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Analysis of deciduous tree species dynamics after a severe ice storm using SORTIE model simulations

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Abstract

Ice storms are frequent natural disturbance events in hardwood forests of eastern Canada and the United States, but their effects on forest dynamics are not well understood. Our objectives were to characterize short- and long-term tree species dynamics after a severe ice storm, and to assess the influence of spatial distribution of trees on these dynamics. SORTIE, a spatially explicit individual tree-based forest model, was used to simulate the effects of a severe ice storm on 300 years old stands. Crown radius was reduced and tree mortality was increased for a 5-year period following the ice storm disturbance. To investigate the influence of the spatial distribution of trees, we repeated the same experiment in a uniformly distributed stand where we systematically assigned coordinates of all trees, saplings and seedlings before the ice storm was modeled. Our results showed that six types of dynamics can be adopted by a species following an ice storm and that spatial distribution of trees influenced the species responses. In summary, we found that a combination of factors, namely, species density and spatial distribution, shade tolerance, growth rate, extent of canopy openness and canopy loss resulting from the ice storm, determine how tree species respond to ice storm disturbance.

Keywords: Ice storm; Forest modeling; SORTIE; Tree species dynamics; Natural disturbances

1. Introduction

In January 1998, the region east of the Great Lakes was subjected to the most severe ice storm ever recorded in Canada and the eastern United States (USA) (Environment Canada, 1998; Federal Emergency Management Agency, 1998). Within a period of 5 days, up to 100 mm of freezing rain intermixed with snow and hail fell causing major damage to both artificial and natural structures in the affected areas (Environment Canada, 1998). In northeastern US an estimated area of 6.9 million forested hectares were

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affected to varying degrees by the ice storm (Miller-Weeks et al., 1999); while in Québec and Ontario, 2.4 million forested hectares were impacted (Canadian Forest Service, 2001). While some trees were folded in two or were broken under the immense weight of the ice, most trees experienced crown loss due to substantial branch breakage (Boulet and Davidson, 1998; Miller-Weeks et al., 1999).

The 1998 ice storm could be considered a freak weather event since no other ice storm of this magnitude has occurred in Canada in recorded history (Environment Canada, 1998). Nevertheless, scientists consider ice storms to be a natural disturbance event that occur frequently in forests of eastern Canada and USA (Abell, 1934; Bennett, 1959; Lemon, 1961; Melonçon and Lechowics, 1987; Seischab et al., 1993; Irland, 2000; Proulx and Greene, 2001). This is supported by climatological studies (Stuart and Isaac, 1999; Cortinas, 2000; Higuchi et al., 2000). Certain regions in eastern Canada are annually exposed to freezing precipitation (Stuart and Isaac, 1999; Environment Canada, 1998). With heavy accumulations of ice, the risk of tree damage is larger and under exceptional circumstances, a major ice storm event like the one in 1998 could occur. The frequency of such an event is not well established but it has been estimated that an ice storm like the one in 1998 could be repeated every 250 years (Proulx and Greene, 2001). However, ice storms of less magnitude that result in the same damage to trees occur more frequently (Lemon, 1961; Melonçon and Lechowics, 1987; Seischab et al., 1993; Irland, 2000). Furthermore, Hengeveld suggests that the frequency of ice storms may increase in response to climate change (Environment Canada, 1998).

Studies undertaken in North America on forests impacted by ice storm disturbances have revealed that several factors, such as the magnitude and orientation of the slope, the frequency of ice storms, wind speed, and the quantity of ice accumulated interact and affect forests in different ways (Lemon, 1961; Siccama et al., 1976; Bruederle and Stearns, 1985; Whitney and Johnson, 1984; Warrilow and Pu, 1999; Melonçon and Lechowics, 1987; Boerner et al., 1988; Seischab and Orwig, 1991; Seischab et al., 1993; Rebertus et al., 1997; Hooper, 1999; Hooper et al., 2001; Brisson et al., 2001). Studies of ice-damaged stands have shown that dominant canopy trees incur more damage than sub-canopy trees after ice storm disturbance (Siccama et al., 1976; Bruederle and Stearns, 1985; Rebertus et al., 1997; Brisson et al., 1999, 2001; Hopkin et al., 2003; Nielsen et al., 2003; Parker, 2003). Still many of those studies have reported conflicting results about the susceptibility of tree species to ice storms. This lack of agreement among studies is likely due to differences in conditions among study sites such as the structure, age, composition and health of the forest stands, topography, and severity of the ice storm.

What is the impact of ice storm damage on the future development of forests? Hypotheses put forth to answer this question are often contradictory. Downs (1938) proposed that ice storms delay forest succession by creating canopy openings that would favour the growth and survival of pioneer species. In contrast, Abell (1934), Carvell et al. (1957) and Lemon (1961) suggested that ice storms increase the rate of forest succession by severely damaging pioneer species. Other researchers have proposed that both of these phenomena (delay or acceleration of succession) can occur within the same forest stand depending on location within the stand (DeSteven et al., 1991; Irland, 2000) since ice storms do not affect forest stands uniformly. Based on these three opposing hypotheses, it is difficult to predict how the forests damaged by the ice storm in 1998 will evolve.

To improve our understanding of the influence of severe ice storms on forest dynamics, long-term monitoring of forest stands affected by the 1998 ice storm is critical. The opportunity to perform such longitudinal studies, however, depends largely on funding to research institutions. Research costs can be high and the results may not be available for hundreds of years. Moreover, environmental factors such as climatic change and air pollution could bias conclusions regarding the long-term effects of the 1998 ice storm on forest dynamics. An alternative approach, which is complementary to field studies, is to use a forest simulation model such as SORTIE.

The objective of our research is to characterize the tree species dynamics following a major ice storm in the short, mid and long-term, using the simulation model, SORTIE. This study is also designed to examine the influence of the spatial distribution of trees on tree species dynamics after ice storm disturbance. Specifically, the objectives of our study are: (1) to verify the three hypotheses proposed by earlier researchers (see discussion above) concerning the effect of the ice storm on the successional development of forests; and (2) to test whether the spatial distribution of trees influences tree species dynamics after an ice storm.

2. Methods

The methods section is divided into three sections. First, the design and structure of the SORTIE model are briefly described. The justification for the choice of this particular model and the major assumptions underlying its application are also presented. The second section reviews the literature on ice storm damage to trees, outlines the major damages to trees, and then explains the modifications done to SORTIE in order to model ice-damaged trees. The third section outlines the three modeling scenarios that were designed to answer specific study objectives.

2.1. The SORTIE model

SORTIE is an individual-based, spatially explicit model, that was developed by Pacala et al. (1993, 1996) from empirical field studies in transition oak-northern hardwood forests of Connecticut, USA. SORTIE models dynamics in undisturbed hardwood forests of northeastern North America comprised of nine tree species: American beech (*Fagus grandifolia* Ehrh.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), yellow birch (*Betula alleghaniensis* Britt.), eastern white pine (*Pinus strobes* L.), red oak (*Quercus rubra* L.), black cherry (*Prunus serotina* Ehrh.) and white ash (*Fraxinus Americana* L.).

The model predicts tree species dynamics over long periods of time by following the fate of each individual tree throughout its life. To do this, SORTIE is composed of four basic sub-models defined by field data: resource availability (light), growth, mortality and seedling recruitment (Pacala et al., 1996). Trees are distributed continuously in space (x and y coordinates) while time is divided into discrete, 5-year intervals. A parameter file controls the forest simulation. The file contains parameters developed for each species, as well as user-specified information about the size and dimensions of the simulation plot. When the simulation is underway, the quantity of light reaching each seedling and sapling is calculated for each 5-year time interval using the resource sub-model. This calculation is performed using characteristics of an individual's neighbourhood and arrangement of nearby tree crowns, and includes sky brightness distribution and light transmission. Tree crowns are represented by three-dimensional cylinders, which have species-specific dimensions and light extinction coefficients. For each young individual, species-specific growth rates are predicted as a function of the amount of light they receive. In contrast, growth rates for mature trees are pre-determined for each species and estimated from repeated sampling of permanent plots. The probability of mortality of each young individual of a given species is estimated as a function of its recent growth rate, based on the idea that growth reflects carbon balance and carbon balance determines mortality. The mortality sub-model also includes a stochastic mortality rate where each individual has a constant probability of dying from density-independent factors. The recruitment sub-model determines the number of seedlings produced by each mature tree that has a diameter greater than 10 cm at breast height (DBH). Seedlings are dispersed around parent trees at a density that is proportional to parent size and inversely proportional to the distance between the seedling and the parent. The function gives the probability that each seedling will disperse to any location based on the coordinates of the parent tree (see Pacala et al., 1996 for further details).

The SORTIE model was selected because it is spatially explicit, it allows the simulation of forest development over hundreds of years, and it assigns species-specific characteristics to each species in the model. In addition, SORTIE possesses two important characteristics in term of its light model. First, it provides predictions with a satisfactory degree of precision and accuracy in a wide range of situations, as it has been demonstrated by validation tests aimed at comparing light predicted by the model to light measured in the field (Beaudet et al., 2001). Second, compared to other light models, SORTIE requires a small number of input data (Beaudet et al., 2001). As an example, the FOREST model developed by Cescatti (1997a,b) to simulate the radiative transfer in discontinuous canopies requires 18 parameters to describe tree crown only, while Pacala et al. (1993) report 10 main parameters to run SORTIE. Although SORTIE was not especially created to model the effects of ice storms on forest stands, its structure is flexible enough to model the changes that forests sustain during a severe ice storm. Therefore we believe that the predicted forest dynamics following simulated ice storm damage will be indicative, for the most part, of the natural phenomena that occur in forests after a severe ice storm. In addition to these aspects, the modeling performed in this study is based on three other assumptions. First, the initial tree species distributions were computer generated. They do not reflect the current state of an existing forest, but rather a hypothetical situation in a northern hardwood forest similar to the sites where the model was calibrated. Second, in order to simulate stands that have been damaged by an ice storm, it is necessary to simplify or omit certain components and calculations of the model. For example, in the model procedure used, all of the long-term mortality occurred during the same year at 5 years after the start of the simulation. Additionally, the bending of small-sized stems is not modeled in the simulation. Third, in SORTIE, the growth of mature trees is a function of pre-determined growth rates, which were calculated in forests lacking large canopy openings. As a result, the growth response of large-sized trees to the opening of the canopy from ice storm damage is not modeled and densities of ice-damaged stands are likely overestimated during the first centuries after the ice storm.

In this study, SORTIE version 4.1 was used and the simulations were performed on a 9 ha (300 m × 300 m) simulation plot.

2.2. Simulation of a forest stand damaged by an ice storm

The critical step in our methodology was to reproduce the characteristics of forest stand that has been affected by a severe ice storm using SORTIE. To do this, we reviewed scientific literature and characterized general patterns of forest change caused by severe ice storms. First, it was found that the susceptibility to ice storm damage varied by tree species and by diameter (DBH) class (Rebertus et al., 1997; Boulet and Aubin, 1999; Brisson et al., 1999; Warrilow and Pu, 1999; Proulx and Greene, 2001). Secondly, it was found that ice storms affected forest stands in three major ways: (1) crown reduction caused by loss of branches, (2) short-term and mid-term mortality of severely damaged trees, and (3) changes in light conditions in the understory during the first few years following the ice storm disturbance. Numerical values were developed to quantify the ice storm changes sustained by each species. These values were then used to create a parameter file in which parameters were modified to simulate the effects of a severe ice storm on each tree species.

2.2.1. Quantification of ice storm damage

The following four sections describe how we quantified ice damage to tree species and stands. Also included are data obtained from the literature that we used to estimate numerical values of ice damage.

2.2.1.1. Tree susceptibility to ice storm damage. The susceptibility of tree species to ice storm damage was established using the work of Seischab et al. (1993). These authors synthesized the results obtained by various researchers and determined an average susceptibility for each of 13 species. Important results presented by Brisson et al. (1999) and Rebertus et al. (1997) were incorporated to update the information found in Seischab et al. (1993). Birch tree susceptibility to ice damage was added by including results of Boerner et al. (1988). The average susceptibility of each species was calculated (Table 1). This permitted us to develop values of crown reduction and the probability of mortality of each species in the SORTIE model without performing detailed field studies of trees damaged by ice storms.

2.2.1.2. Crown reduction and the probability of short-term mortality. Percentages of crown reduction were determined for each tree species and for each diameter class according to the work by Brisson et al. (1999). After the 1998 ice storm, Brisson et al. (1999) characterized the damages caused to trees in Boisé-des-Muir, Quebec, into five classes of crown reduction: 0–5, 2–25, 25–50, and 100% of crown reduction. For each species and for each of three diameter classes, they enumerated all individuals affected by each damage class. We obtained the percentage of damaged trees for three of the tree species that are included in the SORTIE model: sugar maple, American beech and eastern hemlock (Table 2). Because we could not integrate all the information presented in Table 2 in the simulations, it has been condensed to determine the percentages of crown reduction (PCR) by species and diameter class (Table 3).

Table 1
Average susceptibility of tree species to ice storm damage (updated from Seischab et al., 1993)

Studies	1	2	3	4	5	6	7	8	9	10	11	
Year of the ice storm	1998	1997	1991	1986	1979	1976	1973	1956	1948	1936	1923	
Location	QC	MI	NY	OH	VA	WI	CT	WV	NH	PA	WI	
	Study 1	Study 2	Study 3	Study 4	Study 5	Study 6	Study 7	Study 8	Study 9	Study 10	Study 11	Mean
Degree of ice storm susceptibility determined for each study												
Black cherry (*Prunus serotina*)			3	2		3	2	3	3	3	3	2.8
Poplar (*Populus* spp.)			2		3	3			3	3	3	2.8
Willow (*Salix* spp.)			3							3		3.0
Elm (*Ulmus* spp.)	3	3	1						3	2	3	2.4
American linden (*Tilia americana*)		3	2						3	3		2.8
Red maple (*Acer rubrum*)	2		2	2	1	2	3			2		2.0
Sugar maple (*Acer saccharum*)	2	2	2			2	1		2	1		1.7
American beech (*Fagus grandifolia*)		2	2	2		2	1		2	2		1.9
Red and black oaks (*Quercus rubra* and *Q. velutina*)		2	3	1	2	2	2		2			2.0
Birch (*Betula lenta* and *B.* spp.)			1			3	1			1		1.5
White oak (*Quercus alba*)	2	1	1	1	1					1	1	1.0
Hickory (*Carya* spp.)	1	1	1		1	1	2		1	1	1	1.2
Eastern hemlock (*Tsuga canadensis*)			1	3						1		1.5
Ash (*Fraxinus* spp.)		2	1	1		3	2		1	1		1.6

Values were obtained from 11 studies in eastern North America: (1) Brisson et al. (1999); (2) Rebertus et al. (1997); (3) Seischab et al. (1993); (4) Boerner et al. (1988); (5) Whitney and Johnson (1984); (6) Bruederle and Stearns (1985); (7) Siccama et al. (1976); (8) Carvell et al. (1957); (9) Lemon (1961); (10) Downs (1938); (11) Rogers (1923). Location of study sites: QC = Québec (Canada); MI = Michigan (USA), NY = New York (USA), OH = Ohio (USA), VA = Virginia (USA), WI = Wisconsin (USA), CT = Connecticut (USA), WV = West Virginia (USA), NH = New Hampshire (USA), PA = Pennsylvania (USA). Ice storm susceptibility: 3 = highly susceptible, 2 = moderately susceptible and 1 = low susceptibility.

Table 2
Tree damage caused by the 1998 ice storm at the Boisé-des-Muir, Québec (from Brisson et al., 1999)

	15–20 cm DBH					20–35 cm DBH					>35 cm DBH				
	1	2	3	4	5	1	2	3	4	5	1	2	3	4	5
Sugar maple	36.3	37.4	15.4	4.4	6.6	6.5	23.1	48.7	20.6	1.0	0.2	5.9	72.0	20.9	0.9
American beech	26.5	24.5	21.2	15.9	11.9	9.4	12.3	34.1	41.3	2.9	0.0	9.6	55.8	30.8	3.8
Eastern hemlcok	83.3	12.1	4.5	0.0	0.0	80.0	15.6	4.4	0.0	0.0	29.2	70.8	0.0	0.0	0.0

Percent of trees was calculated for three diameter classes (DBH) and for five damage classes (1–5), representing reductions in crown size: 1 = <5%, 2 = 5–25%, 3 = 25–50%, 4 = >50% and 5 = 100%. Only species included in the SORTIE model are presented here.

Table 3
Percentage of crown reduction (PCR) and the probability of short-term mortality (PSTM) by diameter class (DBH) for sugar maple, American beech and eastern hemlock, using Eq. (1)

Species	15–20 cm DBH		20–35 cm DBH		>35 cm DBH	
	PCR	PSTM	PCR	PSTM	PCR	PSTM
Sugar maple	14.0	0.07	33.2	0.01	40.1	0.01
American beech	20.1	0.12	34.3	0.03	39.2	0.04
Eastern hemlock	3.4	–	4.1	–	10.6	–

The equation used to calculate PCR for sugar maple, beech and eastern hemlock is:

$$\text{PCR} = (\text{DC1} * 0) + (\text{DC2} * 0.15) + (\text{DC3} * 0.4) + (\text{DC4} * 0.5) \quad (1)$$

where DC1, DC2, DC3 and DC4 represent the percentage of trees in each of four damage classes, one to four, respectively (Brisson et al., 1999). The multipliers 0, 0.15, 0.4 and 0.5 represent the 'average' percentage of damaged crowns in each of the first four damage classes. The fifth damage class corresponds to a crown reduction of 100% and was used to develop the probability of short-term mortality (PSTM) for the three species (Table 3). PSTM represents the chance that a tree will die from its damages in the same year that the ice storm occurred.

The percentage of crown reduction and the probability of short-term mortality for red maple, red oak, white ash, black cherry and yellow birch (Table 4) were estimated based on comparisons to sugar maple and beech. Eastern hemlock was not taken into account in Eqs. (2) and (3). Since conifers can better support ice weight than deciduous trees, using the PCR of eastern hemlock would have underestimated the PCR of deciduous species. We used the following equations to estimate PCR and PSTM for each of the above species:

$$\text{PCR} = \frac{S \times (\text{PCR sugar maple} + \text{PCR beech})}{1.7 + 1.9} \quad (2)$$

$$\text{PSTM} = \frac{S \times (\text{PSTM sugar maple} + \text{PSTM beech})}{1.7 + 1.9} \quad (3)$$

where S corresponds to the average susceptibility of a given species (Table 1) and where 1.7 and 1.9 represent average susceptibility of sugar maple and beech,

Table 4
Percentage of crown reduction (PCR) and the probability of short-term mortality (PSTM) by diameter class (DBH) and species, using Eqs. (2) and (3)

Species	15–20 cm DBH		20–35 cm DBH		>35 cm DBH	
	PCR	PSTM	PCR	PSTM	PCR	PSTM
Black cherry	26.4	0.14	52.1	0.03	61.6	0.04
Red maple	18.9	0.10	37.2	0.02	44.0	0.03
Red oak	18.9	0.10	37.2	0.02	44.0	0.03
White ash	15.1	0.08	29.8	0.02	35.2	0.02
Yellow birch	14.2	0.08	27.9	0.02	33.0	0.02
White pine[a]	3.4	–	4.1	–	10.6	–

[a] White pine was the only species in which crown reduction and short-term mortality could not be calculated or found in the literature. Given that few data are available for this species, it was assumed that white pine exhibited the same effects as eastern hemlock. Values of crown reduction and mortality for eastern hemlock were therefore assigned to white pine.

respectively. The values for these two species were used in Eqs. (2) and (3) because they have similar susceptibility.

Data for white pine is not presented in Table 1. As a result, we could not use the preceding equations to develop values for mortality and crown reduction for this particular species. It was decided to arbitrarily assign the same PCR and PSTM values to white pine as were calculated for eastern hemlock since these two species were conifers and showed low susceptibility to ice damage.

2.2.1.3. Probability of long-term mortality. Calculation of the probability of long-term mortality (PMLT) is based on the positive linear relationship between the percentage of crown reduction and PMLT. Relatively few data were available concerning the long-term mortality of trees as a result of ice storm disturbance. A report prepared by the Ministry of Natural Resources (2000) estimated that 28% sugar maples that were moderately affected (41–60% of crown reduction) by the ice storm would die within 5 years following the ice storm. Based on this information, the probability of long-term mortality (PMLT) for trees greater than 20 cm DBH was calculated for each species (Table 5):

$$\text{PLTM} = \frac{\text{PCR of given species} \times 0.28}{\text{PCR of sugar maple}} \tag{4}$$

For trees less than 20 cm DBH, no probability of long-term mortality was derived since this category of trees is considerably less affected by crown reduction (Table 3). They tend to either bend or break due to the ice weight.

Table 5
Probability that trees will die within 5 years following the ice storm (probability of long-term mortality; [PLTM]) for each tree species included in the SORTIE model

Species	PLTM (%)
Sugar maple	28.0
American beech	27.3
Eastern hemlock	7.4
Black cherry	43.0
Red maple	30.7
Red oak	30.7
White ash	24.6
Yellow birch	23.6
White pine	7.4

2.2.1.4. Increase in understory light availability. Finally, given that light is a fundamental component of the SORTIE model, it is crucial that light availability in the understory brought about by modifications to trees to simulate ice storm damage is comparable to that observed in the field. Brisson et al. (1999) found that the light availability at 4 m in height was five times higher after the ice storm in 1998 than in 1995. This information will be considered during the sequence of operations required to simulate ice damage in Section 2.2.3.

2.2.2. New parameter files

In order to represent forest stands that have sustained ice storm damage in SORTIE, it was necessary to create a new parameter file in which trees have reduced crowns. SORTIE is limited to a maximum number of 16 species in the parameter file. Presently, there are nine species included and only seven can be added. Each species has a list of parameters that control the behavior of all individuals. In order for individuals of the same species to exhibit different behaviors, it is necessary to represent a species by more than one list of parameters. To represent the difference in susceptibility among size classes, individuals of one species were divided into two diameter classes (Table 6): those with a DBH < 20 cm and those having a DBH ≥ 20 cm.

Table 6
Crown radius to diameter ratios assigned to each species and diameter class for the different modelling scenarios performed in this study

No.	Species	DBH (cm)	Crown radius to diameter ratio	
			Default	Scenarios I and II
1	Red maple	<20	0.108	0.081
2		≥20		0.046
3	Sugar maple	<20	0.107	0.088
4		≥20		0.051
5	Yellow birch	<20	0.109	0.089
6		≥20		0.062
7	American beech	<20	0.152	0.112
8		≥20		0.075
9	White ash	<20	0.095	0.076
10		≥20		0.051
11	Black cherry	<20	0.116	0.076
12		≥20		0.023
13	Red oak	<20	0.119	0.090
14		≥20		0.051
15	White pine	All	0.087	0.075
16	Eastern hemlock	All	0.100	0.860

White pine and eastern hemlock were not divided into two groups because of the limitation of 16 species/size groups and they exhibited comparatively less susceptibility to ice damage than the other species in the model.

A ratio of crown radius to DBH was then assigned to each of the 16 species (or size groups). This ratio predicts crown width as a function of DBH. We hoped to represent, at least in part, the differences in susceptibility to ice storms observed between size classes by assigning different ratios to individuals of the same species and by relating this to the level of crown reduction observed by Brisson et al. (1999) and calculated in Table 3.

The new ratios of crown radius to DBH were calculated using the following equation:

$$\text{Ratio} = \frac{F * ((\text{Normal crown radius})^2 * \text{PCR})^{1/2}}{\text{DBH}} \quad (5)$$

where F is a coefficient of adjustment which adjusts the ratios in order to obtain the 500% increase in light quantity observed by Brisson et al. (1999) at 4 m in the understory. For trees with a DBH < 20 cm, the PCR used to determine the ratio is the one attributed to the class '15–20 cm' in Tables 3 and 4. For trees with a DBH equal or superior to 20 cm, the PCR used is the one attributed to the class 'more than 35 cm' also in Tables 3 and 4. For white pine and eastern hemlock, the PCR for stems greater than 35 cm DBH was used to calculate the crown radius to diameter ratio for all individuals.

2.2.3. Sequence of operations undertaken to simulate ice storms

Fig. 1 illustrates the series of operations that were undertaken to simulate a forest stand damaged by a severe ice storm. This was done for each model simulation. The forest stands were modified for a period of 5 years since it has been proposed that understory light conditions return to pre-disturbance conditions during this time period due to the renewal of branches.

The first step in order to modify an ice-damaged stand was to execute a SORTIE simulation using the default parameter file (unmodified) until the stand has attained the desired stage of succession (after 300 years). At this time, the tree map file (TMF) 'A' and the GLI (global light index) map 'A' at 4 m are created by SORTIE. The TMF is a list of data (e.g. spatial coordinates, DBH, height and species) concerning all of the individuals present in the forest stand. The map of GLI values is two-dimensional and illustrates the distribution of light levels (in units of percent of full sunlight) at a specified height in the understory. Next, a program was executed using IDL 5.4^{TM} software, which used the probability of short-term tree mortality to remove all trees from the TMF 'A' that died immediately after the ice storm occurred. This computer program also divided species into diameter classes in order to obtain the 16 individual groups that comprise the modified parameter file. Then, the resulting TMF 'B', reflecting the modified parameters, is registered in SORTIE and the GLI map at 4 m is extracted again. The average

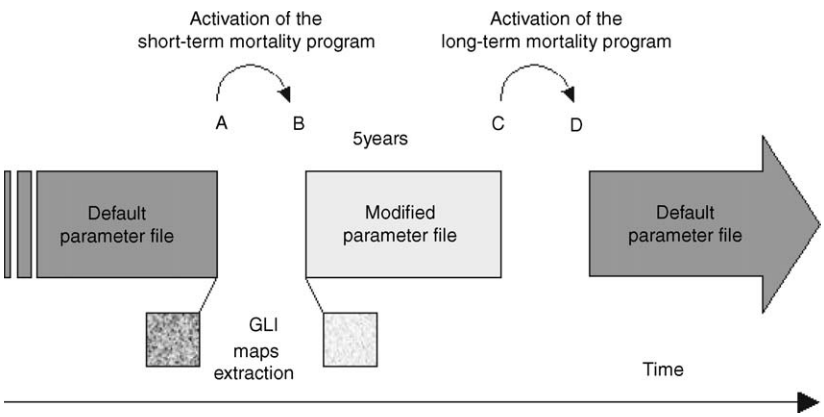

Fig. 1. Schematic diagram of the procedures performed to temporarily transform an undisturbed forest stand into a stand that has been severely damaged by an ice storm. TMF represents the "tree map file" and GLI represents "global light index ".

percentage of light availability at 4 m was calculated for the initial GLI map 'A' as well as for the second GLI map 'B'. If the increase in light availability, resulting from changes made to the forest stands, agreed with the 500% observed by Brisson et al. (1999), the modified parameter file was saved (in practice, an increase in light availability of 490–510% was accepted). If this was not the case, the coefficient of adjustment, *F*, was changed and the process was repeated until the desired light conditions were attained. Once an appropriate modified parameter file was identified from this process, the SORTIE model was executed for a period of 5 years. After this time, the model was stopped and a new TMF 'C' was produced. A second program using the probability of long-term mortality was initiated which removed all trees that died 5 years after the ice storm from TMF 'C'. At the same time, the program regrouped individuals of different diameter classes into one species, which restored nine species in the parameter file. Finally, TMF 'D' was produced, the standard file of parameters for SORTIE was registered, and the forest simulation was initiated.

2.3. Scenarios

Three scenarios were developed in this study. The first scenario was designed to examine forest succession after a severe ice storm. Specifically, we examined how tree species dynamics evolved after we modified forest stands to resemble ice-damaged stands. In the second scenario, we hoped to deepen our understanding of how the spatial distribution of trees influences tree species dynamics after disturbance. Finally, a control scenario (no ice storm) was designed for each of the two initial scenarios presented above. Thirty replicates (i.e. simulations) were performed for each scenario.

For each simulation and for each scenario, SORTIE was run for a period of 300 years using the default parameter files of the model. Initial conditions of the simulation included densities of 900 seedlings per hectare (100 seedlings/species/ha), which were randomly distributed. Ménard et al. (2002) showed that after 300 years, the structure and density of the species in forest stands are not affected by the initial conditions of the simulation. The characteristics of forest stands after 300 years of simulation are presented in Table 7.

For the first scenario, the processes described in Section 2.2.3 were performed on 300-year-old stands and then the model was run for a period of 2000 years using the default parameter files. In the second scenario, the spatial coordinates of all individuals within the 300-year-old stands were systematically assigned using an IDL program. This was done to create a forest stand with uniformly distributed trees. To ensure that the spatial distribution of individuals was the only difference between scenarios I and II, values of crown reduction

Table 7
Structure and composition of the 300-year-old forest stands that were generated by SORTIE to represent initial conditions (before the ice storm simulation)

Species	Seedling density			Sapling density[a]			Tree density[b]		
	Absolute (seedlings/ha)	STD	Relative (%)	Absolute (saplings/ha)	STD	Relative (%)	Absolute (trees/ha)	STD	Relative (%)
Red maple	23.4	3.5	3.2	0.6	0.3	0.8	3.6	0.5	2.7
Sugar maple	28.5	4.8	3.9	1.0	0.4	1.3	5.5	0.6	4.1
Yellow birch	42.8	9.3	5.9	3.1	0.9	3.9	13.5	2.8	10.1
American beech	160.7	14.0	22.2	32.6	3.6	41.4	31.5	2.9	23.7
Eastern hemlock	227.0	23.6	31.3	27.1	6.0	34.4	28.5	3.4	21.5
White ash	39.4	5.6	5.4	0.6	0.4	0.8	5.8	0.9	4.3
Black cherry	65.7	9.7	9.1	4.5	1.3	5.8	22.2	3.4	15.9
White pine	86.8	11.7	12.0	5.8	1.3	7.3	12.6	1.6	9.5
Red oak	50.0	7.7	6.9	3.4	1.1	4.4	10.8	1.7	8.1
Total	724.2	90.0	100	78.8	15.4	100	133.8	17.8	100

Total basal area (m^2/ha) for trees > 15 cm DBH: 66.0, STD: 5.1; average GLI at 4 m in the understory: 1.22, STD: 2.5. STD represents the standard deviation of the mean.

[a] Individuals with DBH ≥ 2.0 and <15.0 cm.

[b] Individuals with DBH ≥ 15.0 cm.

were the same in both scenarios. Therefore, modified parameter files used in scenario I were also used in scenario II. The level of increase in light availability was not considered during the steps to modify stands in scenario II. When the period of transformation was completed, the model was run for a period of 2000 years. For scenarios I and II, the values of F used in Eq. (5) were 1.3.

For the control scenarios, a copy of the initial TMF 'A' for each of scenarios I and II was registered in SORTIE and the model was then run for 2000 years using the default parameter files. For the control scenario for scenario II, the spatial coordinates of individuals were changed systematically within the TMF 'A' to give a uniformly distributed stand before the simulations were run.

Statistical analyses were performed using paired sample T-tests ($\alpha = 0.1$).

3. Results and analyses

Results obtained for each of the scenarios I and II, in comparison with the control scenario, are presented in the following two sections.

3.1. Scenario I: heterogeneous stand

Statistical analyses revealed that during the first 250 years following the ice storm, the species-specific densities of seedlings, saplings and trees in forest stands that had experienced a severe ice storm were significantly different than in control forests (T-test; $\alpha = 0.1$). The period of time during which this difference was observed varied according to species and diameter class. After 300 years, there were very few differences in species-specific densities between the control and the ice-damaged forests (Fig. 2).

3.1.1. Tree species dynamics during the first 300 years

Figs. 3–5 illustrate tree species dynamics for 300 years after an ice storm disturbance in terms of changes in the density of trees, saplings and seedlings.

We observed that mature tree density decreased in disturbed stands 5 years after the ice storm (Fig. 3). This phenomenon can be explained by the short-term and long-term mortality of trees that were severely damaged by the ice storm. Following this drop in density, a recruitment of adult individuals of all species was observed in the ice-damaged stands. A maximum density was attained for each species at approximately 55 years after the ice storm. Black cherry, beech and hemlock showed the largest increases in density. This recruitment of adult individuals may be attributed to the increase in light levels in the understory from damaged tree crowns. In SORTIE, the increase in light

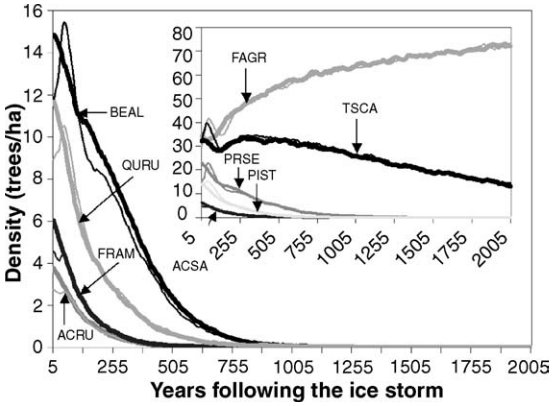

Fig. 2. Species densities over 2000 years of forest succession following the simulation of a severe ice storm: outcome of scenario I. Bolded lines represent mature tree densities in the control stands while unbolded lines are densities in the ice-damaged stands. *Acer saccharum* (ACSA), *Acer rubrum* (ACRU), *Fagus grandifolia* (FAGR), *Quercus rubra* (QURU), *Tsuga canadensis* (TSCA), *Pinus strobus* (PIST), *Prunus serotina* (PRSE), *Betula alleghaniensis* (BEAL), *Fraxinus americana* (FRAM).

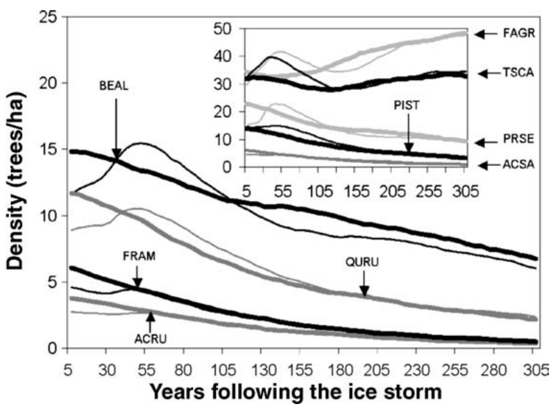

Fig. 3. Mature tree densities over 300 years of forest change following the simulation of a severe ice storm. See Fig. 2 for the legend.

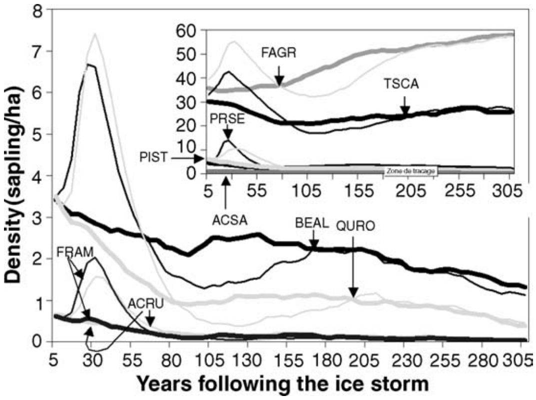

Fig. 4. Sapling densities over 300 years of forest change following the simulation of a severe ice storm. See Fig. 2 for the legend.

availability favors the growth and survival of seedlings and saplings. These higher light levels for 5 years following the ice storm and consequent improved growth and survival of young trees (Fig. 4) may have resulted in higher numbers of individuals reaching the forest canopy.

Between 100 and 200 years after the ice storm (Fig. 3), tree density was either significantly lower (yellow birch, beech, black cherry), equal (sugar maple, red maple, white ash and eastern hemlock) or was higher (white pine, red oak) than the control forest stands. In the former case, the decline in density of trees can be explained by two phenomena. First, seedling density decreased following the transformations made to the stands to simulate ice storm damage (Fig. 5). This decrease in seedling numbers occurred to species that had short-term and long-term mortality probability greater than 7.4 % (Tables 3–5). When the number of mature trees was reduced by the mortality relationships, seedling production was also decreased because there were fewer mature trees in the forest to produce seedlings. Consequently, fewer trees were able to reach the forest canopy, causing the decrease in density of developing stands. Secondly, it is likely that light levels at the forest floor in ice-damaged forests have dramatically decreased 55 years after the ice storm given the high densities of trees at this stage in forest development. This reduction in light availability would be detrimental to the growth and survival of individuals in the understory. This same phenomenon could explain why the density of saplings decreases slightly after 30 years of forest development (Fig. 4).

3.2. Scenario II: uniform distribution

As in scenario I, there were significant differences in species-specific densities between stands modified by ice storm damage and the control stands. However, these differences were evident throughout the full duration of the model simulation (Fig. 6).

Like in scenario I, mature tree densities of several species decreased immediately after the ice storm as a result of the mortality functions. This was also followed by an increase in tree densities (Fig. 7); although

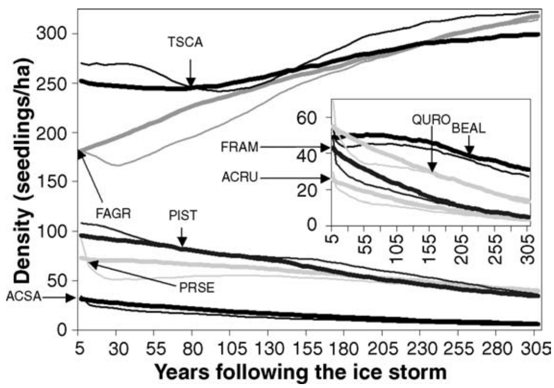

Fig. 5. Seedling densities over 300 years of forest change following the simulation of a severe ice storm. See Fig. 2 for the legend.

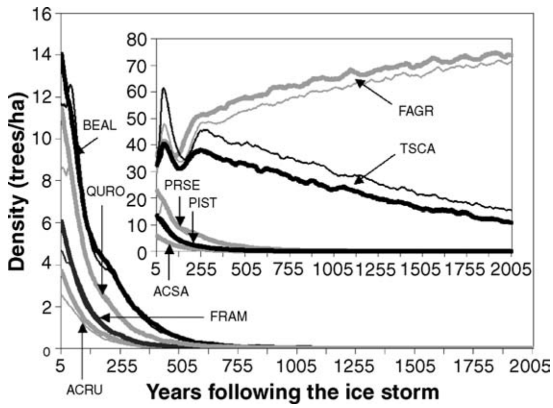

Fig. 6. Species densities over 2000 years of forest succession following the simulation of a severe ice storm in a uniformly distributed stand: outcome of scenario II. See Fig. 2 for the legend.

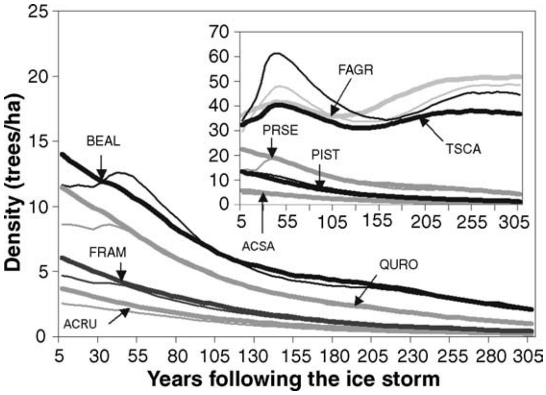

Fig. 7. Mature tree densities over 300 years of forest succession following the simulation of a severe ice storm in a uniformly distributed stand: outcome of scenario II. See Fig. 2 for the legend.

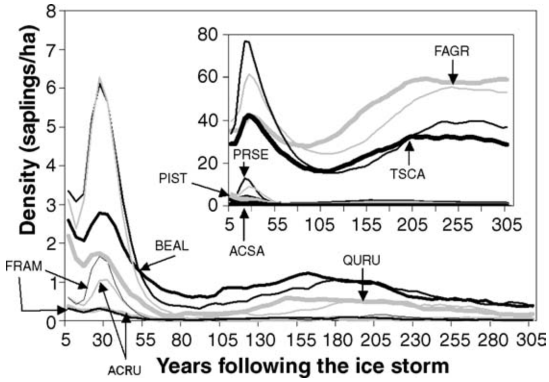

Fig. 8. Sapling densities over 300 years of forest succession following the simulation of a severe ice storm in a uniformly distributed stand: outcome of scenario II. See Fig. 2 for the legend.

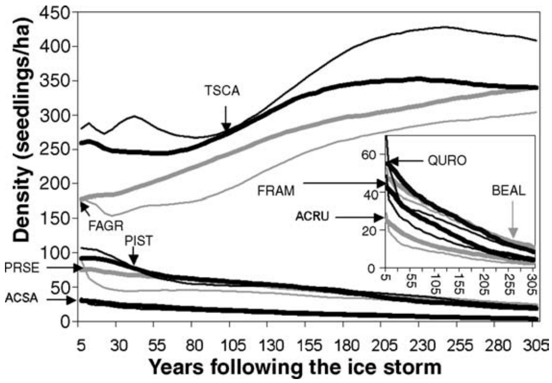

Fig. 9. Seedling densities over 300 years of forest succession following the simulation of a severe ice storm in a uniformly distributed stand: outcome of scenario II. See Fig. 2 for the legend.

increases were not as pronounced as in scenario I for black cherry, American beech, red oak, yellow birch, red maple and white pine. In contrast, eastern hemlock showed a great increase in density in scenario II. Differences in the spatial distribution of the trees likely explain the different tree species dynamics observed in scenarios I and II. Individuals of a given species were more likely to cluster in scenario I compared to scenario II. In scenario I, the increase in light levels in the understory was concentrated where the tree species most affected by the ice storm were clustered. The seedlings of these species benefited from the increase in light availability given that they were located close to their parents (in accordance with the recruitment function of the model). In contrast, the change in light conditions had little effect on seedlings of species that were less affected by the ice storm, resulting in limited growth of seedlings of these species. In scenario II, seedlings, saplings and trees were distributed more uniformly within the forest matrix, which results in a uniform distribution of light levels. Consequently, seedlings of all tree species had the same chance of being exposed to increased light conditions. The species seedlings subjected to the most favorable light conditions overall would have greater increases in densities at the expense of other species. In scenario II, light conditions created by the ice storm favored the development of young hemlock individuals (Figs. 8 and 9) so hemlock densities were significantly higher during the entire period of simulation than they were at the time that the ice storm occurred (Fig. 6).

4. Discussion and conclusion

4.1. Inter-specific successional dynamics

Overall, we observed six patterns of post-ice storm tree dynamics (Fig. 10). However, other responses can be observed when site conditions, tree species and the severity of ice storm damage are different. Additionally, it would be wrong to conclude, on the basis of our results, that a given species adopts one particular response following an ice storm. For this reason, the six post-ice storm dynamics that we observed are presented in a general manner, accompanied by the conditions that can lead a species to adopt a particular pattern of response.

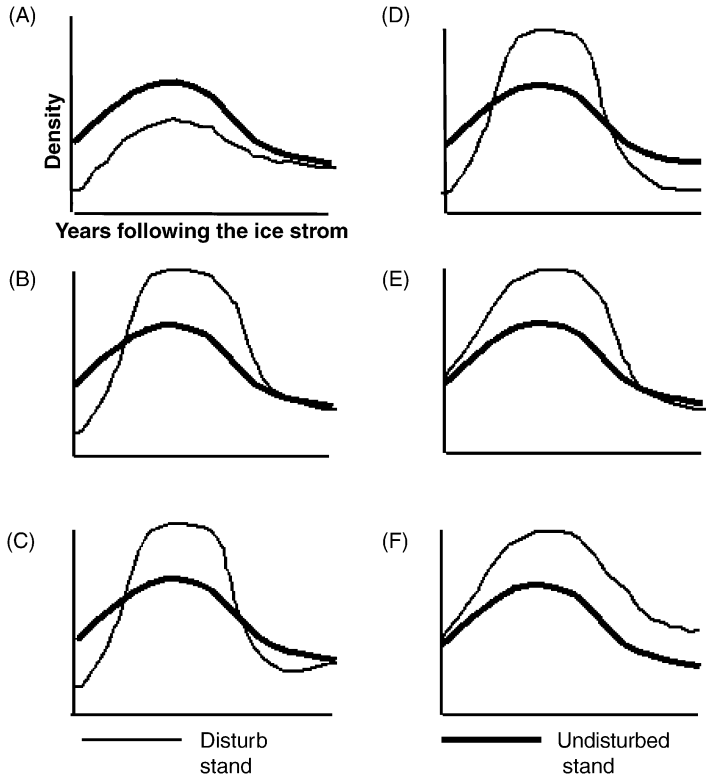

Fig. 10. Simplified representation of six types of tree dynamics following a severe ice storm disturbance.

The species that adopt the patterns A, B, C and D of Fig. 10 sustain a decrease in density during the first years following the ice storm. These species are moderately to severely susceptible to ice storm damage. The type of behavior adopted (A, B, C or D) following this immediate decline in density depends on the growth potential of the species. In A, the potential for growth was low since density remained lower than in control stands for a certain period of time before recovering. The maples showed this response in scenarios I and II. In the case of B, C and D, the potential for growth of species was higher. In fact, following the initial drop in density caused by the ice storm, the density increased and remained higher than the control stands for a certain period of time. This increase in density can be explained by the strong response of advanced regeneration to canopy openings caused by the ice storm. Following this rise in density, patterns B, C and D differ. In B, densities were restored to the same levels as in control stands while in C and D, the densities returned to significantly lower levels than found in control stands. In C, tree density remained lower for a while before recovering, but in D, it remained lower than the control densities for the entire simulation. One can expect that the canopy closure that occurred 55 years after the ice storm, when tree densities were at their maximum, could have caused, after a delay, this return to low densities in patterns B, C and D. When the stand density was high, the canopy was closed and the seedlings grew slowly in the understory. If the species was sufficiently shade-tolerant, its chances of adopting dynamic B were greater because seedlings will survive during this period of canopy closure. If the species was not shade tolerant, patterns C and D were exhibited. Beech showed behavior C during scenario I (Fig. 3), and behavior D in scenario II (Fig. 4). In the second scenario, where extreme conditions favored high densities of hemlock, densities of beech were very low. Finally, patterns E and F illustrate the response of species that showed low susceptibility to ice storm damage. These species also responded well to forest canopy openings. When conditions were very favorable for these species, pattern F was adopted. That is, the species was found at higher densities in the ice-damaged stand throughout the period of simulation. Eastern hemlock exhibited this response in scenario II. When conditions were slightly less favorable for the species, species showed a great increase in density, which was then followed by a decline to levels similar to control stands. Eastern hemlock showed this pattern in scenario I.

4.2. Ecological interpretations

The type of response adopted by a species therefore depends on species-specific characteristics and life history traits such as shade tolerance, crown damage sustained from the ice storm, growth rates, crown openness, abundance and spatial distribution of regeneration and trees. Indeed, tree species composition and spatial distribution can influence the strength and the type of response adopted by a species. Consequently, it is possible that within a particular stand, the response of a species to the ice storm may vary depending on its location within the stand. This result supports the work of DeSteven et al. (1991) and Irland (2000) who reported that the ice storms can delay forest succession in certain cases by creating canopy openings and favoring early successional species, while in other cases, increase the rate of succession by damaging early successional species.

The lack of any long-term effects on the structure and composition of this temperate deciduous forest following such a severe ice storm may seem surprising at first. However, these forests tend to be very resilient to autogenic and allogenic factors (Webb and Scanga, 2001). The severe ice storm reported here had only a limited effect on light availability and long-term tree mortality. Obviously, 5 years of increased light availability, even if the increase is as much as 500%, is not enough to trigger large changes in species composition and structure. In our modeling experiments, we did not examine the effect of ice storms on soil disturbance because we believed that ice storms do not normally disturb the soil. Lack of long-term responses can also be explained by the absence of a dense understory shrub and tree vegetation in the model. Dense shurb and tree understory can be found in other similar hardwood forests of eastern North America (Beaudet and Messier, 2002; Majcen and Richard, 1992). Dense understory vegetation has been shown to rapidly occupy the understory following any dramatic increase in light availability (Beaudet and Messier, 2002). Many shade intolerant species such as *Quercus, Betula* and *Fraxinus* did initially increase their seedling and sapling densities following the ice storm, but the lack of any subsequent major disturbance presumably impeded further development of this functional group in our simulations.

This simulation study supported dendrochronological and simulation studies in old-growth temperate deciduous forests (Woods, 2000a,b; Brisson et al., 1994; Poulson and Platt, 1996; Pacala et al., 1996) that found that extremely shade tolerant species such as *Fagus grandifolia* and *Tsuga canadensis* would tend to completely dominate these forests if catastrophic or episodic large-scale disturbances do not occur regularly. Our work also supported Webb and Scanga (2001) who proposed that patch dynamics do not always result in an increase in shade intolerant species as has been traditionally believed (Pickett and White, 1985). We therefore agree with them that stand structural and compositional patterns following such a severe ice storm depend on a suite of factors that include: initial density and spatial distribution of shade tolerant understory shrub species, seedlings, saplings and mature trees of different species, crown cover of different species, inter-specific differences in susceptibility of tree crown and tree mortality to ice storm damage, growth and survival rates in different light environments.

4.3. Contribution brought to ecological modeling

The purpose of modeling is to capture the essential characteristics of a system in order to better understand how it works. Models are used as exploring tools to decipher the dynamics of a system, determine the key parameters that are responsible for its functioning and maintenance, and test what-if scenarios to evaluate the consequences of particular actions on the system. Models seldom provide unequivocal answers, but rather are useful at opening our mind to new conceptual frameworks and hypotheses that could be further tested in a more rigorous manner (Landsberg, 2003; Grimm, 1999).

SORTIE belongs to a specific class of models referred to as individual-based models (IBMs), in which a discrete individual that has at least one unique characteristic is the fundamental modeling unit. Such a unique feature might simply be its spatial location (Berek, 2002). In contrast to top-down models that aim at developing a general conceptual framework applicable to virtually all kinds of populations and ignore individual variability, IBMs are at the foundation of the bottom-up approach, which goal is to determine what individual properties and actions are essential for generating the characteristics of the population dynamics (Fahse et al., 1998). An IBM takes explicitly into account four main elements: the unique individuals composing a population, the individual's life cycle, the number of individuals rather than the population density, and the resource available in the system (Uchmanski and Grimm, 1996). SORTIE is also a spatially explicit (individual trees have a unique location), a dynamic (describes how the state of a system changes across a time span), and an empirical model (based on multivariate regressions fitted on data acquired from field measurements). While such models are dependent on the dataset used for parameter fitting, they can be very accurate in their predictions and can be judiciously applied to investigate the likely response of a system to changes in a range of environmental situations (Porté and Bartelink, 2002; Robinson and Ek, 2000; Jarvis, 1993).

Progress achieved in ecological modeling through the use of IBMs such as SORTIE can be described within a paradigmatic and a pragmatic perspective, according to the terms proposed by Grimm (1999). Individual-based modeling is part of a novel paradigm in ecology and other sciences that considers individual variability, local interactions, and the explicit consideration of space as key components to generate the global dynamics of a system. SORTIE has all the characteristics to contribute to this new kind of scientific investigation that may lead to a different view and understanding of forest dynamics.

From a pragmatic point of view, some research questions related to forest dynamics are almost impossible to test in the field because they would require a high amount of resources and a period of time that might extend a life span. It is the case with the investigation of the impact of severe disturbances like ice storms. Also, the influence of external factors such as climatic changes may jeopardize the conclusions of a long-term study. To address these research questions, a model like SORTIE represents a valuable tool to test different scenarios, verify hypotheses proposed by earlier researchers, and generate new insights about species responses and global forest dynamics that could be further tested in a more rigorous manner using field data.

Our study revealed that the response of a tree species to the ice storm depends on species-specific characteristics and life history, and may vary depending on its location within a stand. Such a result represents a typical contribution that can only be achieved with the use of an individual-based, spatially explicit model. It can lead to a systematic investigation in the field, and contribute to a significant increase in knowledge about species response to ice storm and potentially other kinds of forest disturbances.

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