.e. no specific and precise trajectory is able to adequately characterize them. The challenge in our simulations is to verify if, starting from different conditions, the simulated system will tend towards the same species spatial structure response envelopes at the SSD scale. SSD scale of observation refers to areas similar in size to the areas occupied by SSD. If the model exhibits similar dynamics between initial conditions then our confidence in the results will be strong. Moreover, if the dynamics between initial conditions converge, the time steps of this convergence will indicate in which initial time span is sensitivity to initial conditions present. Future SSD local studies would have to be performed after that convergence.

It is also important to examine the SSD impact on global ecosystem dynamics. In our study, we introduce minor disturbances at two different moments in time to verify if they would significantly affect the species densities generated by SORTIE. Since our goal is to eventually study the spatio-temporal dynamics of introduced SSD, it is imperative to verify if, in the presence of these SSD, SORTIE models the forest natural response to SSD and not the forest reaction to a succession-disrupting disturbance. Our belief is that the model should produce converging and stable dynamics in conformity with field observations (Runkle, 1990; Coates and Burton, 1997).

2.3. METHODOLOGY

The model used in this study is SORTIE BC v. 4.1(Pacala *et al.* 1993; 1996; Papaik, 1999). Based on large sets of empirical observations (Great Mountain Forest in northwestern Connecticut) on nine species of the northern hardwoods forests (Pacala *et al.* 1994; Ribbens *et al.* 1994; Canham *et al.* 1994; Kobe *et al.* 1995), SORTIE simulates the evolution of all individual trees through their competition with others for light. The broad-scale forest dynamics emerges as the collective result of the localized interactions among seedlings, saplings and mature canopy trees (Levin et al., 1998; Deutschman and Devine, 2000). The model discretizes time in iterations of five years but treats space in a continuous and explicit fashion. For every time step, SORTIE uses the following five operating submodels (in order of their execution): 1) Harvesting – applies any predefined harvest regime; 2) Light availability – attributes a GLI value (Gap Light Index: Canham *et al.*, 1990) to every tree as a function of species specific light extinction coefficients and height; 3) Tree growth – as a function of the GLI values; 4) Reproduction – seedling recruitment as a function of parent tree proximity, and 5) Tree mortality – as a function of previous growth rates and stochasticity. The model was also analysized for its sensitivity to species and sub-model parameters in their assessment of non-spatial descriptors of forest dynamics (Deustchman *et al.*, 1997; 1999).

All the species modeled by SORTIE have been used in the study (*Acer rubrum* L. (ACRU), *Acer saccharum* Marsh. (ACSA), *Betula alleghaniensis* Britton (BEAL), *Fagus grandifolia* Ehrh. (FAGR), *Fraxinus americana* L. (FRAM), *Pinus strobus* L. (PIST), *Prunus serotina* Ehrh. (PRSE), *Quercus rubra* L. (QURU) and *Tsuga canadensis* (L.) Carr. (TSCA)) to ensure realistic stand composition. Simulations were performed using a toroïdal matrix of 120 x 120 m over a temporal extent of 1000 to 1600 years depending on the set of simulations performed. A 1,44 ha matrix was selected because the focus of the study is very local and because of storage and processing capacities.

2.3.1. Analysis of initial condition influence

To evaluate the model sensitivity to initial conditions, we first defined two different scenarios of initial conditions for which we performed 15 replicates each. "Since SORTIE is stochastic, multiple simulations (with different random number seeds) are needed to describe the behavior of the model for each set of parameter values" (Deutschman and Devine, 2000). Our scenarios do not represent a wide range of initial conditions but the

purpose of this study is to evaluate the model's potential for SSD local studies, not to do an exhaustive account of initial condition sensitivity.

The two scenarios differ in their species initial spatial configuration. The Random scenario is modeled by generating a random initial seedling distribution of the nine species with a seedling density of 100 individuals per ha for each species. This density was chosen based on earlier runs where we observed that simulations had a tendency to stabilize around a density of 900 ind./ha. Fifteen simulations of 1000 years (200 time steps) were then performed. The randomness of the distribution originates from the pseudo-random number generator of SORTIE. For the Aggregated scenario, the same initial considerations were used (randomness and density) but after 200 years of simulations (40 time steps), a severe partial-cut (every individual with a diameter at breast height (dbh) larger than 1 cm was removed) was applied to the entire matrix. This partial-cut allows almost 90% of the individuals in the matrix to survive. The purpose of this intervention is to generate an aggregated spatial distribution of the remaining seedlings, the species having a much more clustered and natural spatial configuration after two centuries (Dubé *et al.*, 2001). Then, 1000 years of simulation were added to the first 200 years (total simulation = 1200 years) to obtain a millennium of development to compare the two scenarios (Figure 1). For each of the total 30 replicates, temporal density outputs and playback files (spatial coordinates, dbh, and species affiliation of every individual at each time step of a simulation) were produced (Figure 1).

Step 1

Step 2
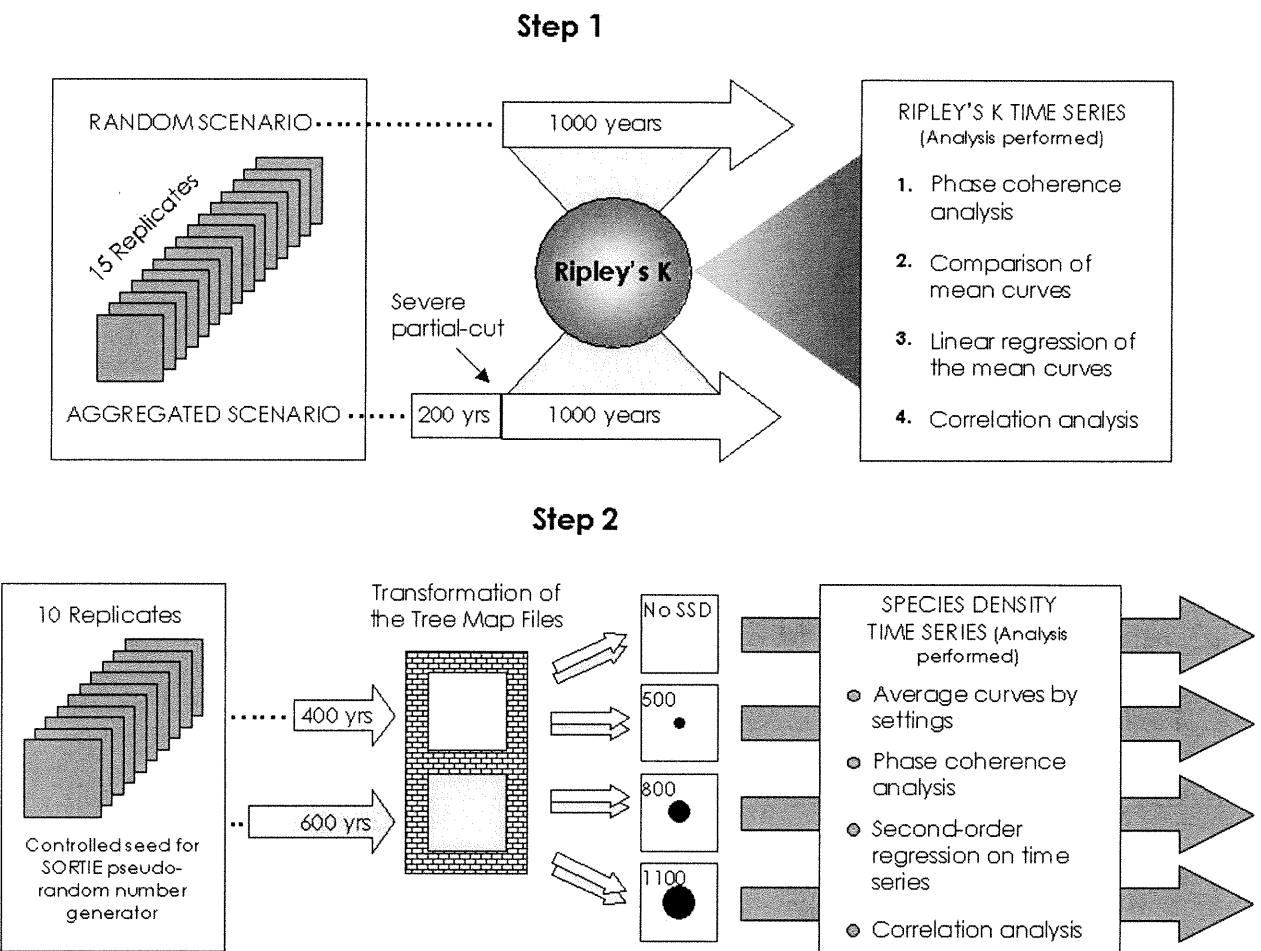
Figure 1 *Illustration of the simulation and analytical processes.*

To assess the sensitivity to initial conditions, we measured the species spatial structure generated by the model at different radial distances from each individual tree corresponding to the sizes of SSD (300 to 1300 m²). The local spatial structure was characterized using Ripley's K statistic (Bailey and Gatrell, 1995; Fortin, 1999). The Ripley's K is a point pattern method for categorical data that essentially counts the number of events that occur in an area within a distance t of a given event. At each time step for a given species and for a specific radial distance around each individual, the Ripley's K statistics was computed (Figure 2). It quantifies the intensity and scale of the spatial structure of a given variable, and is given by:

$$K(t) = (R / N^2) \sum\sum I_t(d_{ij}) \quad \text{for } i \neq j$$

where R is the area, N is the number of points analyzed, and I_t (d_{ij}) is an indicator function which corresponds to 1 if d_{ij} (distance between points) $< t$ and 0 otherwise. To linearize the plot of K (t) against t, as well as for stabilizing the variance, L(t) is used instead:

$$L(t) = \sqrt{(K(t) / \pi)} - t$$

L(t) takes negative values in the presence of segregation, positive values when clustering is present, and is null if the structure is the result of randomness. This method offers unique advantages. First, it is not affected by the unit size since it is not based on sampling units (x,y coordinates). In this study, Ripley's K is particularly interesting since it allows us to evaluate the spatial structure of species at different scales of observation, therefore for different hypothetical sizes of SSD. To avoid the sensitivity of this statistic to edge effects, we selected a sub-matrix that has a surrounding buffer superior to the largest t employed. Ripley's K was computed for radial distances (t) of 10 m to 20 m from each individual, with a 1 m increment, representing areas going from 314 to 1256 m^2. These areas correspond well to large extrinsic natural gaps and to management cuts.
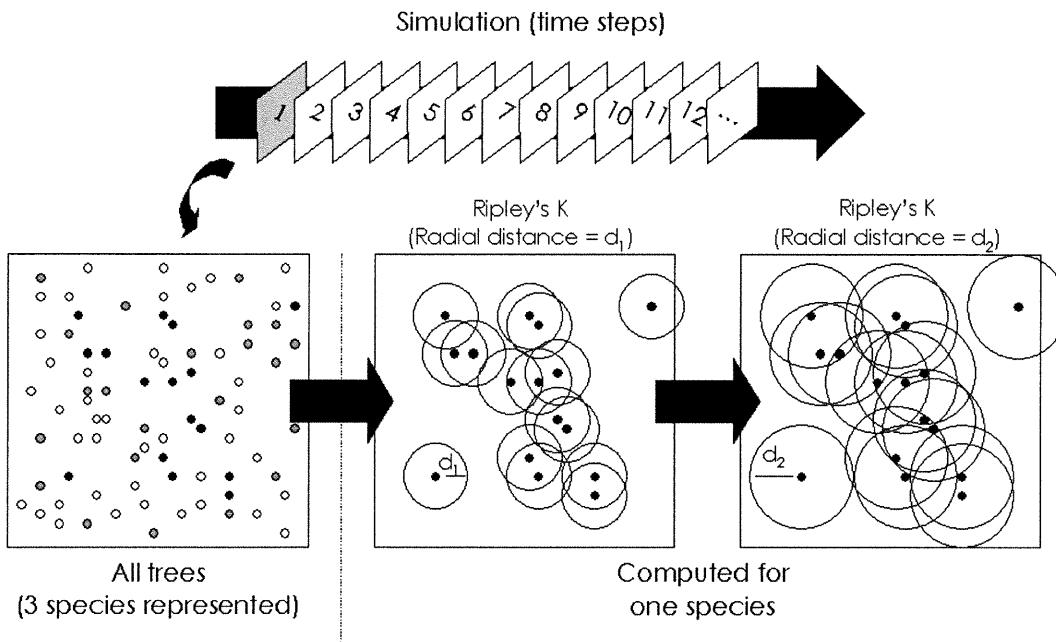
Figure 2 *Illustration of the Ripley's K statistic computation.*

The resulting Ripley's K values were plotted against time. Each replicate was then analyzed to detect periodicity using the phase coherence method (Lindstörm et al., 1997). This method reveals periods in data series by grouping data points according to

periods (p to $p + (n/2)$) and calculating the standard deviation of those grouped data points from their zero-mean values. If a period p, compared to randomized times series, significantly reduces the standard deviation then a phase p exists. Our phase coherence results were compared for statistical significance with 200 permutations of the time series with a confidence level of 95%. This method is very efficient for dealing with short and noisy time series compared to other temporal autocorrelation statistics. Secondly, the trends of the averaged curves for each scenario were extracted using linear regression for direct comparison. Finally, correlation analysis (Spearman Rank Correlation) was performed on these trends to estimate the association between curves of the two scenarios and ultimately evaluate the model sensitivity.

2.3.2. Assessing the impact of SSD on global species dynamics

To evaluate the impact of SSD on species densities, we designed an experiment in two steps. First, we performed simulations based on the Random scenario described in the earlier section in which we introduced circular, punctual and lattice-centered disturbances of different sizes (500, 800 and 1100 m²). We used the Random scenario because it is the simpler of the two and because results from the sensitivity analysis suggested that they were equivalent in the context of our objective. We chose the circular shape based on the observations made by Runkle (1990) and Brokaw (1985) that gaps are approximately circular. Only the adult trees were removed (dbh > 15 cm) since a SSD is usually characterized by openings in the canopy caused by the death of mature trees. Secondly, we introduced the disturbances at two different time steps, 80 and 120, corresponding to 400 and 600 years respectively (Figure 1). The selection of these two moments was based on results obtained for the sensitivity to initial conditions suggesting that the first few centuries should be overlooked.

To isolate the SSD impact in our six settings (two moments in time X three disturbance sizes), we executed the following actions: 1) we imposed ten different seeds in the pseudo-random number generator of SORTIE in order to replicate the exact same ten simulations for the six scenarios; 2) for both moments of disturbance (400 and 600 years), we halted the simulations to extract the SORTIE Tree Map Files (files containing the information related to the trees spatial position and size at a specific time step); 3) using a programming software, we removed the trees corresponding to our criterion of disturbance; and finally, 4) we used these altered Tree Map Files as initial conditions for the rest of the simulations (1000 years) (Figure 1). For every simulation, we extracted

density outputs in order to quantify the SSD impact on species density. The statistical and analytical tools used for this section are similar to those employed in the preceding one: phase coherence analysis, regression and correlation analysis.

2.4. RESULTS AND DISCUSSION

The results are presented in four subsections. The first two relate to our first inquiry, that is sensitivity to initial conditions. The next two correspond to the model response to introduced disturbances.

2.4.1. General and visual assessment of the species density responses

To better understand the results and analytical choices we have made, it is necessary to briefly describe the species behaviors. Figure 3 shows the average density curves of the species for both scenarios (Random and Aggregated). The values at year 0 distinguish clearly the two scenarios, one associated to identical initial densities for each species (Random) and the other to a severe partial-cut after 200 years (Aggregated). Species density starts to rise rapidly at the beginning of the simulations because the individuals already have a few centimeters in dbh at year 0. *Tsuga canadensis* and *Fagus grandifolia* are co-dominant in both scenarios and in almost the same proportions. This situation typically corresponds to a non-disturbed forest dominated by the two most shade tolerant species of the model (Pacala *et al.*, 1996). Similar trends were found in a unique old-growth forest of southern Quebec (Brisson *et al.*, 1994). Furthermore, the shade intolerant *Prunus serotina* remains a low profile third place competitor while the other species slowly disappear, mostly after 500 years. These proportions are similar to model results obtained by the authors of SORTIE (Pacala *et al.*, 1996). Also, the uncommon weak competitiveness of *Acer saccharum* can be attributed in part to the sandy and acidic soils where SORTIE has been calibrated, since its survival at low light is "much higher on […] calcareous soils" (Pacala *et al.*, 1996). While these are averaged curves and do not account for the variations between replicates, they reveal coherent species behavioral responses for both scenarios (Figure 3).
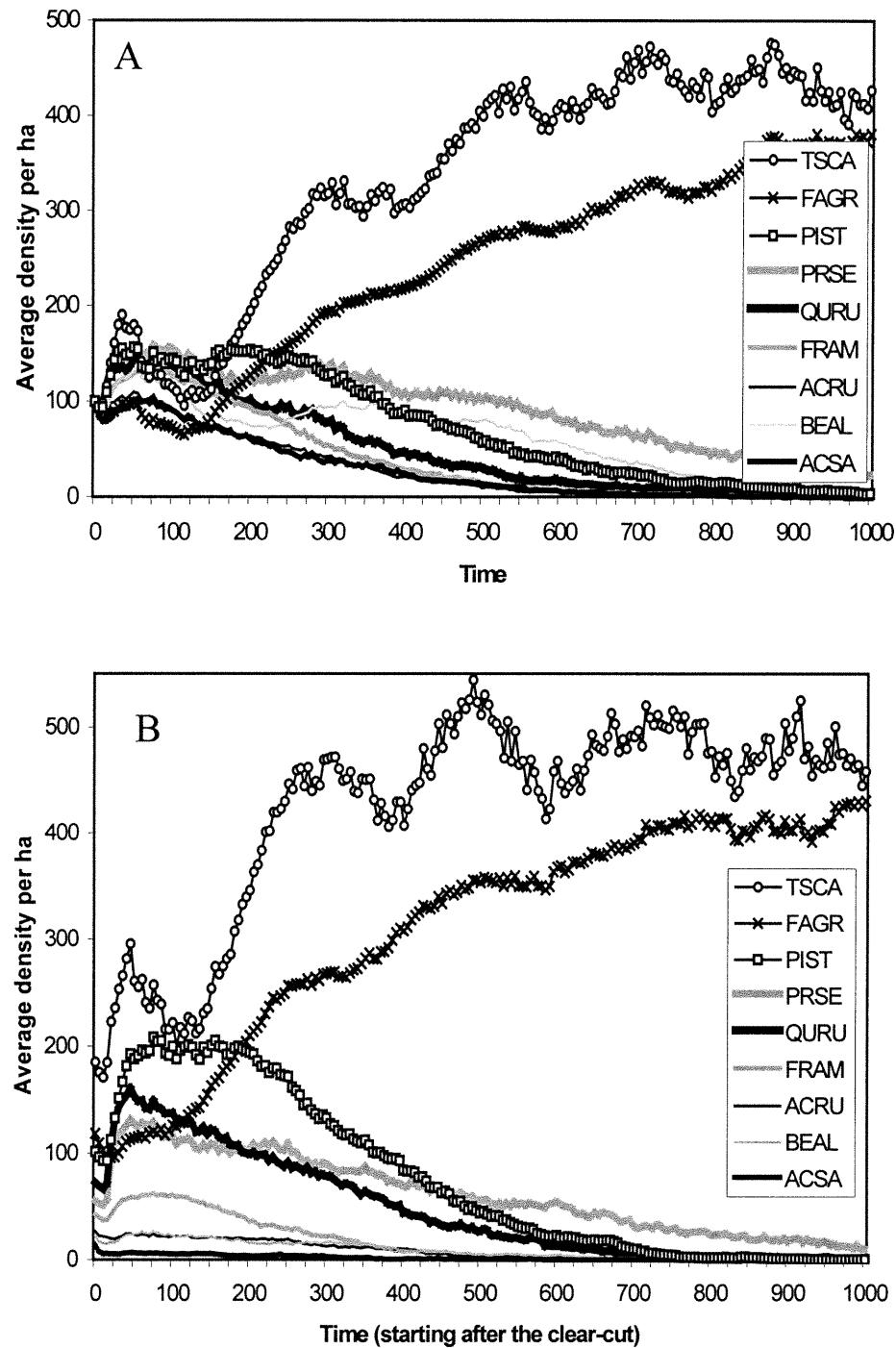
Figure 3 *Averaged density results for both scenarios of initial conditions (A. Random scenario; B. Aggregated scenario).*

2.4.2. Ripley's K results

To ensure statistical validity, the Ripley's K statistic was computed only for the two main species, *Tsuga canadensis* and *Fagus grandifolia*. It is calculated for small radial distances, and a sufficient number of individuals for a given species at the SSD scale is crucial for statistical validity. Also, only the results for radial distances 10 m, 15 m and 20 m are shown to lighten the displays.

Figure 4 shows a typical example of Ripley results for all replicates of one species and scenario combination (*Fagus grandifolia*, random scenario, 10 m of radial distance). Only this example is shown since all species and scenario combination visually exhibit a similar behavior in terms of replicate variability. A first observation is that almost all the Ripley values are positive, indicating clustering of the species individuals. Also, there are large variations in Ripley's K intensity through the replicates of a species and scenario combination as seen by the extent of the actual L values (from 0 to 10). Phase coherence analysis performed for all replicates revealed no significant period.
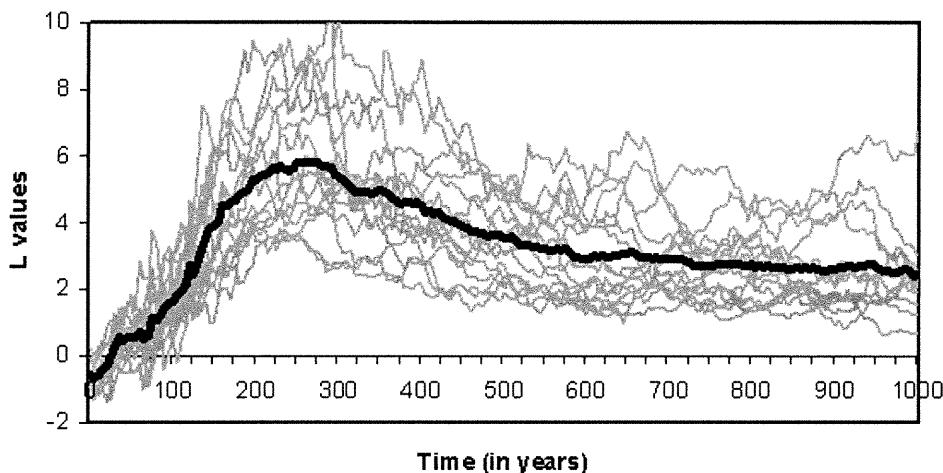
Figure 4 *Example of Ripley's K (L) results for all replicates of a species-scenario combination: values for FAGR – Random scenario and for radial distance = 10 m (the black curve corresponds to the averaged time series).*

To verify the sensitivity to initial conditions, the mean curves of the Ripley's statistic were compared between scenarios. For the two species, the comparison between the Random and the Aggregated scenario reveals strong convergence (Figure 5). For *Fagus grandifolia*, the curves are almost the same after 300 years, experiencing a slow descent of L values from around 5 to 2,5. As for *Tsuga canadensis*, the curves tend towards a

constant L value of 5, and the curves for the same radial distances for both scenarios are similar after 300 years. Yet, all the *Tsuga canadensis* curves do not overlap as much and as fast as in the case of *Fagus grandifolia*. Figure 6 illustrates the absolute difference between scenarios and supports this visual assessment of the convergence. By 200-225 years (40-45 time steps), the differences have already reached their minimum and are staying small for the rest of the simulations. This observation concerning sensitivity of SORTIE to initial conditions limited to the first few centuries was also observed by Dubé *et al.* (2001).

If we remove the first 300 years of simulations where sensitivity is witnessed, are the Ripley's K curves statistically similar between scenarios? To answer this question, we performed a Spearman's *r* correlation (Legendre and Legendre, 1998) analysis between the trends (linear regression) of the averaged Ripley series of the two scenarios. The use of this non-parametric coefficient was dictated by the verification, through the Kolmogorov-Smirnov test, of the data series non-normality. The Spearman's *r* results are shown in Table 1. All the values are significant (rejection of the null hypothesis of absence of correlation: a = 0.05, n = 140) and indicate good rank correlation. The negative values (inverse relationship) of Spearman's *r* found in the case of *Tsuga canadensis* for radial distances 10 m and 15 m can be attributed to the closeness of the curve slopes to 0. Table 1 also shows the results of the linear regressions (slope and ordinate intercept) on the 300-1000 years curves and this inverse relationship is clearly visible. While all the associated slope values are close and coherent, the slope values for TSCA (10) and TSCA (15) are in opposition. This situation emerges from the very small slope values in the Ripley's K behavior for *Tsuga canadensis*.

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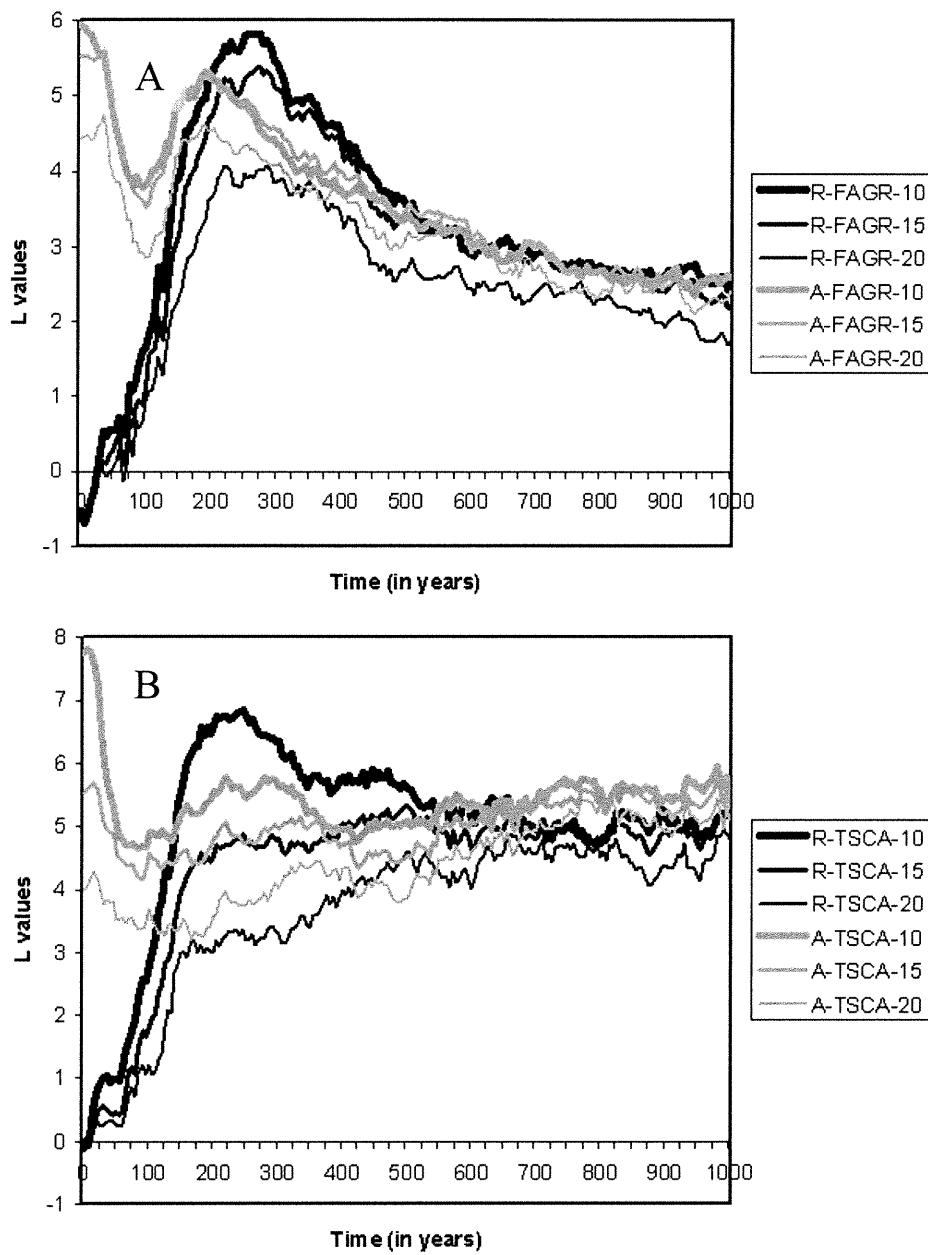
Figure 5 *Averaged Ripley's K (L) values for (A) FAGR and (B) TSCA (R = Random scenario, A = Aggregated scenario; 10, 15 and 20 are radial distances in m).*
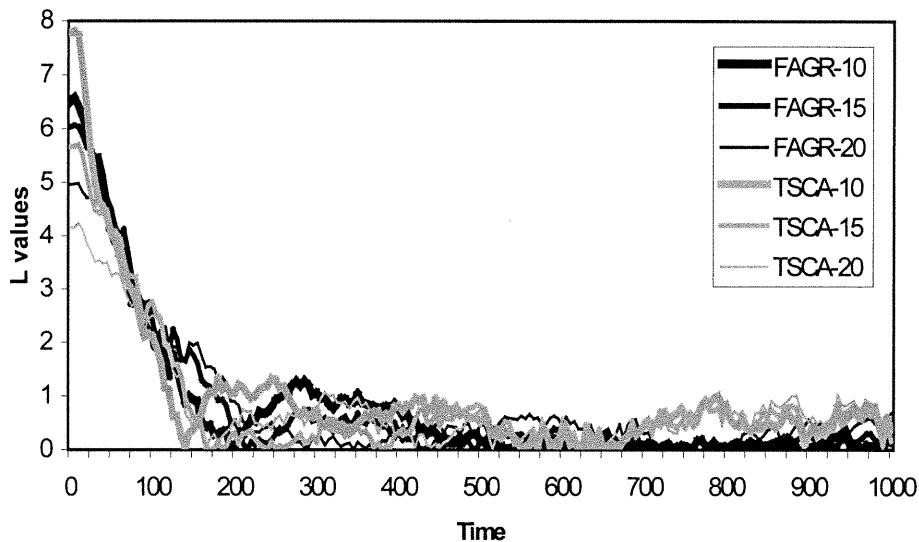
Figure 6 *Difference between mean Ripley's K (L) time series of both scenarios (10, 15 and 20 are radial distances in m).*

Table 1

SPEARMAN'S RANK CORRELATION RESULTS

Species	Random	Aggregated	Results	
Fagus grandifolia	10	10	0,949	All significantly
	15	15	0,966	different of 0
	20	20	0,919	r_c = 0,180
Tsuga canadensis	10	10	-0,635	
	15	15	-0,349	
	20	20	0,546	

LINEAR REGRESSION RESULTS

Scenarios	R.D.	*Fagus grandifolia*		*Tsuga canadensis*	
		Slope	Ord. intercept	Slope	Ord. intercept
Random	10	-0,018	4,54	-0,007	5,82
	15	-0,017	4,37	-0,002	4,93
	20	-0,013	3,50	0,007	3,86
Aggregated	10	-0,012	3,97	0,005	5,05
	15	-0,014	4,15	0,006	4,66
	20	-0,012	3,75	0,010	4,02
Note: 10, 15 and 20 are radial distances in the Ripley's K computation					

Table 1 *Spearman's rank correlation and linear regression results*

Therefore, SORTIE seems to generate, after three centuries, coherent spatial pattern across scales regardless of the initial conditions of simulation. Moreover, SORTIE exhibits local species spatial structures comparable to logical tree behavior (positive values corresponding to clustering).

2.4.3. Density results by settings

In the evaluation of the SSD impact on species density, we first focus on the averaged density responses for all settings (combination of moment and size of disturbance). Results for the main two species are presented in Figure 7. Mean density curves for the other species cannot be evaluated because they eventually experience very low densities and, accordingly, they all disappear before the simulation ends. *Fagus grandifolia* is characterized by an ascending trend that is similar for all SSD sizes and moments of disturbance. After the decrease right at the time of logging, it takes *Fagus grandifolia* 175 and 125 years in the 400 years and 600 years respectively to catch up the non-disturbed cases. This difference in impact length could be explained by the fact that in the 600 years settings, the more shade-intolerant and mobile species are in a smaller proportion than in the 400 years settings. Since *Fagus grandifolia* has the largest SORTIE mean dispersal distance compared to *Tsuga canadensis*(FAGR: 5,9 m vs TSCA: 4,1 m), when fewer other species competitors are present, *Fagus grandifolia* takes advantage of the space more effectively than *Tsuga canadensis*, and therefore reaches back the undisturbed case faster.

Similar observations can be made for *Tsuga canadensis*. In fact, the disturbed cases tend to follow the same trends as the non-disturbed ones but exhibit more variability than in *Fagus grandifolia*. An interesting fact emerges from the two graphs of *Tsuga canadensis*. In the 400 years scenarios, the density in the disturbed cases stays relatively lower compared to the undisturbed one while in the other scenario this situation is clearly not present. This dichotomy can indicate the level of stand competition present at both moments of disturbance and can be linked to the difference in impact length for *Fagus grandifolia*. In the 400 years settings, even if they possess relatively small densities, the other six species are much more present and their competition more felt than in the 600 years settings. Their presence, added to the fact that they are more shade intolerant and invasion-prone, could explain the differential responses of *Fagus grandifolia* and *Tsuga canadensis*, the 600 years settings offering less competitive environments.

These averaged results show us that the SSD seem to not have disrupted the general species tendencies. We will now analyze the results on a replicate basis for a more detailed investigation.
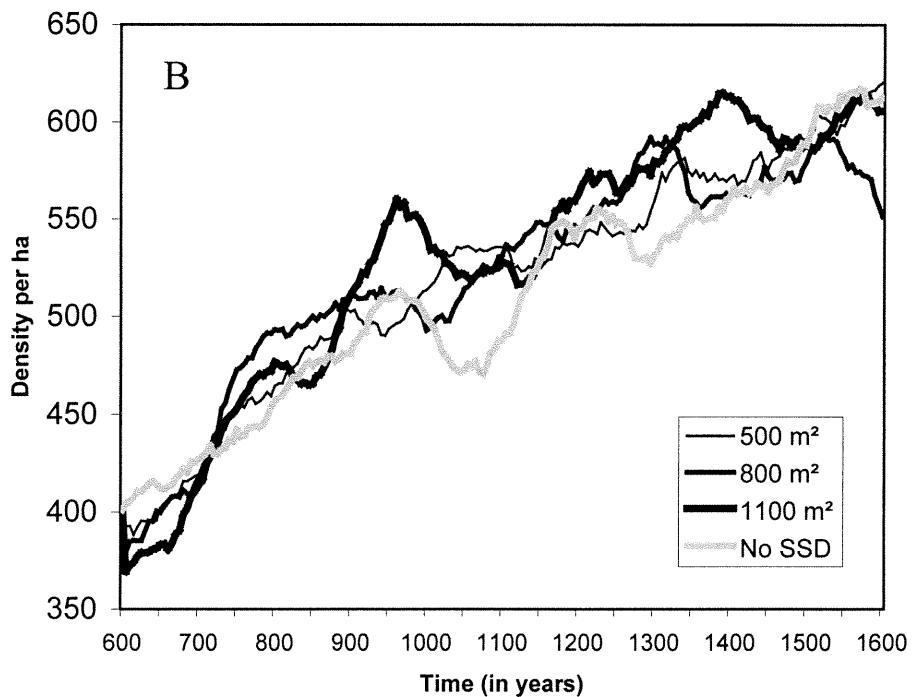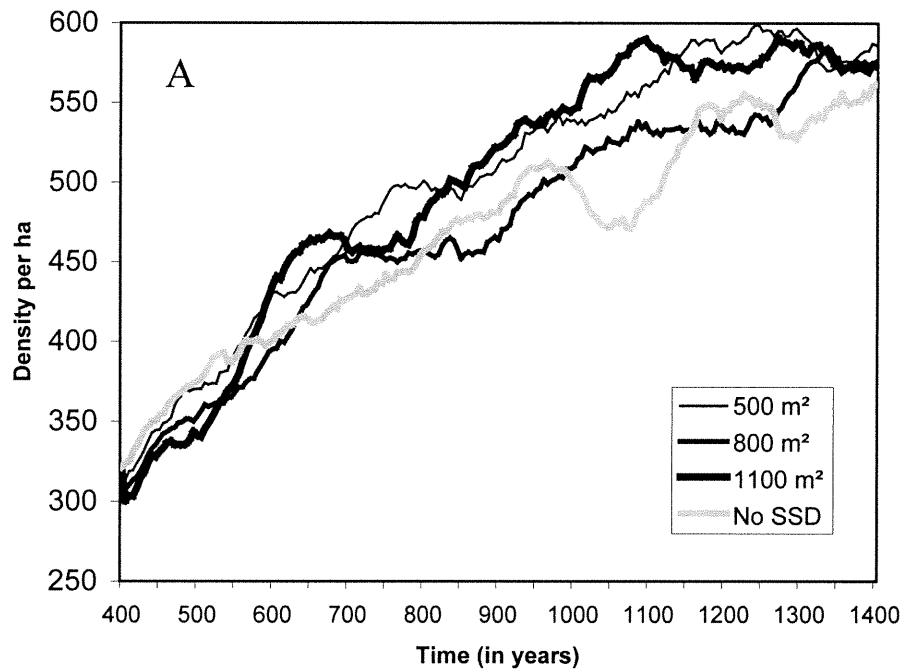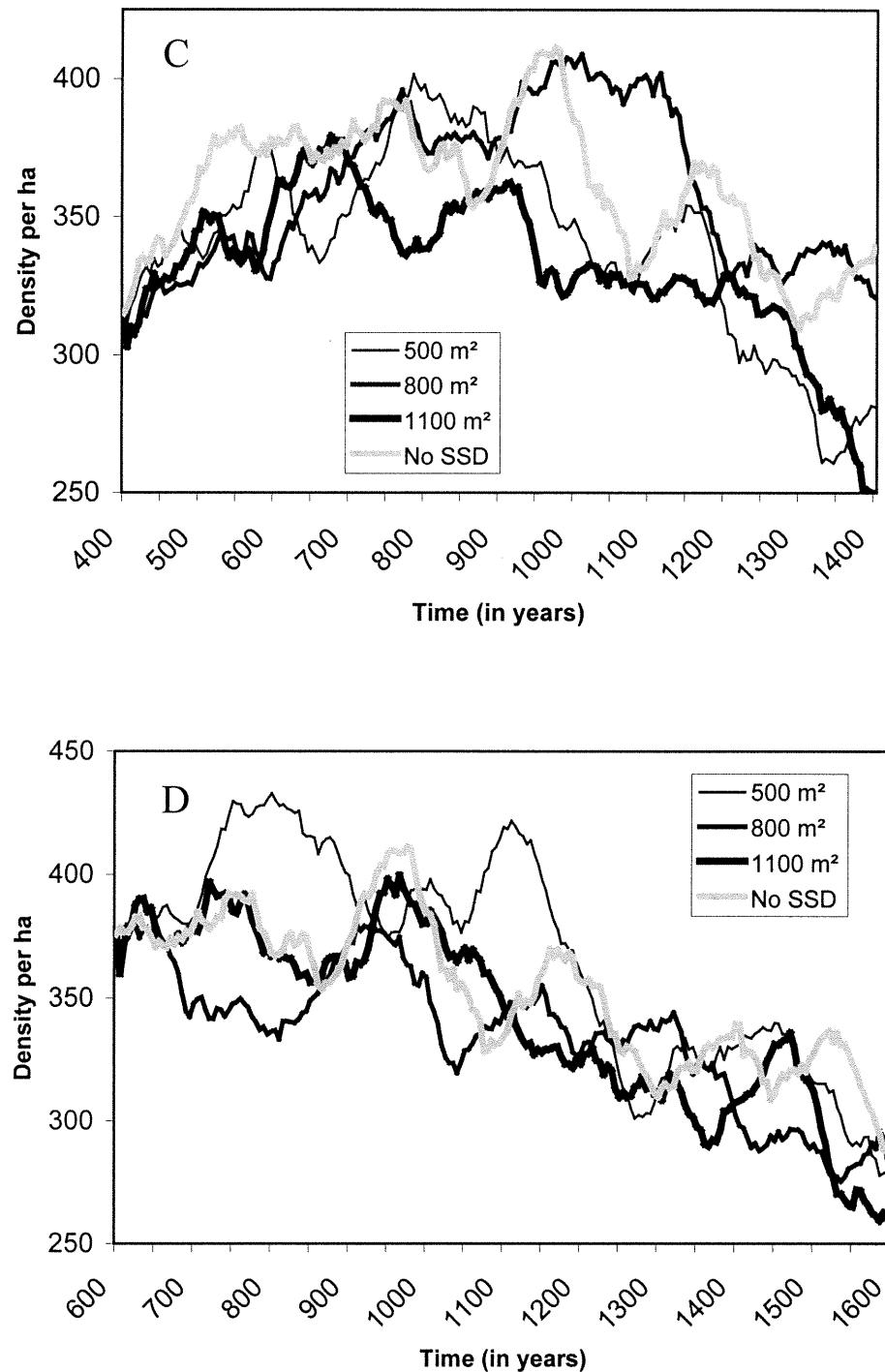
Figure 7   *Averaged density after the introduction of disturbance for all SSD treatments: A. FAGR - Year 400, B. FAGR – Year 600, C. TSCA – Year 400 and D. TSCA – Year 600.*

2.4.4. Replicate-based analysis

As shown in the replicate time series on Figure 3, variability is present in the replicate density curves. We performed phase coherence analysis on each time series to detect the presence of periodicity. Almost no significant phases were found. This indicates two possibilities: 1) that the temporal window we used limits the periodic expression of the disturbed and undisturbed density dynamics or 2) that they simply do not experience clear phases.

We then focused our attention on the trends of the species density curves to detect the presence and eventually the intensity of the SSD impact. We extracted the second-order polynomial regression curve out of the original data sets. The trends in hand, we performed 120 Spearman's Rank Correlation tests (two most abundant species (FAGR, TSCA) X six scenarios (two moments of disturbance X three SSD sizes) X ten replicates) between the disturbed trends and their associated undisturbed ones. These results are presented in Table 2. The Spearman test was used because the null hypothesis was rejected after performing Kolmogorov-Smirnov normality tests on the trends. It shows the degree of association between the disturbed trends and their undisturbed counterparts.

The statistical significance (r_c = 0,18 or –0,18; a = 0.05, n = 200) of all the values (except one: TSCA (5th replicate, 400-1100 setting)) suggests that a strong relationship (positive or negative) exists in all the couplings. For *Fagus grandifolia* the correlation results are very high, as revealed by the mean values (0,8867 to 0,9572) and by the small intra-setting variance (0,0036 to 0,021). The correlations are positive indicating that the disturbed cases are evolving in the same direction as the non-disturbed ones. However, no differential impact can be observed between SSD sizes of a setting since no pair of means (400-500 VS 400-800, 400-500 VS 400-1100, 400-800 VS 400-1100; same pairs for the 600 year settings) are significantly different. This situation was evaluated using two sample T (Student) tests (a = 0.01, Critical t= 2,88: FAGR = -0,14; 0,03; 1,28; 0,20; 0,37; 0,19).

Table 2

Spearman's rank correlation results

Species	Replicates	Scenarios					
		400-500	400-800	400-1100	600-500	600-800	600-1100
	1	1,00	1,00	0,78	0,88	0,83	0,83
	2	1,00	0,81	0,98	0,63	0,95	0,83
	3	0,82	1,00	1,00	1,00	0,77	0,88
F	4	0,95	0,95	0,72	0,99	0,94	0,88
A	5	1,00	1,00	1,00	1,00	1,00	1,00
G	6	0,54	0,97	0,97	0,89	0,95	0,95
R	7	0,96	0,96	0,86	0,69	0,69	0,69
	8	0,98	0,98	0,98	1,00	0,99	0,97
	9	0,99	1,00	0,91	1,00	1,00	1,00
	10	0,98	0,91	0,91	0,99	0,84	0,84
	Mean	**0,92**	**0,96**	**0,91**	**0,91**	**0,90**	**0,89**
	1	0,56	0,99	-0,99	0,82	0,80	1,00
	2	0,80	0,67	0,43	0,35	0,78	0,97
	3	-0,34	-0,98	-0,40	0,82	0,96	0,82
T	4	0,92	0,66	0,83	0,32	0,53	0,99
S	5	0,93	0,93	-0,14	0,31	0,93	0,30
C	6	0,95	0,44	0,42	0,25	0,97	0,77
A	7	-0,45	0,36	0,76	-0,76	-0,89	-0,48
	8	0,46	0,93	0,18	-0,67	0,82	0,82
	9	0,83	0,80	0,26	0,99	0,94	-1,00
	10	1,00	-0,73	1,00	0,86	0,98	0,97
	Mean	**0,57**	**0,41**	**0,24**	**0,33**	**0,68**	**0,51**

Table 2 *Spearman's rank correlation results for all replicate comparison between disturbed and undisturbed cases. (Settings are a combination of a time and a size of SSD; the first number corresponds to the time (in years), the second to SSD sizes (in square meters)*

The mean results for *Tsuga canadensis* are somewhat smaller with values oscillating around 0,4 and 0,5. These results show the influence of two factors: 1) a less intense but still strong positive correlation, and 2) the presence of one, two or three negative correlations in each scenario. Both factors can be explained in part by the fact that *Tsuga canadensis* has more constant density values than the other species in our temporal window and only a small decreasing tendency. This situation can increase the chances of finding opposing time series in terms of correlation due to the inherent variability characterizing each replicate. This situation was also present in the earlier Ripley results. Again, no differential impact can be observed between SSD sizes (T tests results: 0,57; 1,28; 0,58; -1,34; -0,63; 0,59) but this time it is mainly due to high variance caused by the rare negative correlation values.

This analysis has shown that a strong positive relationship exists between disturbed and non-disturbed simulations and that no significant difference in impact between disturbance sizes was registered.

2.5. CONCLUSION

This study represents one of the first attempts at using a modeling tool for the study of local scale SSD. Until recently, such studies were impossible to realize since forest succession models were not spatially-explicit and individual-based. SORTIE design and structure allows the inherent complexity of forested ecosystem to emerge.

In our simulations, the species spatial structures at the SSD level are insensitive to initial conditions (Random spatial structure VS Aggregated spatial structure) after 300 years of simulation. Furthermore, the SSD impact on species densities is weak and does not significantly affect their global tendencies. This situation is coherent with field observations. Coates and Burton (1997) mentioned that selective group cuts (100 to 1000 m^2) did not change the stand conditions. Runkle (1990) observed that forest area experiencing gap episodes at all times (7 to 14% of forest area depending on gap definition) was of the same magnitude as what was present in our disturbed simulations. Therefore, we can conclude that SSD local studies performed after three centuries of evolution on matrices similar to the one we used (120 m X 120 m) are free of initial conditions sensitivity problems and are based on observations of stable species stand density conditions.

The implications of our findings are very important. First, SORTIE could become a valuable complementary tool to SSD field studies. Field study limitations can be overcome by SORTIE simulations. SORTIE considers the precise location of each tree and can be used to simulate species dynamics over a long period of time. This implies that forest managers can investigate the local and global impact of their interventions and that ecologists can deepen their understanding of SSD processes.

Finally, this study of sensitivity issues establishes simulation guidelines for future research in modeling SSD impacts. It can be seen as a preliminary step towards the achievement of exhaustive accounts of SSD local and global impact on forest dynamics. Future studies will aim at characterizing the effects of SSD sizes, morphologies, severities, and frequencies on forest dynamical properties.

2.6. ACKOWLEDGEMENTS

PARAGRAPHE DE LIAISON

Le chapitre 2 vise à vérifier le potentiel du modèle SORTIE pour l'analyse spatio-temporelle des perturbations de petite envergure (PPE) à l'échelle locale. Les conclusions de cette recherche préliminaire démontrent les capacités du modèle à cette échelle d'observation et servent de base à l'exécution des recherches traitant de l'impact des PPE. Le chapitre 3 a pour sujet la caractérisation spatiale de l'impact périphérique des PPE par l'entremise du modèle SORTIE.

CHAPITRE 3: SAPLING RELEASE EPISODES AT THE PERIPHERY OF SMALL-SCALE DISTURBANCES (SSD): A MODELING ASSESSMENT OF SSD IMPACT EXTENT

3.1. ABSTRACT

Small-scale disturbances (SSD) are recognized as important features of temperate forests dynamics and have been extensively studied in the last decades. Their definition has progressively evolved from the simplistic physical projection of the canopy opening to a more resource-based and functional approach (extended and species extended gaps). But to truly define SSD extent, the peripheral impact of SSD on the trees has to be considered. This study was undertaken to characterize the impact extent of SSD on their periphery using the SORTIE forest succession model. The sapling growth responses to SSD of different sizes (500 to 2000 m²) was used as an indicator of the impact extent. Ten replicates of a simulation were performed (305 years, 25 ha lattice). The SSD were introduced after 300 years. From files that were extracted from the model five years before and after the SSD, pre-SSD and post-SSD growth values were computed for each sapling. These values were used to create a growth ratio that was compared to a release threshold to determine sapling release episodes (SRE). These SRE were analyzed to assess the extent of SSD impact. Results indicate that SSD effect extends significantly into the adjacent forest. Release orientations are concentrated in the northern hemisphere and SRE mostly appear in the first 20 m from SSD. Based on different degrees of SRE occurrence, new SSD areas were defined and compared to areas from SSD existing definitions. The differences are substantial and have important implications for forest managers and ecologists.

KEYWORDS: forest modeling, small-scale disturbances, gaps, release, SORTIE.

3.2. INTRODUCTION

Small-scale disturbance (SSD) is a recent expression that refers to two different entities: forest natural gaps and gaps generated by silvicultural treatments. Natural gaps refer to canopy openings caused by the death of trees (Barden, 1989), originating from windstorm, thunderstorm light-burst, and mainly, natural death. Their importance in temperate forest dynamics is well recognized (Bormann and Likens, 1979; Brokaw, 1985;

Runkle, 1985; Platt and Strong, 1989; Whitmore, 1989). They represent the first step towards tree maturity for saplings (Canham, 1988; Poulson and Platt, 1989), they alter light regimes (Chazdon and Fetcher, 1984; Canham, 1988), and help diversify forest species composition (Runkle, 1985; Lorimer, 1989; Spies and Franklin, 1989; Whitmore, 1989). Silvicultural treatments represent a management tool designed to help gap phase species regeneration (Gouvernement du Québec, 1997), enhance productivity (Coates and Burton, 1997) or the presence of old-growth forest features (Runkle, 1991). Some of the SSD designed by forest managers are similar to natural gaps in terms of size and shape. But while there is a lot of literature on forest natural gaps (Runkle and Yetter, 1987; Veblen, 1989; Lorimer, 1989; Brokaw and Schneider, 1989; Runkle, 1990; Runkle, 1991; Dahir and Lorimer, 1996), a debate still lingers concerning their definition.

Watt (1947) first proposed that a gap is a site where a canopy tree had died and active recruitment of new individuals into the canopy is occurring. In the '80, Runkle pioneered by emphasizing the importance of incorporating the notion of size in the definition of gaps. Size is important because ecological processes linked to gaps vary depending on gap size, and also because a solid and standard size outlining preludes any attempts at gap comparative studies. Runkle (1982) consecutively formalized two new definitions: the "canopy gap" and the "extended gap". The canopy gap refers to the vertical projection of the canopy opening. The extended gap consists of the canopy gap plus the area extending to the base of the surrounding trees. Runkle's second definition is based on the fact that a gap should include all the portions of space where the light regime is altered. Recently, Dubé *et al.* (2001) went a step further by proposing the "species extended gap concept". Such a gap includes the portions of space in which the light regime is suitable for the establishment and growth of a particular species. Another approach has been proposed by Payette *et al.* (1990), in a dendrochronological assessment of disturbance regimes, who used radial growth patterns to establish gap sizes and chronology. These studies reveal that the focus has progressively shifted from the physical definition of gaps and SSD to a more functional one. This approach puts aside the traditional view of the forest as a uniform matrix perforated by discrete SSD and accentuates a vision of interacting SSD that create complex forest dynamics (Lieberman *et al.*, 1989). Sharing this vision, we advocate that SSD impact on tree growth at the SSD periphery is substantial and extends considerably into the adjacent forest. Therefore, the entire surface where the SSD translates into enhanced tree growth should be included into a realistic SSD definition.

This evolution in the conceptualization of SSD is very recent and partly explains the lack of knowledge about the external impact of SSD. Most of the SSD studies of the last decades have focused on SSD inner processes and on SSD cumulative global impact on forests. Knowledge about SSD external impact would help ecologists to better understand species behaviors and would greatly contribute to the forest managers who need to know the consequences of the SSD they produce in order to better plan their treatments and strategies. Which species will be more affected? Which spatial orientations will benefit the most from the sudden light increase? At which distance will the SSD presence be felt?

Another reason explains this absence of studies on SSD periphery: the experimental limitations of field studies. Field studies that locally investigate SSD dynamics are normally characterized by tedious data collecting periods, and by limited spatio-temporal dimensions. Runkle's (1990) longitudinal study of 36 forest gaps is a good example of this situation. Spanning over 12 years, this study of gaps inner processes necessitated considerable time and financial investments even though the precise spatial positioning of the trees was not acquired. Moreover, this study was based on limited tree samples, therefore limiting the comprehension of the dynamics that was occurring. A way to overcome these limitations is to use a forest model.

Following the pioneer work of Botkin *et al.* (1972) who designed the first gap model, JABOWA, several scientists have since developed forest simulation models that discretize space by using spatial cells corresponding approximately to the size of a stand or a gap (e.g.: FORET – Shugart and West, 1977; SILVA – Kercher and Axelrod, 1984; FORSKA - Leemans and Prentice, 1989). More recent models (e.g.: FORMOSAIC - Liu and Ashton, 1998; LANDIS - He *et al.*, 1999) have tackled larger observation scales and incorporate more spatial interactions but they still discretize space. Also, in all these models, the role of individual trees, the true key players in forest dynamics, is not considered, thus affecting aspects of growth, recruitment and competition. Forest dynamics emerge as the basic simulation units (trees) interact, revealing the need for individual-based models supported by solid and considerable species field data. Unfortunately, most forest models do not fulfill these requirements.

The SORTIE model used in this study incorporates all of the elements needed to take into account the complexity of forest ecosystems (continuous space, individual-based (Judson, 1994)). SORTIE (Pacala *et al.* 1993; 1996), a stochastic and mechanistic spatially-

explicit and individual-based temperate forest succession model, is particularly well suited for simulating SSD. Its spatial characteristics and its simple design, added to its reliance on considerable empirical data makes it very popular for forest modelers. SORTIE models the evolution of forests affected by small intrinsic naturally-created gaps. It has been proven to consistently and realistically mimic the dynamics of such undisturbed forests (Pacala *et al.*, 1996).

The objective of this study is to characterize the impact extent of SSD on their periphery through saplings growth reaction. Specifically, the sapling release episodes (SRE) located outside SSD of varying sizes (500 to 2000 m^2) are used as indicators of SSD impact. A release episode is defined by a sharp increase in growth not associated with climatic variations (Glitzenstein et al. 1986). All individuals that possess a diameter at breast height (DBH) of 2 to 15 cm are considered saplings. The decision to only study sapling release responses is based on two facts: first, adult trees will practically never be affected by SSD since they already have access to abundant light, and second, seedlings represent a numerically stable but demographically volatile (high mortality and birth rates) population that is never studied for DBH values in the field. Our interest lies in the SRE spatial configuration (distance from SSD and orientation) by SSD sizes and species.

3.3. METHODOLOGY

SORTIE BC v. 4.1(Pacala *et al.* 1993; 1996; Papaik, 1999) is the model used in this study. Based on large sets of empirical observations on nine species of the northern hardwood forests (Pacala *et al.* 1994; Ribbens *et al.* 1994; Canham *et al.* 1994; Kobe *et al.* 1995), SORTIE simulates the evolution of all individual trees through their competition with others for light. The temporal dimension is segmented in time steps of five years but space is continuous, tri-dimensional and explicitly considered. For every time step, SORTIE uses the following five operating submodels (in order of their execution): 1) Harvesting – applies any predefined harvest regime; 2) Light availability – attributes a GLI value (Gap Light Index: Canham *et al.*, 1988) to every tree as a function of species specific light extinction coefficients and height; 3) Tree growth – as a function of the GLI values; 4) Reproduction – seedling recruitment as a function of parent tree proximity, and 5) Tree mortality – as a function of previous growth rates and stochasticity.

The nine species modeled by SORTIE are the following: *Acer rubrum* L. (ACRU), *Acer saccharum* Marsh. (ACSA), *Betula alleghaniensis* Britton (BEAL), *Fagus grandifolia* Ehrh. (FAGR), *Fraxinus americana* L. (FRAM), *Pinus strobus* L. (PIST), *Prunus serotina* Ehrh. (PRSE), *Quercus rubra* L. (QURU) and *Tsuga canadensis* (L.) Carr. (TSCA). Simulations were performed using a toroïdal matrix of 500 x 500 m (25 ha) over a temporal extent of 305 years and all nine species were used to ensure realistic stand composition.

Figure 1 summarizes our experimental framework. The initial simulation conditions and the temporal extent have been chosen based on conclusions achieved in a preliminary study (Ménard *et al.*, 2001). This study revealed that the species local spatial structures generated by the model were insensitive to initial conditions (initial spatial configuration) after 250 years and that species densities were unaffected by artificially-introduced SSD. Therefore, ten replicates of a simulation characterized by an initial random distribution of individuals and a density of 100 ind. / ha per species were performed. The simulation was then stopped after 295 years (time step #59) for the extraction of a Tree Map File (TMF) representing the pre-SSD situation. A TMF is a file generated on request by SORTIE that contains information (spatial coordinates, diameter at breast height (DBH), height, species) on every individual on the matrix at that moment. The simulation was restarted for another five years (time step #60) and at that time (year 300) another TMF was extracted. Using the IDL 5.3™ software, four new TMF were created from each of the ten TMF extracted at 300 years. By removing all the individuals inside a matrix-centered circle of 12.615 m, 17.841 m, 21.851 m and 25.231 m of radius, SSD of respectively 500, 1000, 1500 and 2000 m² were artificially introduced into the forest scene. These modified TMF and the non-disturbed one were then reentered into SORTIE and simulated for another five years, until year 305 (time step #61). At that point, five new TMF containing the post-SSD information were finally extracted.

This methodology allowed us to acquire the following information: for every replicate and every tree, we possess pre-SSD DBH values, DBH values at the time the SSD were introduced, and post-SSD DBH status for all five scenarios (no SSD and the four SSD sizes). The no-SSD scenario at year 305 only serves for a comparison purpose. The modified tri-dimensional light structures of the SSD scenarios at year 305 are the only element influencing the DBH values since SORTIE mortality and reproduction sub-models are applied after light and derived growth are computed. Everything else being controlled, it is possible to reveal the SSD pure impact on growth by comparing the behavior of trees in SSD scenarios to their behaviors in the associated non-disturbed settings.
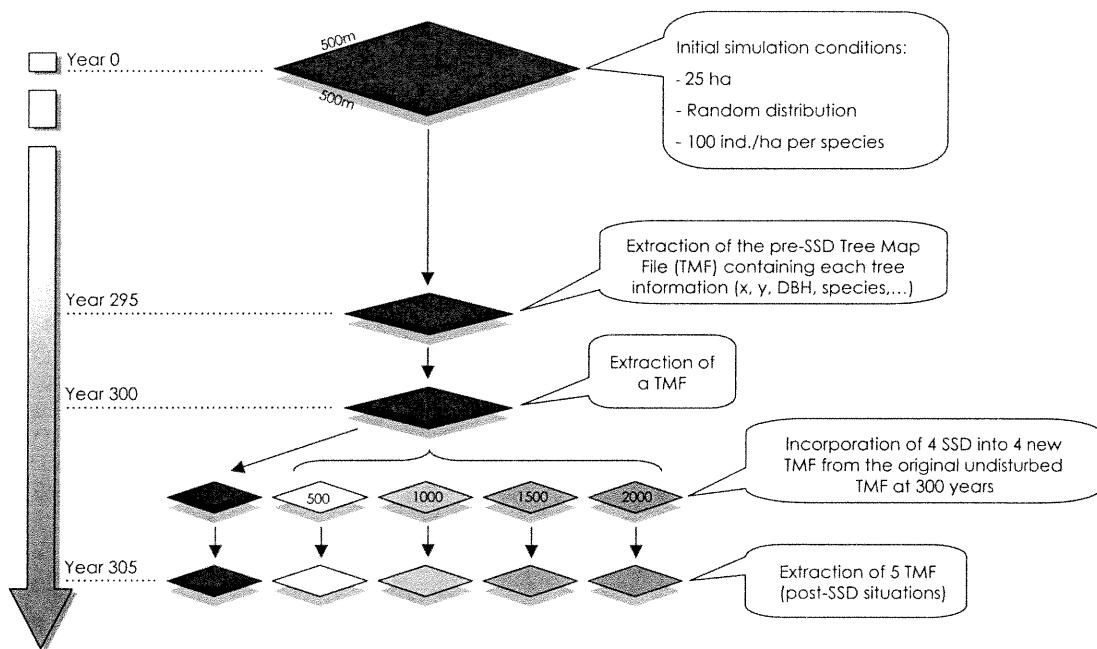
Figure 1 *Illustration of the experimental framework.*

A widely used approach in determining release from dendrochronological records is based on the use of a threshold growth ratio (Canham, 1985; Lorimer, 1985; Lorimer and Frelich, 1989; Cho and Boerner, 1995; Cherubini, 1996; Poulson and Platt, 1996). The method used in this study is derived from this approach and was developed by Henry and Swan (1974) and later reused by Payette *et al.* (1990): a 2,5 or more increase rate in tree-ring width over the previous rate (for at least four consecutive years – five in our case) is considered a release. From the three DBH values gathered on each individual tree, the pre-SSD growth (300 – 295) and the post-SSD growth (305 – 300) were established. A growth ratio was then computed by dividing the post-SSD growth by the pre-SSD growth. If the ratio was higher than 2.5, it was concluded that this tree had experienced a release episode. If a tree had a release ratio value higher than 2.5 in a SSD scenario and did not have one in the associated no-SSD scenario, then this tree had experienced a release episode entirely caused by the SSD. By comparing the SSD scenarios release values to their no-SSD counterparts, the release episodes naturally occurring in the forest matrix were left aside and only the true outside SSD impact was captured.

3.4. RESULTS AND ANALYSIS

A total of 331 SRE were found in the 40 disturbed forest scenes created by the ten replicates and the four SSD sizes. These SRE are first analyzed by SSD sizes to examine the relationship between SSD size and peripheral impact intensity, extent and orientation. Then, they are analyzed by species to verify if specific differences exist for these three attributes.

3.4.1. Sapling release episodes (SRE) by small-scale disturbance (SSD) sizes

The distribution of the 331 SRE by SSD sizes for the ten replicates is the following: 500 m² = 29, 1000 m² = 81, 1500 m² = 113 and 2000 m² = 108. In average, 2,9; 8,1; 11,3 and 10,8 saplings experience release in the periphery of SSD. To verify if the increasingly larger SSD had a significant impact on the number of SRE, t tests for mean comparison ($\Delta = 5\%$) were performed. Only the average for 500 m² is significantly different from the others, revealing that the number of SRE may be reaching a plateau from 1000 m² to 2000 m².

Where are these SRE located in terms of orientation and distance from the SSD? To answer this question, space in the periphery of SSD was discretized by dividing the spectrum of orientations into six sectors of 60 degrees, and the distance from the SSD into six rings of five meters. For each of the resulting 36 spatial sections, the number of SRE was divided by the number of present saplings. These SRE relative frequencies indicate the intensity of the release process in each section and the general spatial configuration of SRE in relation to SSD sizes. Figure 2 shows maps of SRE relative frequencies for the four SSD sizes. These maps reveal a north and south hemisphere dichotomy, a relative east-west spatial symmetry, and the presence of highest SRE relative frequency in the first five meters of the north sector. These observations are consistent with light regimes around SSD at the latitudes of northern hardwood forest (Canham et al., 1990).

500 m² 1000 m²

330 30 330 30
25 25
20 20
15 15
10 10
5
270 90 270 90
210 150 210 150

LEGEND

0 – 9%
10 – 29%
30 – 49%
50 – 69%
70 – 100%

1500 m² 2000 m²

330 30 330 30
25 25
20 20
15 15
10 10
5
270 90 270 90
210 150 210 150
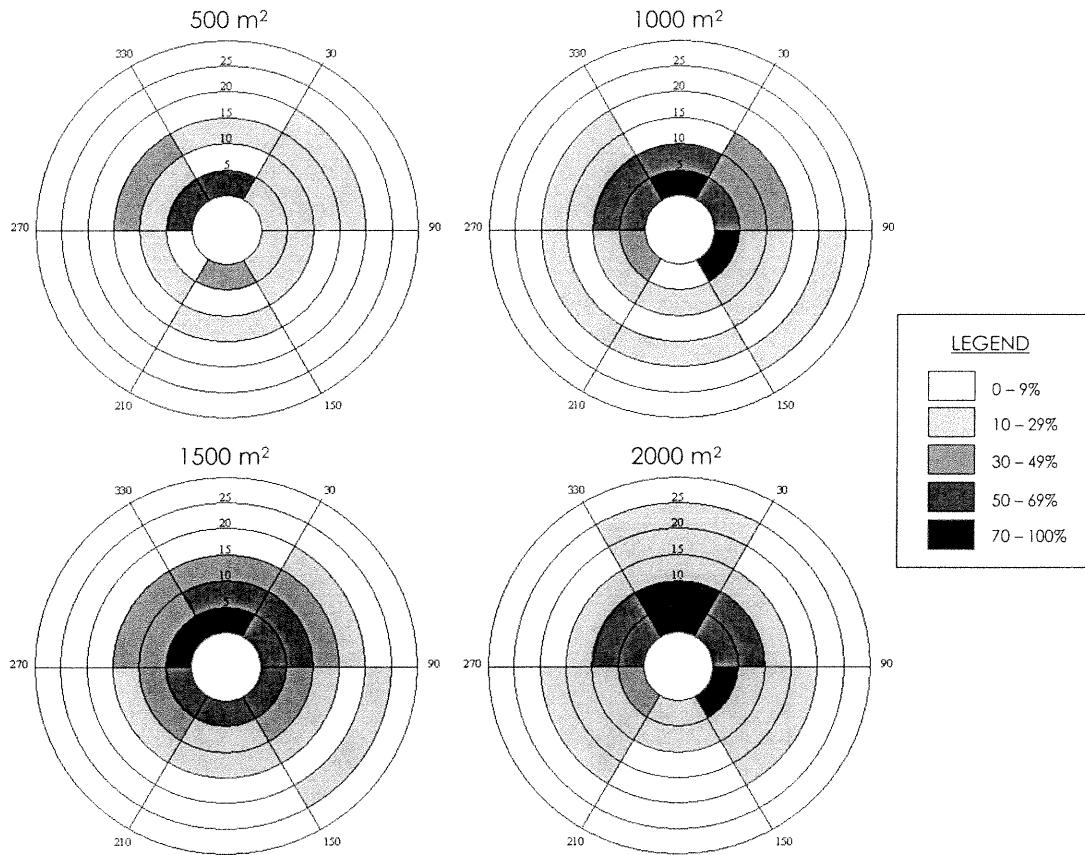
Figure 2 *Spatial representation of SRE relative frequencies for the four SSD sizes.*

The map for 500 m² shows few SRE, a weak east-west axis, and an overall discontinuous impact. The 1000 m² map reveals a considerable increase in SRE relative frequencies, an intensification of the release impact in the first 10 m (mainly in the north hemisphere), and few SRE in the south sector. With the 1500 m² map, the impact reaches its highest intensity. The impact pattern is very continuous; over 50% of all saplings within 5 m and over 30% of the ones situated within 15 m in the north hemisphere experience release episodes. The impact slightly declines in the 2000 m² map, but the impact pattern stays continuous also with high values in the north hemisphere (over 50% in the first 10 m).

While these maps illustrate the general behavior of SRE in SSD periphery, Figures 3 and 4 present a more detailed analysis of the distance from SSD and orientation, respectively. Figure 3 shows that SSD sizes of 1000, 1500 and 2000 m² have similar behaviors in terms of release impact distance in the adjacent forest. Near 50% of all saplings in the first 10 m experienced release in these three SSD sizes, while the percentage drops to around 20% in the 10 to 15 m class. In the 500 m² case, the values oscillate around 20% from 0 to 15 m,

which is notably lower than the other three sizes in the 0 to 10 m classes. After 15 m, all SSD sizes have similar behaviors with values under 10%.
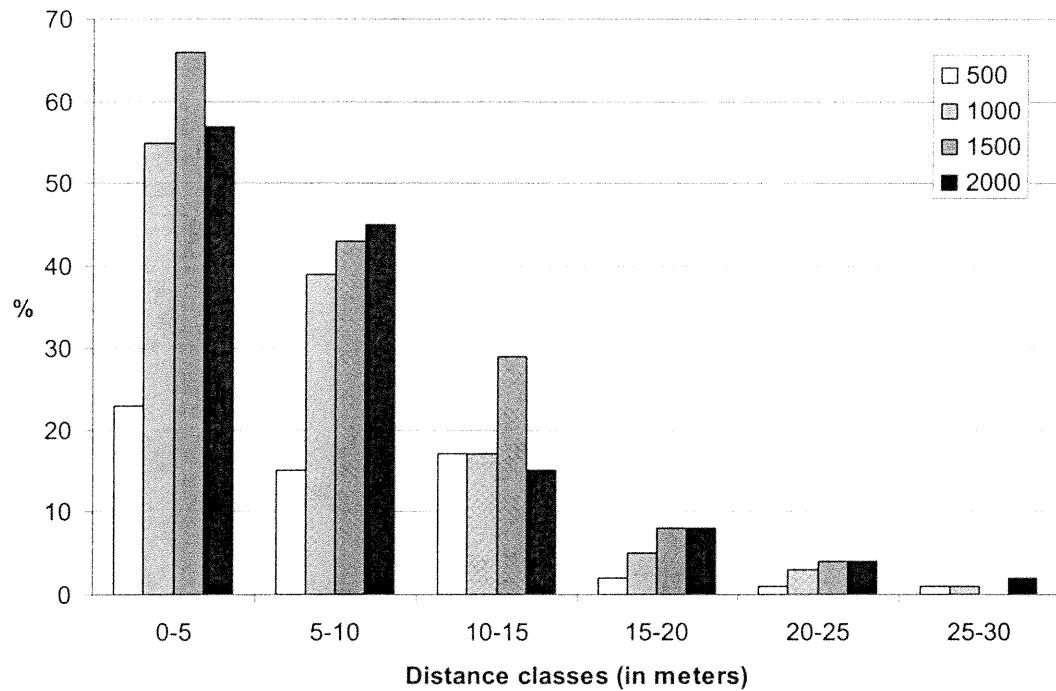

Figure 3 *SRE relative frequencies by distance from SSD for the four SSD sizes.*

Why is the 500 m² distribution so different from the others in the first 10 m while similar after that? This situation could be explained by the presence of diffuse and direct-beam radiation. Diffuse radiation drops off uniformly in all directions with increasing distance from the SSD center (Canham *et al.*, 1990; Runkle *et al.*, 1995), and after 10 m it could be the sole contributing radiation to SRE in every SSD size scenarios. Direct-beam radiation is spatially heterogeneous in and around SSD but its impact is very concentrated in the first few meters of the SSD northern periphery (Canham *et al.*, 1990). The small size of the 500 m² SSD may inhibit the full penetration of direct-beam radiation, which explains the threshold occurring between 500 m² and 1000 m².

Figure 4 reveals the orientation distributions of SRE relative frequencies for each SSD sizes. An interesting dichotomy exists between the two first sizes and the last two in terms of which sector dominates. For the 500 and 1000 m² SSD, the north-west + north-east sectors have the highest SRE proportion, while it is the north sector who takes over in the 1500 and 2000 m² SSD. The north-west + north-east sectors remain constant after 1000 m² while the north sector reaches values over 30% for the same SSD sizes. Again, the direct-beam

radiation explains this transition. This radiation forms a horizontal ellipse of increase illumination in the northern hemisphere of SSD (Canham et al., 1990). However, the highest light values are located in the ellipse center, right in the north sector. These values get so high as SSD size increases that a very large proportion of the saplings in the first 10 m experience release episodes. Finally, like mentioned earlier, very small SRE frequencies (around 5%) are present in the south hemisphere (south-west + south-east and south sectors).
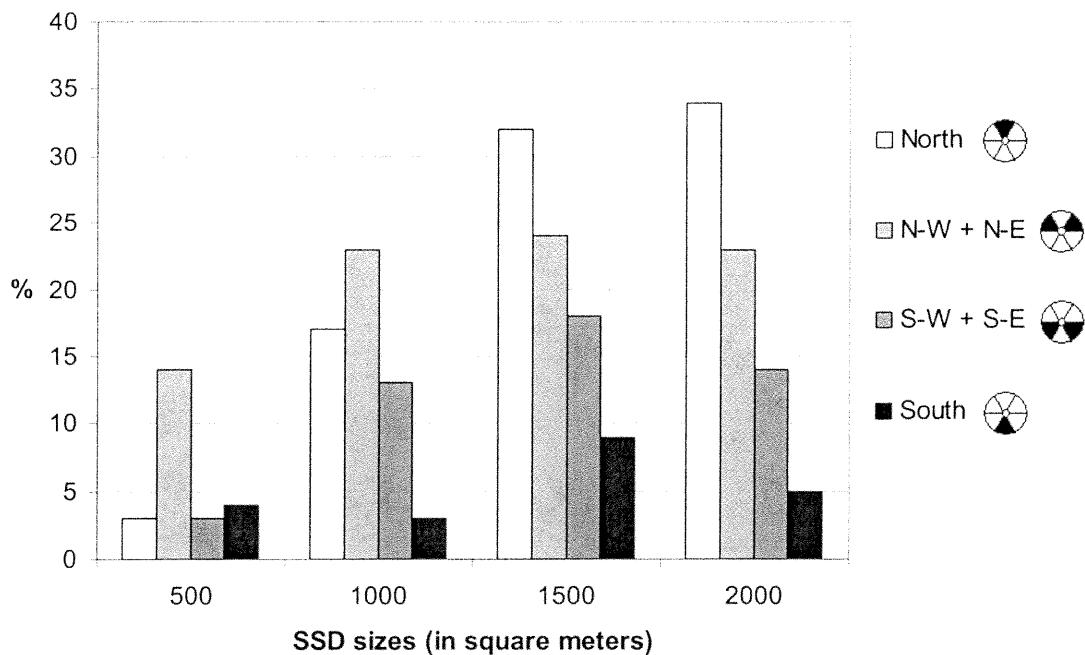

Figure 4 *SRE relative frequencies by orientation sectors for the four SSD sizes.*

3.4.2. Sapling release episodes (SRE) by species

The distribution of the 331 SRE by species is the following: *Fagus grandifolia* = 150, *Tsuga canadensis* = 88, *Pinus strobus* = 39, *Quercus rubra* = 34, *Prunus serotina* = 16, Other species = 4. These results reveal that, out of the averaged 8,275 SRE per SSD, almost half are *Fagus grandifolia* (3,75 per SSD or 45,3% of the SRE), a quarter are *Tsuga canadensis* (2,2 per SSD or 26,6% of the SRE) and all the other species make up the last quarter (2,325 per SSD or 28,1% of the SRE). These proportions are in good agreement with simulations global densities. Since the trees of a particular replicate can have experience release episodes in more than one SSD size, it is imperative that we interpret the results both by species and by SSD size. However, this obligation splits our sampling size by 12 (three

species X four SSD sizes) instead of four like in the preceding section. Therefore, orientations and distance from SSD classes were respectively grouped in order to preserve satisfactory sample sizes.

Figure 5 illustrates the penetration of SRE into the forest in relation to species. The three graphs show the same overall behavior. After an initial 10 m with values around 50%, SRE relative frequencies for all species decline to values around 10 and 20% in the second distance class (10 – 20 m). The results for the 500 m² SSD size do not follow this trend; values in the first 10 m are considerably inferior to the other sizes for all species. The results in the 20 – 30 m distance class reveal important species differences. While *Tsuga canadensis* and the other species do not surpass the 20 m mark, *Fagus grandifolia* present SRE relative frequencies around 5%. This situation is consistent with species knowledge. *Fagus grandifolia* is the most tolerant species of the model (Tubbs and Houston, 1990), and possess the smallest probability of mortality at zero growth (Pacala *et al.*, 1996). Therefore, his ability to convert small amount of light into enhanced growth (Canham, 1989) and to survive long periods of closed canopy is very good.

Figure 6 reveals important species differences in terms of preferential SRE orientation. The highest SRE relative frequencies for *Fagus grandifolia* are located in the north-west + north-east sectors. Also, the south sector for this species has SRE frequencies that are high compared to the other species. This leads to the conclusion that the diffuse radiation created by SSD is sufficient for *Fagus grandifolia* to achieve release, even to the South. *Tsuga canadensis* exhibits a dual behavior. In the first two SSD sizes, the north-west + north-east sectors are dominant and in the last two sizes, it is the north sector who is. Also, the SRE frequencies of this species in the north sector are the highest SRE sector proportions of any species, with values surpassing 40% and 60%. The SRE proportions of the other species also exhibit a dual behavior, but the transition from the north-west + north-east sectors to the north sector takes place at the 1000 m² SSD size. Contrary to *Fagus grandifolia*, *Tsuga canadensis* and the other species seem to benefit from the increase of direct-beam radiation as SSD sizes increases.
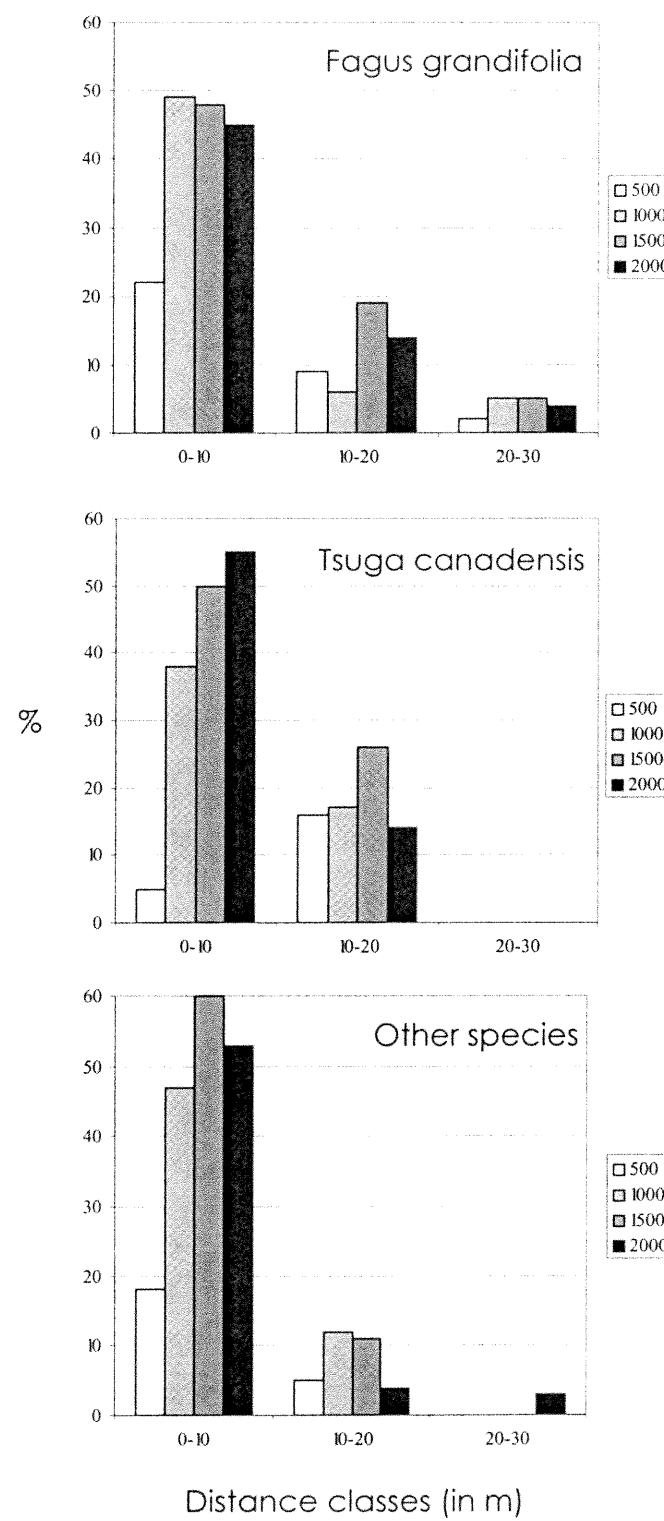
Figure 5 *SRE relative frequencies by distance from SSD for the three species.*
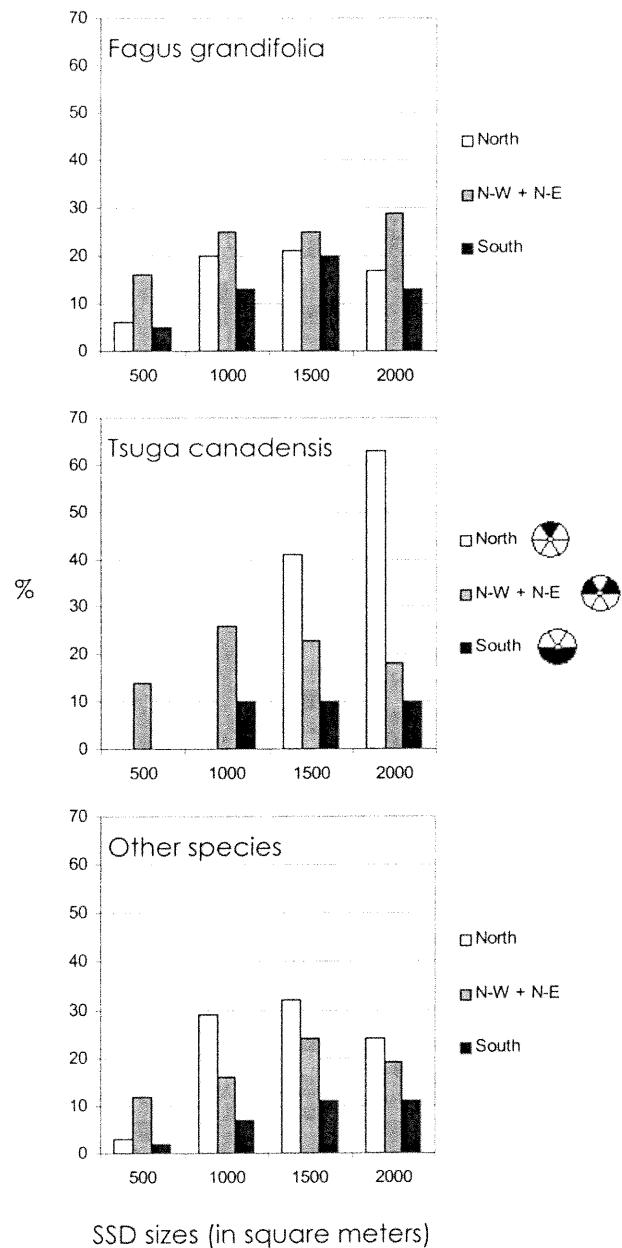
Figure 6 *SRE relative frequencies by orientation sectors for the three species.*

Finally, Figure 7 shows each species proportion in the number of SRE by SSD sizes compared to each species mean proportion in the saplings of the entire simulation matrices. The matrices are the ten 25 ha lattices onto which the simulations were performed. If SSD did not have any favorable impact on any species, the species proportions in the number of SRE would be equivalent to their proportions in the

simulation matrices. *Fagus grandifolia* is advantaged by SSD but this advantage vanishes (from 55% to 41%) as SSD sizes increases. The reverse situation is present for *Tsuga canadensis*, with its proportion in SRE rising to the matrix mean as the SSD sizes increase (from 24% to 32%). The other species combined have a behavior somewhat similar to *Tsuga canadensis* with the exception that their proportions in SRE surpasses their matrix mean (from 21% to 28%). Again, *Tsuga canadensis* has a behavior closer to the other species than to *Fagus grandifolia*. Traditionally, small SSD are said to favor established and dominant species while larger ones benefit to opportunists and shade intolerant species (Bazzaz and Pickett, 1980). This situation is present in Figure 7.
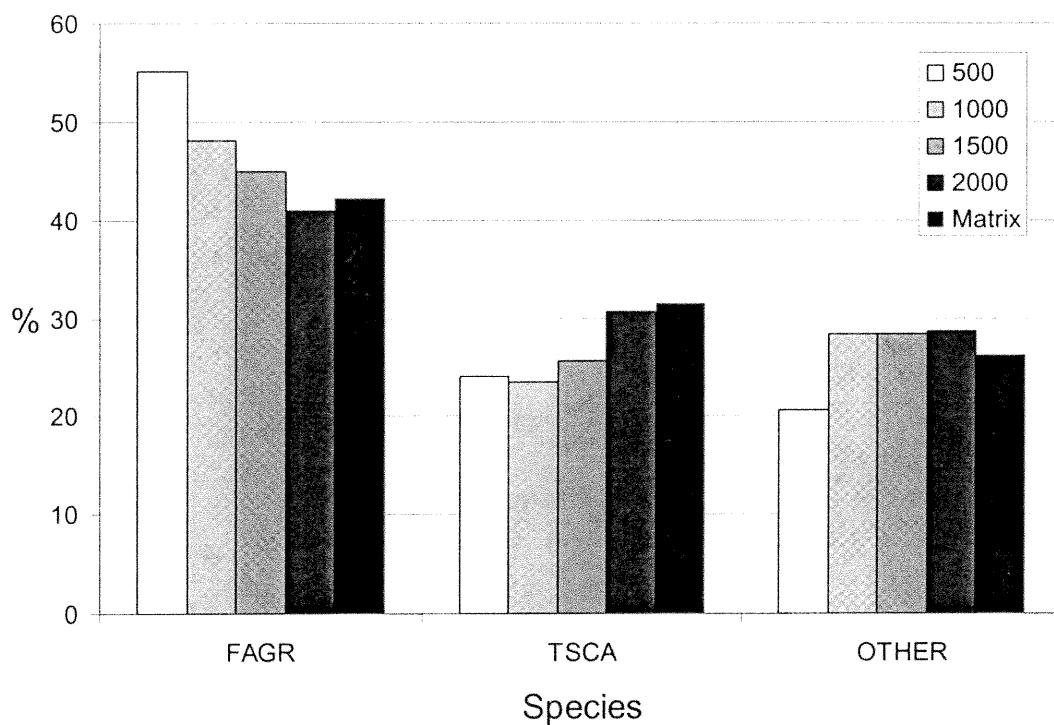
Figure 7 *Species proportions in SRE and simulation matrices.*

3.5. DISCUSSION AND CONCLUSION

This research represents one of the first attempts to study local forest dynamics using a forest succession model. It sheds new light on a traditionally neglected region of potential SSD impact, the outside periphery. While this region has been examined through light level regimes (Canham *et al.* 1990) and has slowly reached the scientific community's recognition as a logical part of the SSD concept, nothing has been done to quantify the reaction of saplings in SSD periphery. The results presented here offer an

interesting picture of SSD external impact on SRE attributes. Whilst this picture seems to be ecologically-based with results that are in agreement with field studies literature, it also adds valuable information to the SSD size and extent debate.

3.5.1. Consistency between field knowledge and model results

The purpose of simulation models is to produce new information, and forest modeling can be seen as a complementary tool to field studies. However, the confidence that is associated with model results is strongly linked to its confrontation with real world data. Even if the validation process of ecosystem models was recently criticized (Oreskes *et al.,* 1994; Rykiel, 1996), it is still regarded as important "for building model credibility in the user community"(Rykiel, 1996). To that regards, the majority of the results presented above can effectively be compared to field knowledge.

The spatial configuration of SRE in the outside periphery of SSD is consistent with prior facts on SSD light regimes. Many researches on SSD interior light modulations (Minckler *et al.* 1973; Collins and Pickett, 1987; Poulson and Platt, 1989; Runkle *et al.* 1995) support the modeled assessment of SSD overall light regimes done by Canham *et al.* (1990). They maintain that in northern temperate forests, light gradually decreases from the north edge of SSD, to the SSD center, to the south edge. The presence of an opposition between the north and south hemispheres in the SRE proportions and the occurrence of the highest SRE proportions in the first 10 m to the north of SSD are consistent with their observations.

The SRE results related to species behavior can also be explained by field knowledge. SRE for *Fagus grandifolia* occur further from the SSD than those of all the other species (Figure 5). This situation arises because very small increases in light can trigger in *Fagus grandifolia* important growth responses (Canham, 1989), and because a small growth looks important in comparison to this species very low growth under the canopy. However, as a true shade-tolerant, *Fagus grandifolia* does not react to more intense light increases. This situation explains his low SRE proportions in the north sector and his relatively strong SRE presence in the south sector (Figure 6). *Tsuga canadensis* is also classified as a shade-tolerant but, to the contrary of *Fagus gandifolia*, its reaction to small light increases is slow (Canham, 1989) while more intense increases affect it greatly (specimens planted for horticultural purposes, Bouchard, personal observations). Those circumstances explain this species strong SRE proportions in the north sector (Figure 6).

Finally, the other species (mainly *Pinus strobus*, *Prunus serotina* and *Quercus rubra*) are considered more shade-intolerant than the other two species and this trait is apparent in the SRE. Like *Tsuga canadensis*, they do not respond to small light increases but not for the same reason. When present in the understory, the saplings of these species already have considerable growth since they cannot withstand moderate periods of suppression. Therefore, small light increases found far from SSD edges (after 20 m) are not sufficient to generate a release ratio superior to 2,5 (Figure 5). Moreover, shade-intolerant species usually react favorably to high illumination environments; this fact explains why their highest SRE proportions are in the north sector, Still, these proportions are smaller than the ones obtained by *Tsuga canadensis* because of these species superior base-line growth.

3.5.2. From extended gap to SSD based on release episodes

The major contribution of this research lies in its examination of SSD impact extent as a new basis for SSD definition. The SSD concept has largely evolve in the last decades, from a discrete physically-defined disturbance (canopy gap) to a resource-defined one (extended and species extended gap). However, none of these conceptualizations link the resources regimes alterations caused by SSD to their impact on the trees. It is possible to evaluate the impact through the use of dendrochronology like Payette *et al.* (1990) did, but as in all forest field studies, data collection is expensive and tedious. Our results show the pertinence of the forest modeling approach in SSD local studies and the real extent and size of SSD.

To evaluate the differences in SSD size between SSD definitions, the areas corresponding to the different definitions were compared. First, the canopy gap area (vertical projection of the canopy opening - Figure 8.a) of each SSD was calculated. Then, the extended gap area (canopy gap plus the area extending to the base of the surrounding trees – Figure 8.c) was considered, but since our experimental SSD (Figure 8.b) are similar in size to the extended gap conception, these experimental areas were used instead. Finally, SSD based on the inclusion of peripheral areas of different SRE proportions (Figure 8.d) were computed from the maps on Figure 2. These areas correspond to the true impact extent of SSD.
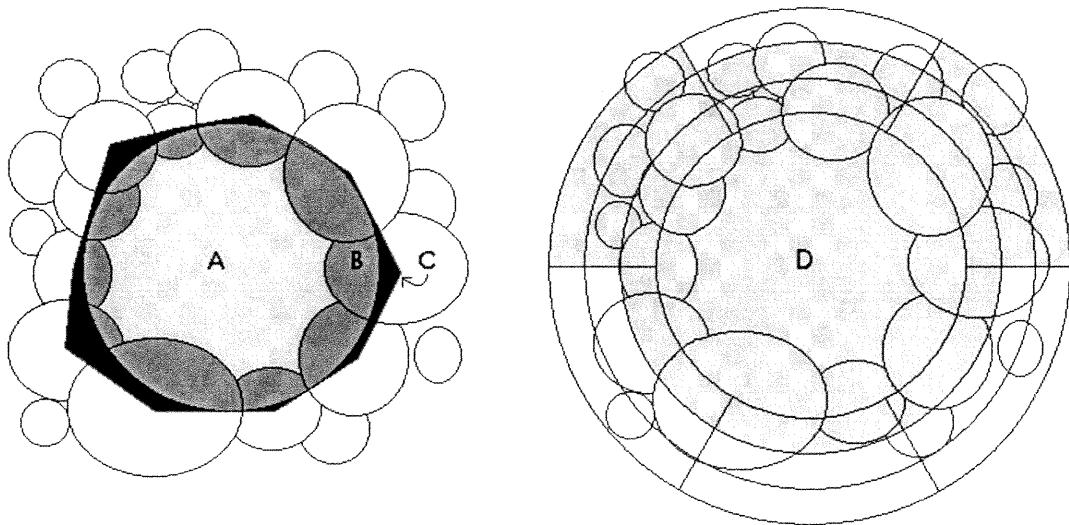
Figure 8 *Schematic representation of SSD definitions. (A: canopy gap; B: our experimental SSD; C: extended gap, and D: SRE based SSD).*

The areas are presented in Table 1. First, the relationship between the experimental SSD areas and the mean of their associated canopy gap areas concords with Runkle's results (1982; 1990). He found that canopy gaps usually double their size when treated as extended gaps but as gaps become larger the factor becomes less than two. This situation is explained by the decline in the relative importance of the area extending to the base of the SSD surrounding trees as the perimeter/area ratio declines. While this concordance with literature is interesting, the most important aspects of the Table 1 results are the differences between our experimental SSD areas and the areas generated by the addition of peripheral areas of SRE proportion levels. As the SRE proportion criterion is lowered, the resulting areas increase consequently (ex.: the 50% SRE area contains the experimental SSD areas and the sections with SRE proportions higher than 50%). If we consider the areas where 70% and more of the saplings experience release episodes, there is a 0-20% increase in SSD size depending on the initial experimental SSD. The areas expand 30-71% if the 50% and more sections are considered, 61-138% if the 30% and more sections are included, and 190-290% if we go down to the 10% threshold. The areas in which SSD are felt can be almost four times larger than Runkle's extended gap.

Table 1

SSD sizes according to definition (in square meters)					
Mean canopy gap		256	653	1114	1552
Experimental extended SSD*		500	1000	1500	2000
	70% SRE	500	1213	1755	2461
Experimental	50% SRE	658	1691	2572	3093
extended SSD + ...	30% SRE	868	2089	3571	3238
	10% SRE	1996	3567	4702	5800

* Sizes close to extended gap definition

Table 1 *SSD sizes according to definitions*

Thus, SRE areas represent an important region and should receive considerations in any SSD related topic. They have significant implications for forest managers and ecologists. Forest management aims at disturbing the forest for timber productivity while limiting and maximizing the number and type of interventions. The SRE based SSD could lead to a reconsideration of forest management treatments since reduced sizes of SSD can produce similar impacts. Also, this innovative vision of SSD may encourage ecologists to reexamine some SSD theories and conclusions. Among them, the gap partitioning theory (Denslow, 1980; Runkle *et al.* 1995; Kobe, 1999) which, from our results, could be extended to the peripheral areas of SSD and the spatial interactions of the SSD entities and their global impact on forest dynamics. Much work has to be done on forests ecosystems and the SSD that drives them in order to detail, extend and revisit the SSD notion in this new perspective.

3.6. ACKOWLEDGEMENTS

CHAPITRE 4 : DISCUSSION ET CONCLUSION

Les résultats des recherches effectuées dans le cadre de ce mémoire permettent de faire ressortir trois grands constats. Premièrement, SORTIE possède les caractéristiques requises pour l'étude spatio-temporelle des perturbations de petite envergure (PPE) à l'échelle locale. Deuxièmement, ce modèle génère des résultats réalistes concernant la caractérisation spatiale de l'impact des PPE sur les gaules. Enfin, les superficies associées à l'impact des PPE, évaluées par les épisodes d'essor des gaules, sont considérablement plus grandes que les superficies normalement attribuées aux PPE.

4.1. SORTIE À L'ÉCHELLE DES PPE : POTENTIEL D'UTILISATION ET RÉALISME VÉRIFIÉS

Quoique les PPE aient été étudiées par plusieurs chercheurs, elles ne l'avaient pas été par l'approche de la modélisation pour une échelle locale. Jusqu'à tout récemment, les modèles forestiers ne possédaient pas l'architecture adéquate pour atteindre le niveau de détail nécessaire aux études locales. De plus, les avancées technologiques en informatique des dernières années permettent maintenant d'effectuer des simulations comportant un très grand nombre de données. Par exemple, pour déterminer les épisodes d'essor des gaules décrits dans le chapitre 3, plus de 3 375 000 valeurs de diamètre à hauteur de poitrine ont dû être enregistrées et traitées. Il y a quelques années, ce genre de traitement aurait été difficile à réaliser.

Cette situation explique pourquoi les vérifications présentées dans le chapitre 2 ont été exécutées. La sensibilité des patrons spatiaux locaux générés par le modèle aux conditions initiales de simulation et la sensibilité des espèces aux perturbations introduites devaient être évaluées pour vérifier le potentiel du modèle SORTIE pour des études portant sur les PPE. L'évaluation de ce potentiel était donc une étape préliminaire à la réalisation de notre étude. Les résultats obtenus démontrent que ces patrons spatiaux ne sont pas sensibles aux conditions initiales (distribution spatiale initiale) après 250 ans et que les densités des espèces ne sont pas significativement altérées par l'incorporation de PPE. Les directives expérimentales découlant de ces résultats permettent à l'ensemble des chercheurs qui utilisent SORTIE à l'échelle locale d'éviter d'avoir à composer avec la sensibilité du modèle lors de l'interprétation des résultats de simulation.

Les résultats obtenus au niveau de l'impact des PPE sur la croissance des gaules et même ceux traitant de la structuration spatiale locale des espèces montrent que SORTIE modélise de manière réaliste à cette échelle d'observation. Le patron spatial de l'impact observé à travers les épisodes d'essor s'inscrit dans la continuité des recherches de terrain étudiant la segmentation des zones d'impact à l'intérieur des PPE. À nos latitudes, l'impact à l'intérieur des PPE décroît graduellement du nord vers le sud. Or, les résultats obtenus présentent aussi une forte dichotomie entre les périphéries nord et sud des PPE. Le comportement des espèces en périphérie des PPE est aussi en lien avec la littérature les concernant. *Fagus grandifolia* fait partie des espèces tolérantes à l'ombre. Il possède les épisodes d'essor les plus éloignés des PPE (faible lumière) et ne réagit pas à l'augmentation de la taille des PPE (zones de forte illumination). *Tsuga canadensis* a curieusement un comportement en présence de PPE qui pourrait l'apparenter aux espèces de mi-succession. Il réagit fortement aux PPE de 1500 et 2000 m² avec des proportions d'épisodes d'essor très élevées dans le secteur nord. Cependant, il n'est guère favorisé par les PPE puisque ses proportions dans les épisodes d'essor générés par toutes les tailles de PPE sont toujours inférieures à ses proportions moyennes dans les gaules des matrices de simulation non-perturbées. Enfin, même l'évolution temporelle des valeurs de la statistique du K de Ripley du premier article est conforme à l'écologie de la reproduction arborescente (d'un patron aléatoire à un patron agrégé). Cette confrontation réussie entre les dynamiques modélisées et la réalité ajoute à la confiance dans le modèle SORTIE et permet ainsi de proposer plus aisément des hypothèses alternatives.

La génération par SORTIE de dynamiques locales et globales (Dubé *et al.* 2001) complexes à partir de la compétition des individus arborescents pour la ressource lumineuse témoigne de l'immense pouvoir des interactions simples dans l'émergence de la complexité dans les systèmes vivants. Bien que SORTIE néglige certains aspects des écosystèmes forestiers, tels que la compétition pour l'eau et pour les nutriments du sols, la présence d'arbres morts (chicots ou au sol) et la flexibilité des houppiers, les résultats présentés au chapitre 2 montre que ces limitations n'altèrent pas la qualité des dynamiques forestières locales générées par le modèle. Cette situation permet de croire que bons nombres de phénomènes locaux pourraient être étudiés par l'entremise de SORTIE comme, par exemple, le processus de fermeture des PPE, l'étude temporelle de l'impact périphérique des PPE, l'impact à long terme des PPE répétitives, etc.

4.2. L'ÉTENDUE DES PPE : VERS UNE NOUVELLE DÉFINITION?

Le troisième et dernier constat de cette étude, et aussi la contribution la plus originale, est la proposition d'une nouvelle manière de définir l'étendue des PPE. Formulée par Payette *et al.* (1990), la méthode basée sur les réactions de croissance des arbres en périphérie des PPE ne peut que difficilement être appliquée en forêt étant donnée la quantité de données devant être recueillies. L'approche par la modélisation permet de remédier à ce problème et permet aussi de contrôler toutes les variables pour ne conserver que l'impact pur des PPE sur la croissance des gaules. Les superficies de PPE qu'engendre cette nouvelle optique sont considérablement supérieures à celles provenant des approches traditionnelles. Dépendamment de la proportion d'épisodes d'essor des gaules utilisée pour définir les nouvelles PPE (10, 30, 50 ou 70%), des augmentations de superficie variant entre 0 et 300% peuvent être observées sur les aires de PPE selon la définition étendue (Runkle, 1982). Ces différences attestent de l'écart existant entre les conceptions plus physiques des PPE et celles plus fonctionnelles auxquelles se rattache cette étude. Cependant, l'importance de cette approche dépasse le cadre théorique de la définition des PPE. Elle incite les aménageurs forestiers à revoir leurs méthodes sylvicoles étant donné l'allure plus continue de l'impact des PPE et devrait amener les écologistes à redéfinir l'ampleur de l'implication des PPE dans la dynamique forestière. Cette recherche s'inscrit dans le rôle que peut tenir la modélisation dans la compréhension des écosystèmes forestiers : elle se veut instigatrice de débats et génératrice d'idées à vérifier.

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