

Release episodes at the periphery of gaps: a modeling assessment of gap impact extent

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Abstract: Gaps are recognized as important features of temperate forest 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). However, to truly define gap extent, the peripheral impact of gaps on the trees has to be considered. This study was undertaken to characterize the impact extent of gaps on their periphery using the SORTIE forest succession model. The sapling growth responses to gaps of different sizes (500–2000 m²) was used as an indicator of the impact extent. Ten replicates of a simulation (for each gap size) were performed (305 years, 25-ha lattice). Gaps were introduced after 300 years. Growth ratios (pregap/postgap growth) for each sapling were computed and compared with a release threshold to determine sapling release episodes. These release episodes were analyzed to assess the extent of gap impact. Results indicate that gap effect extends significantly into the adjacent forest. Release episode orientations are concentrated in the northern hemisphere of gaps, and release episodes mostly appear in the first 20 m from gaps. Based on different degrees of release occurrence, new gap areas were defined and compared with areas from existing gap definitions. The differences are substantial and reveal that gap spatial extent observed through release patterns surpasses gap areas defined by traditional definitions.

Résumé : Les trouées sont reconnues comme des composantes importantes de la dynamique des forêts feuillues tempérées et ont été très étudiées au cours des dernières décennies. Leur définition a évolué, passant de la simple projection verticale de l'ouverture dans la canopée à une vision plus fonctionnelle (trouée étendue et trouée étendue spécifique). Cependant, pour véritablement définir l'étendue spatiale des trouées, l'impact sur les arbres en périphérie doit être considéré. L'objectif de cette étude est de caractériser l'étendue de l'impact périphérique des trouées par l'intermédiaire du modèle de succession forestière SORTIE. La croissance des gaules en réponse à des trouées de différentes dimensions (500–2000 m²) a été utilisée comme indicateur de l'impact. Dix réplicats d'une simulation (pour chaque taille de trouées) ont été effectués (305 ans; matrice de 25 ha). Les trouées ont été introduites après 300 ans. Des ratios de croissance (croissance pré-trouée/post-trouée) pour chaque gaule ont été calculés et comparés à un seuil théorique de regain de croissance pour relever les épisodes de regain de croissance des gaules. Ces épisodes ont été analysés pour caractériser l'impact des trouées. Les résultats indiquent que les épisodes de regain de croissance se concentrent surtout dans l'hémisphère nord de la périphérie et dans les premiers 20 m autour des trouées. Sur la base de différentes intensités de regain de croissance, de nouvelles superficies de trouées ont été calculées et celles-ci s'avèrent substantiellement plus grandes que les superficies basées sur les définitions traditionnelles des trouées.

Introduction

In forest science, gap is a concept 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, lightning, insects, ice storms, 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; Withmore 1989). They represent the first step towards tree maturity for saplings (Canham 1988; Poulson and Platt 1989), alter light regimes (Chazdon and Fetcher 1984; Canham 1988), and help diversify forest species composition (Runkle 1985; Lorimer 1989; Spies and Franklin 1989; Withmore 1989). Silvicultural treatments represent a management tool designed to help gap phase species regeneration (Gouvernement du Québec 1997) and enhance productivity (Coates and Burton 1997) or the presence of old-growth forest features (Runkle 1991). Some of the gaps designed by forest managers are similar to natural gaps in terms of size and shape. However, 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, 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 1980s, Runkle pioneered

Received 4 December 2001. Accepted 21 May 2002.
Published on the NRC Research Press Web site at
<http://cjfr.nrc.ca> on 7 September 2002.

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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 precludes 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 to a more functional one. This approach puts aside the traditional view of the forest as a uniform matrix perforated by discrete gaps and accentuates a vision of interacting gaps that create complex forest dynamics (Lieberman et al. 1989). Sharing this vision, we advocate that gap impact on tree growth on gap periphery is substantial and extends considerably into the adjacent forest. Therefore, the entire surface where gaps translate into enhanced tree growth should be included into a realistic gap definition.

This evolution in the conceptualization of gap is very recent and partly explains the lack of knowledge about the external impact of gap. Most of the gap studies of the last decades have focused on gap inner processes and on gap cumulative global impact on forests. Knowledge about gap 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 gaps they produce 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 gap presence be felt?

Another reason explains this absence of studies on gap periphery: the experimental limitations of field studies. Field studies that locally investigate gap dynamics are normally characterized by tedious data collecting periods and by limited spatiotemporal dimensions. Runkle’s (1990) longitudinal study of 36 forest gaps is a good example of this situation. Spanning over 12 years, this study of gap 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 pioneering 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;

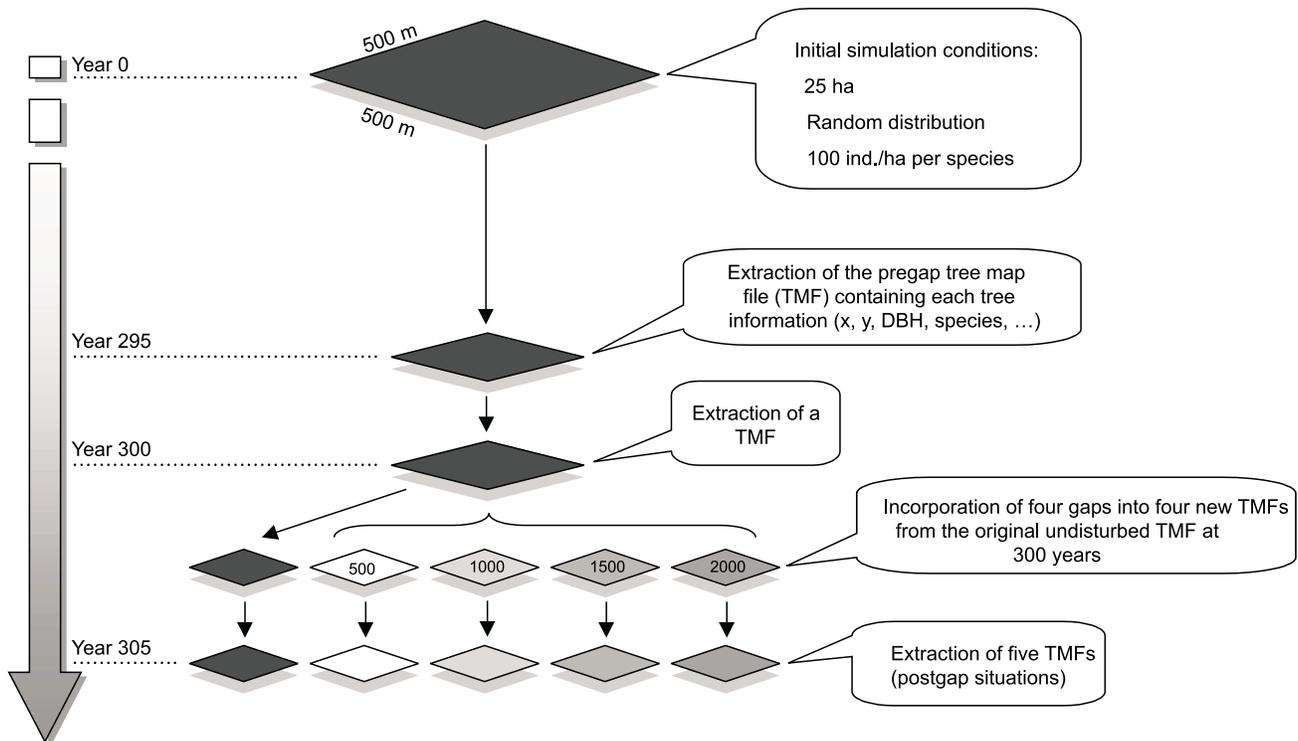
FORSKA, Leemans and Prentice 1989). More recent models (e.g., FORMOSAIC, Liu and Ashton 1998; LANDIS, He et al. 1999) tackle larger observation scales and incorporate more spatial interactions but they still discretize space. Also, in all these models, the role of individual trees, the true key players 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 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 gaps. 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 gaps on their periphery through sapling growth reaction. Specifically, the sapling release episodes located outside gaps of varying sizes (500–2000 m²) are used as indicators of gap 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 2–15 cm are considered saplings. The decision to only study sapling release responses is based on two facts: (i) adult trees will practically never be affected by gaps, since they already have access to abundant light; and (ii) 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 spatial configuration of release episodes (distance from gap and orientation) by gap sizes and species.

Methodology

SORTIE BC version 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 5 years, but space is continuous, tridimensional, and explicitly considered. For every time step, SORTIE uses the following five operating submodels (in order of their execution): (i) harvesting, applies any pre-defined harvest regime; (ii) 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; (iii) tree growth, as a function of the GLI values; (iv) reproduction, seedling recruitment as a function of par-

Fig. 1. Illustration of the experimental framework.

ent tree proximity; and (v) tree mortality, as a function of previous growth rates and stochasticity.

The nine species modeled by SORTIE are the following: *Acer rubrum* L., *Acer saccharum* Marsh., *Betula alleghaniensis* Britt., *Fagus grandifolia* Ehrh., *Fraxinus americana* L., *Pinus strobus* L., *Prunus serotina* Ehrh., *Quercus rubra* L., and *Tsuga canadensis* (L.) Carrière. Simulations were performed using a toroidal matrix of 500 × 500 m (25 ha) over a temporal extent of 305 years, and all nine species were used to ensure realistic stand composition. Also, the forests simulated are all considered by the model to be at 41°30'N.

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. 2002). 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 gaps. Therefore, 10 replicates of a simulation characterized by an initial random distribution of individuals (DBH randomly distributed between 0.2 and 3 cm) and a density of 100 individuals/ha per species were performed. The simulation was then stopped after 295 years (time step No. 59) for the extraction of a tree map file (TMF) representing the pre-gap situation. A TMF is a file generated on request by SORTIE that contains information (spatial coordinates, DBH, height, species) on every individual on the matrix at that moment. The simulation was restarted for another 5 years (time step No. 60) and at that time (year 300) another TMF was extracted. Using a programming software, 4 new TMFs were created from each of the 10 TMF extracted at 300 years. By removing all the indi-

viduals inside a matrix-centered circle of 12.615, 17.841, 21.851, and 25.231 m radius, gaps of 500, 1000, 1500, and 2000 m², respectively, were artificially introduced into the forest scene. These gap areas are closer to Runkle's extended gap than to his canopy gap definition. The modified TMF and the undisturbed one were then reentered into SORTIE and simulated for another 5 years, until year 305 (time step No. 61). At that point, five new TMFs containing the post-gap information were finally extracted.

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

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 et al. 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 times 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-gap growth (300 – 295) and

the postgap growth (305 – 300) were established. A growth ratio was then computed by dividing the postgap growth by the pregap 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 gap scenario and did not have one in the associated no-gap scenario, then this tree had experienced a release episode entirely caused by the gap. By comparing the gap scenario release values to their no-gap counterparts, the release episodes naturally occurring in the forest matrix were left aside and only the true outside gap impact was captured.

Results and analysis

A total of 331 sapling release episodes were found in the 40 disturbed forest scenes created by the 10 replicates and the 4 gap sizes. These release episodes are first analyzed by gap sizes to examine the relationship between gap size and peripheral impact intensity, extent, and orientation. Then, they are analyzed by species to verify if specific differences exist for these three attributes.

Sapling release episodes by gap sizes

The distribution of the 331 release episodes by gap sizes for the 10 replicates is the following: 500 m², 29; 1000 m², 81; 1500 m², 113; and 2000 m², 108. On average, 2.9, 8.1, 11.3, and 10.8 saplings experience release in the periphery of gaps. To verify if the increasingly larger gaps had a significant impact on the number of release episodes, *t* tests for mean comparison ($\alpha = 5\%$) were performed. Only the mean for 500 m² is significantly different from the others, revealing that the number of episodes may be reaching a plateau from 1000 to 2000 m².

Where are these release episodes located in terms of orientation and distance from the gaps? To answer this question, space in the periphery of gaps was discretized by dividing the spectrum of orientations into six sectors of 60°, and the distance from gaps into six rings of 5 m. For each of the resulting 36 spatial sections, the number of release episodes was divided by the number of present saplings. These release relative frequencies indicate the intensity of the release process in each section and the general spatial configuration of release in relation to gap sizes. Figure 2 shows maps of release relative frequencies for the four gap sizes. These maps reveal a northern and southern hemisphere dichotomy, a relative east–west spatial symmetry, and the presence of highest release relative frequency in the first 5 m of the northern sector. These observations are consistent with light regimes around gaps at the latitudes of northern hardwood forest (Canham et al. 1990).

The map for 500 m² shows few release episodes, a weak east–west axis, and an overall discontinuous impact. The 1000-m² map reveals a considerable increase in release relative frequencies, an intensification of the release impact in the first 10 m (mainly in the northern hemisphere), and few episodes in the southern hemisphere. 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 northern 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 northern hemisphere (over 50% in the first 10 m).

While these maps illustrate the general behavior of release episodes in gap periphery, Figs. 3 and 4 present a more detailed analysis of the distance from gaps and orientation, respectively. Figure 3 shows that gap 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 gap 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 gap sizes have similar behaviors with values under 10%.

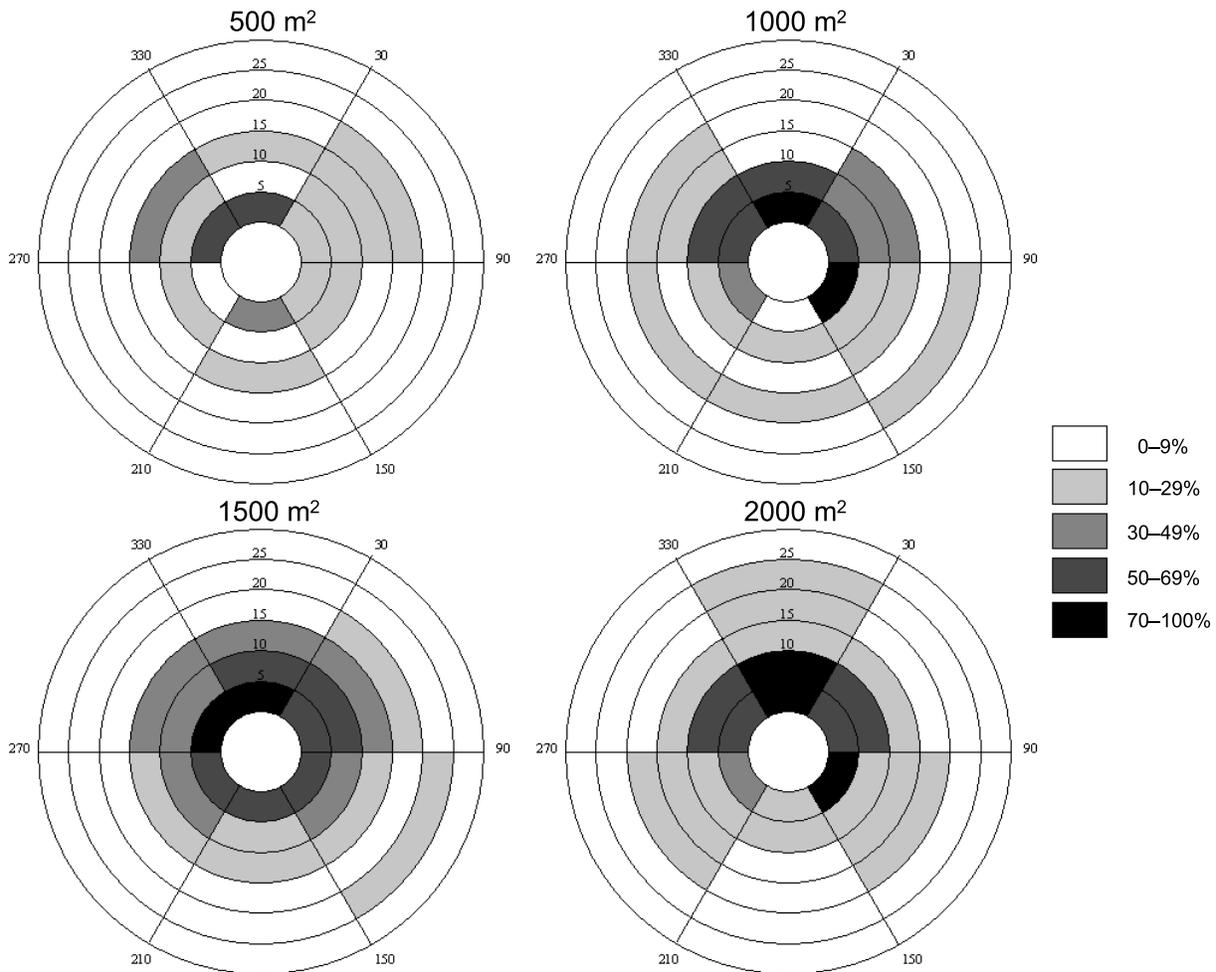
Why is the 500-m² distribution so different from the others in the first 10 m while similar after that? This situation could be explained by the presence of diffuse and direct-beam radiation. Diffuse radiation drops off uniformly in all directions with increasing distance from the gap center (Canham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

Figure 4 reveals the orientation distributions of release relative frequencies for each gap size. 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 gaps, the northwestern and northeastern sectors have the highest release proportion, while it is the northern sector who takes over in the 1500- and 2000-m² gaps. The values for northwestern and northeastern sectors remain constant after 1000 m², while the northern sector reaches values over 30% for the same gap sizes. Again, the direct-beam radiation could explain this transition. This radiation forms a horizontal ellipse of increased illumination in the northern hemisphere outside of gaps (Canham et al. 1990). However, the highest light values are located in the ellipse centre, right in the northern sector. These values get so high as gap size increases that a very large proportion of the saplings in the first 10 m of the northern sector experience release episodes, therefore elevating the release percentage of the whole north sector. Finally, as mentioned earlier, very small episode frequencies (around 5–10%) are present in the southern hemisphere (southwestern, southeastern, and southern sectors).

Sapling release episodes by species

The distribution of the 331 release episodes by species is the following: *F. grandifolia*, 150; *T. canadensis*, 88; *Pinus strobus*, 39; *Q. rubra*, 34; *Prunus serotina*, 16; other species, 4. These results reveal that of the mean of 8.275 episodes per gap, almost half are *F. grandifolia* (3.75 per gap or 45.3% of the episodes), one-quarter are *T. canadensis* (2.2 per gap or 26.6% of the episodes), and all the other species make up the last quarter (2.325 per gap or 28.1% of the episodes). The group of all other species can be viewed as a

Fig. 2. Spatial representation of release relative frequencies for the four gap sizes. The percentages in the key are calculated from the following equation: (no. of release episodes/no. of saplings) × 100.



group of more shade-intolerant species than *F. grandifolia* and *T. canadensis*, who are the two most shade-tolerant species in North America temperate forest. These proportions are in good agreement with simulation species densities (*F. grandifolia*, 42%; *T. canadensis*, 32%; and the other species, 26%). Since the trees of a particular replicate can have experienced release episodes in more than one gap size, it is imperative that we interpret the results both by species and by gap size. However, this obligation splits our sampling size by 12 (three species × four gap sizes) instead of four as in the preceding section. Therefore, orientations and distance from gap classes were respectively grouped to preserve satisfactory sample sizes.

Figure 5 illustrates the penetration of the release episodes into the forest in relation to species. The three graphs show the same overall behavior. After an initial 10 m with values around 50%, the release 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 gap 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- to 30-m distance class reveal important species differences. While *T. canadensis* and the other species do not surpass the 20-m mark, *F. grandifolia* presents release relative

frequencies around 5%. This situation is consistent with species knowledge. *Fagus grandifolia* is the most shade-tolerant species of the model (Tubbs and Houston 1990) and possesses the smallest probability of mortality at zero growth (Pacala et al. 1996). Therefore, its 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 release orientation. The highest release relative frequencies for *F. grandifolia* are located in the northwestern and northeastern sectors. Also, the southern hemisphere for this species has release frequencies that are high compared with the other species. This leads to the conclusion that the diffuse radiation created by gaps is sufficient for *F. grandifolia* to achieve release even to the south. *Tsuga canadensis* exhibits a dual behavior. In the first two gap sizes, the northwestern and northeastern sectors are dominant, and in the last two sizes, it is the northern sector who is. Also, the release frequencies of this species in the northern sector are the highest release proportions by sector of any species, with values surpassing 40 and 60%. The release proportions of the other species also exhibit a dual behavior, but the transition from the northwestern and northeastern sectors to the northern sector takes place at the 1000-m² gap size. Contrary

Fig. 3. Release relative frequencies by distance from gap for the four gap sizes. The percentages on the ordinate are calculated from the following equation: (no. of release episodes/no. of saplings) × 100.

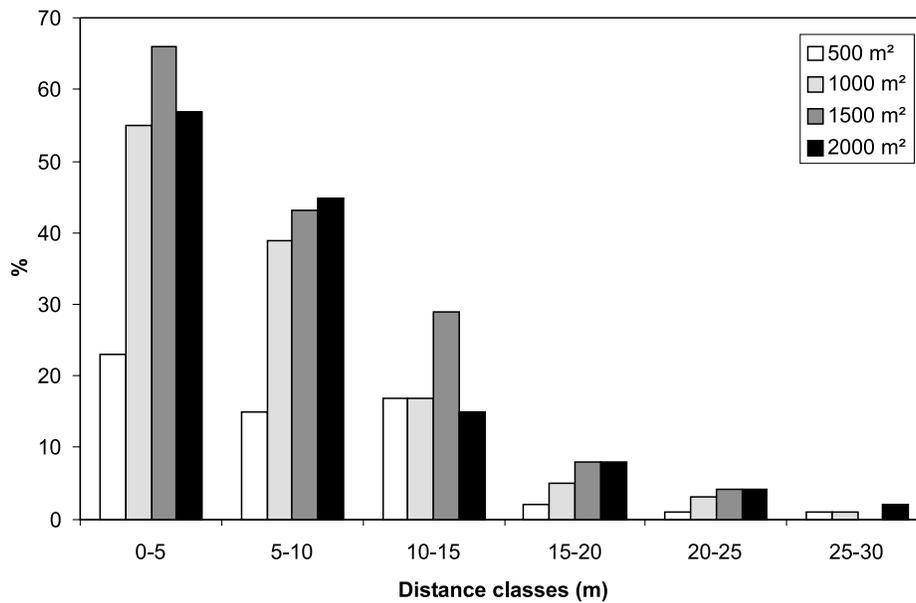
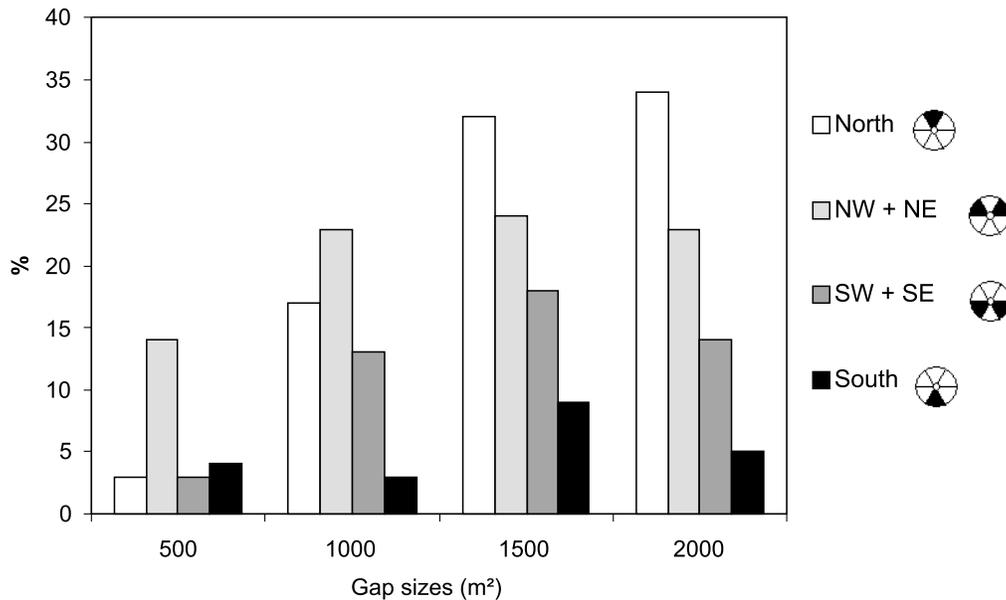


Fig. 4. Release relative frequencies by orientation sectors for the four gap sizes. The percentages on the ordinate are calculated from the following equation: (no. of release episodes/no. of saplings) × 100.



to *F. grandifolia*, *T. canadensis* and the other species seem to benefit from the increase of direct-beam radiation as gap sizes increase.

Finally, Fig. 7 shows each species proportion in the number of release episodes by gap sizes compared with 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 gaps did not have any favorable impact on any species, the species proportions in the number of release episodes would be equivalent to their proportions in the simulation matrices. *Fagus grandifolia* is advantaged by gaps but this advantage vanishes

(from 55 to 41%) as gap sizes increase. The reverse situation is present for *T. canadensis*, with its proportion in release episodes rising to the matrix mean as the gap sizes increase (from 24 to 32%). The other species combined have a behavior somewhat similar to *T. canadensis* with the exception that their proportions in release episodes surpass their matrix mean (from 21 to 28%). Again, *T. canadensis* has a behavior closer to the other species than to *F. grandifolia*. Traditionally, small gaps 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 Fig. 7.

Fig. 5. Release relative frequencies by distance from gap for the three species. The percentages on the ordinate are calculated from the following equation: (no. of release episodes/no. of saplings) × 100.

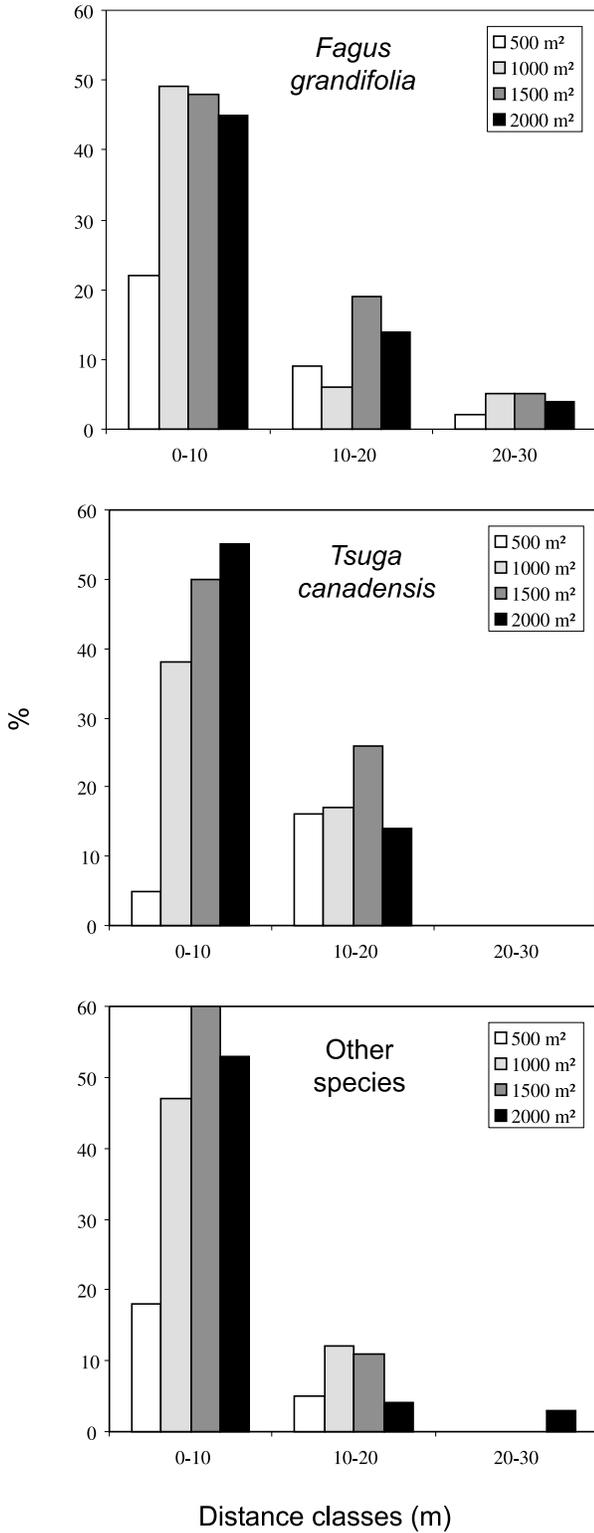


Fig. 6. Release relative frequencies by orientation sectors for the three species. The percentages on the ordinate are calculated from the following equation: (no. of release episodes/no. of saplings) × 100.

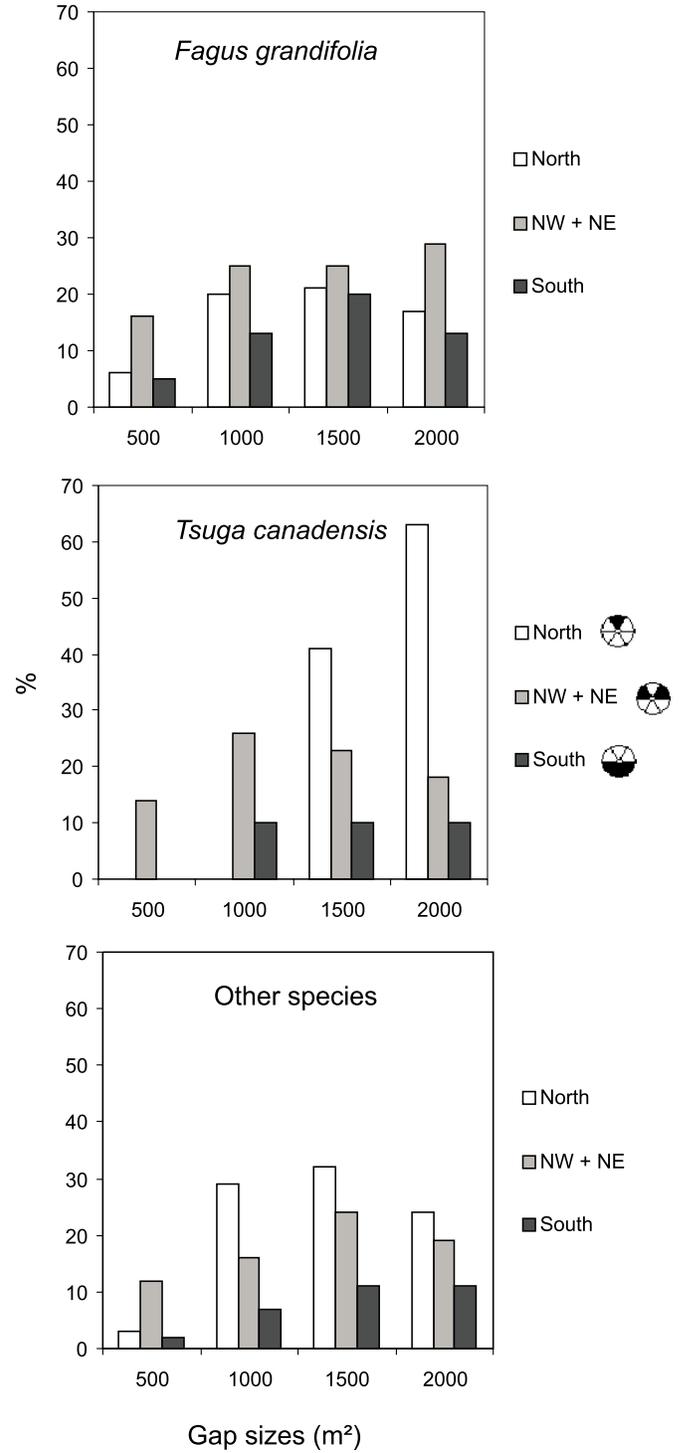


Fig. 7. Species proportions in release episodes and simulation matrices.

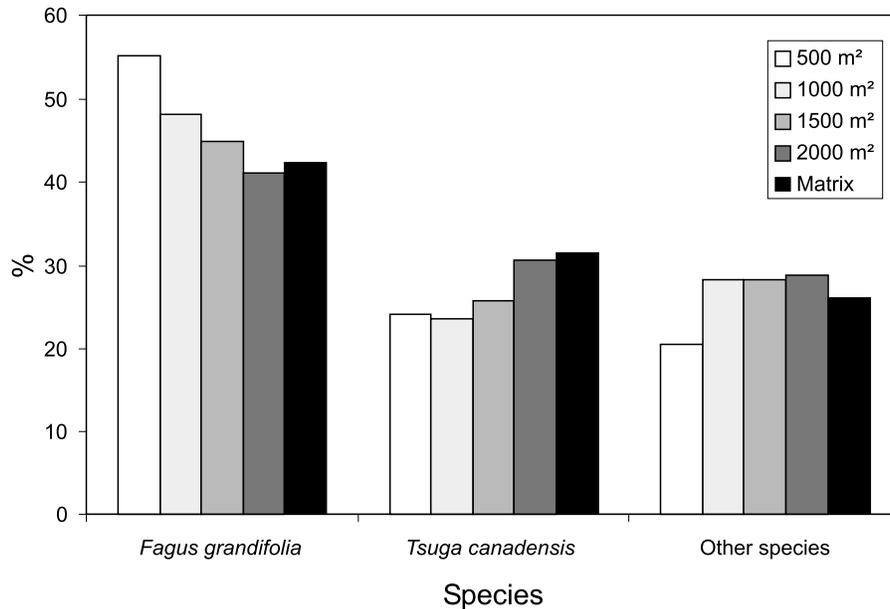
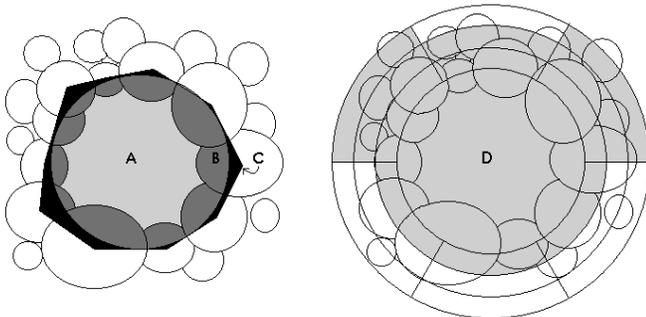


Fig. 8. Schematic representation of gap definitions: (A) canopy gap; (B) our experimental gap; (C) extended gap; and (D) release-extended gap.



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 gap 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 gap concept, nothing has been done to quantify the reaction of saplings in gap periphery. The results presented here offer an interesting picture of gap external impact on release 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 gap size and extent debate.

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 con-

frontation 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 with field knowledge.

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

The release results related to species behavior can also be explained by field knowledge. Release episodes for *F. grandifolia* occur further from the gaps than those of all the other species (Fig. 5). This situation arises because very small increases in light can trigger important growth responses in *F. grandifolia* (Canham 1989) and because a small growth looks important in comparison with this species very low growth under the canopy. However, as a true shade tolerant, *F. grandifolia* does not react to more intense light increases. This situation explains his low release proportions in the northern sector and his relatively strong release presence in the southern hemisphere (Fig. 6). *Tsuga canadensis* is also classified as a shade tolerant, but in contrast with *F. grandifolia*, its reaction to small light increases is slow (Canham 1989), while more intense increases affect it greatly (specimens planted for horticultural purposes; A. Bouchard, personal observations). Those circumstances explain this species strong release proportions in the northern sector (Fig. 6). Finally, the other species (mainly *Pinus*

Table 1. Gap sizes according to definitions (m²).

Gap type	Nominal gap size (m ²)			
	500	1000	1500	2000
Mean canopy gap	256	653	1114	1552
Experimental extended gap ^a	500	1000	1500	2000
Experimental extended gap + 70% RRFA ^b	500	1213	1755	2461
Experimental extended gap + 50% RRFA	658	1691	2572	3093
Experimental extended gap + 30% RRFA	868	2089	3571	3238
Experimental extended gap + 10% RRFA	1996	3567	4702	5800

^aSizes close to extended gap definition.

^bRelease relative frequency areas: areas of Fig. 2 where the release relative frequencies are superior to the percentage mentioned.

strobis, *Prunus serotina*, and *Q. rubra*) are considered more shade intolerant than the other two species, and this trait is apparent in the release episodes. Like *T. 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 gap edges (after 20 m) are not sufficient to generate a release ratio superior to 2.5 (Fig. 5). Moreover, shade-intolerant species usually react favorably to high illumination environments; this fact explains why their highest release proportions are in the northern sector. Still, these proportions are smaller than the ones obtained by *T. canadensis* because of these species superior baseline growth.

From extended gap to release-extended gap

The major contribution of this research lies in its examination of gap impact extent as a new basis for gap definition. The gap concept has largely evolved 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 resource regime alterations caused by gaps 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 gap local studies and the real extent and size of gaps.

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

The areas are presented in Table 1. First, the relationship between the experimental gap areas and the mean of their associated canopy gap areas agrees 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 gap 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 gap areas and the areas generated by the addition of peripheral areas of release proportion levels. As the release proportion criterion is lowered, the resulting areas increase consequently (e.g., the 50% release area contains the experimental gap areas and the sections with release 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 gap size depending on the initial experimental gap. The areas expand 30–71% if the 50% and more sections are included, and 190–290% if we go down to the 10% threshold. The areas in which gaps are felt can be almost four times larger than Runkle's extended gap.

Thus, release areas represent an important region and should receive considerations in any gap-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 release-extended gap could lead to a reconsideration of forest-management treatments, since reduced sizes of gaps can produce similar impacts. Also, this innovative vision of gaps may encourage ecologists to reexamine some gap theories and conclusions. Among them is the gap partitioning theory (Denslow 1980; Runkle et al. 1995; Kobe 1999) from which our results could be extended to the peripheral areas of gaps and the spatial interactions of the gaps and their global impact on forest dynamics. Much work has to be done on forests ecosystems and the gaps that drive them to detail, extend, and revisit the gap notion in this new perspective.

Acknowledgements

The authors are very grateful to the team at the Geocomputing Laboratory in Montréal for its assistance and support. A special thank to three colleagues for their critics and comments (S. Banal, C. Le Guerrier, and M. Tremblay). This research has been funded by a Natural Sciences and Engineering Research Council of Canada (NSERC) scholarship awarded to A.M. and a NSERC research grant awarded to D.J.M.

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