

UNIVERSITÉ DU QUÉBEC À MONTRÉAL

ÉVALUATION DU RÉGIME DE PERTURBATIONS NATURELLES
PAR PETITES TROUÉES DANS LES FORÊTS
DE SAPINIÈRES À BOULEAU BLANC ET À BOULEAU JAUNE
EN GASPÉSIE, QUÉBEC

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
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AOÛT 2005

REMERCIEMENTS

Je voudrais remercier les personnes qui ont rendu possible mon étude de la forêt durant les deux dernières années. Le directeur du Groupe de Recherche en Écologie Forestière interuniversitaire (GREFi), Docteur Christian Messier, qui m'a accueilli au sein de cet organisme. La Chaire Industrielle en Aménagement Forestier Durable (Chaire AFD), le gouvernement du Québec (Bourses de recherche en milieu de pratique, du Fonds pour la Formation de Chercheurs et l'Aide à la Recherche (FCAR)), et la compagnie Produits Forestiers Temrex (division Gaspésie), qui m'ont généreusement offert un soutien financier. J'ai apprécié surtout l'assistance des ingénieurs forestiers Philippe Leblanc, Damien Allard et Katherine Court de la compagnie Temrex.

Je voudrais particulièrement remercier mon directeur d'étude, Docteur Daniel Kneeshaw, qui m'a toujours soutenu, avec générosité dans ses conseils, et pour sa patience, tout en appliquant la pression nécessaire. Je remercie mon co-directeur, Docteur Yves Bergeron, et les membres de mon comité d'orientation, les Docteurs Brian Harvey, Louis De Grandpré et Han Chen pour la correction de mes rapports. Plusieurs étudiants travaillants dans le laboratoire du Dr. Kneeshaw m'ont beaucoup aidé, et sans leur assistance mon travail aurait été au moins considérablement plus difficile. Les doctorants et post-doctorants Docteur Yves Claveau, Docteur Ernest Lo, Patrick Lefort, Gerardo Reyes et particulièrement Mathieu Bouchard. Je salue et remercie au passage ceux à la maîtrise, et ceux en voie de l'être ou qui ont terminé, Dominic Sénécal, Vincent D'Aoust, Ève Lauzon, Jonatan Belle-Isle, Iulian Dragotescu et Julie Mercier. David Lagacé, Maude Beauregard et surtout Frédéric Lewis qui m'a offert son assistance inestimable lorsqu'il le fallait, ont été des aides de terrain très appréciés. Je voudrais remercier Susana Maya. Finalement je voudrais remercier mes parents et mes frères pour leur soutien et leur générosité.

AVANT PROPOS

Cette étude a été conçue, comme d'autres projets de recherche au sein du Groupe de Recherche en Écologie Forestière interuniversitaire (GREFi) et de la Chaire industrielle en Aménagement Forestier Durable (Chaire AFD), avec l'intention de développer éventuellement des méthodes d'aménagement forestier écosystémique, c'est-à-dire un aménagement qui se base sur et cherche à imiter jusqu'à un certain point les caractéristiques du régime des perturbations naturelles de la forêt. Notre projet constitue une évaluation préliminaire des caractéristiques et des conséquences des perturbations par petites trouées dans la canopée, dans plusieurs types de forêts en Gaspésie. Les connaissances sur les perturbations secondaires dans la forêt boréale ne sont pas très développées, encore moins en Gaspésie où il se fait relativement peu de recherche sur la forêt. Malgré les grands espaces de la péninsule habités par l'homme, l'impact de l'exploitation industrielle de la forêt est considérable, et il est impératif d'étudier les vestiges de forêts encore plus ou moins intactes pour pouvoir encore concevoir une gestion proche de la nature.

L'auteur de ces lignes a proposé et réalisé les études décrites dans ce mémoire, avec l'assistance de son directeur Dr. Daniel Kneeshaw et co-directeur Dr. Yves Bergeron. Le présent document est composé de trois chapitres, chacun écrit en anglais et sous forme d'article à soumettre pour publication dans une revue scientifique. L'introduction et la conclusion générales, ainsi que le résumé, sont en français. Un abrégé des hypothèses émises et des résultats obtenus est placé au début de chacun des trois chapitres. Les textes de chaque volet sont par ailleurs structurés pareillement, comprenant les sections Introduction et objectifs d'étude, Aire d'Étude, Méthodes, Résultats, et Discussion. Six appendices présentent des informations supplémentaires sur la méthodologie, ou bien mettent en lumière certains aspects du régime limitrophes aux sujets spécifiquement mentionnés mais qui sont tout de même importants à considérer.

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Résumé

La préservation des attributs essentiels et l'aménagement efficace de la forêt nécessitent une connaissance approfondie de l'état et du fonctionnement de la forêt dite naturelle. L'étude des processus de mortalité des arbres est une approche intéressante, puisque ces événements déclenchent et contrôlent le taux et les caractéristiques du remplacement des arbres. Les régimes de perturbations naturelles de petites envergures dans la forêt boréale nord-américaine sont peu connus, surtout ceux de la région gaspésienne où pourtant l'hétérogénéité de l'environnement rendrait l'exercice particulièrement profitable.

Dans cette étude le régime de perturbations naturelles par petites trouées (<0.1ha) dans les Sapinières à bouleau blanc et à bouleau jaune en Gaspésie (Canada), entre 140m et 770m d'altitude, a été évalué à partir de transects linéaires dans 27 sites. Trois sujets sont spécifiquement étudiés. Le premier chapitre vise à vérifier l'importance des trouées pour le fonctionnement de la forêt, dans le but d'assurer qu'une évaluation de la dynamique des petites trouées peut être utile. Dans le deuxième chapitre, la variabilité régionale des régimes de perturbations par petites trouées est expliquée en considérant certaines caractéristiques dendrométriques et environnementales. Dans le troisième chapitre, la cause de mortalité des arbres de la canopée, le patron temporel des perturbations, et l'impact du régime de perturbations sur l'évolution de la forêt sont considérés.

Sans toutefois jouer un rôle crucial, les trouées ont eu un effet quantifiable sur l'établissement, la composition, la structure et le taux de croissance des arbres en sous-bois. La récente épidémie de la Tordeuse des bourgeons de l'épinette (Tbe) (1973-1991) est la principale cause de mortalité des arbres, suivi par le vent. Les trouées ont des caractéristiques (dimension, orientation, forme géométrique) semblables parmi les sites, mais la sévérité des perturbations varie grandement (18% à 64% de forêt ouverte) et est en moyenne élevée (42%). Les sapinières pures sont généralement moins perturbées, bien qu'elles aient été proportionnellement plus attaquées par la Tbe. Les peuplements sont plus perturbés lorsqu'ils sont composés en partie d'épinettes noires (*Picea mariana* (Mill.) B.S.P.), sont plus affectés par le vent, et sont localisés sur les versants ouest. Il est surprenant que les peuplements davantage perturbés n'étaient pas davantage composés de sapins baumiers (*Abies balsamea* (L.) Mill.) et qu'ils n'avaient pas été plus sévèrement attaqués par la Tbe. Il est surprenant aussi que l'altitude des sites n'ait eu aucun effet sur la sévérité des perturbations. En moyenne 2.1% de la forêt est ouverte annuellement, mais le taux est très variable durant cette période, principalement à cause de l'activité de la Tbe. Le sapin est l'espèce dominante des arbres morts (72%) et des arbres en régénération (77%), soit en proportion beaucoup plus élevée que dans la canopée actuelle (57%). Dans les peuplements mixtes ou composés d'épinettes noires, des cohortes de sapins très distincts de la composition générale du peuplement ont été tués pour par la suite être remplacés par une composition semblable. Dans les peuplements composés de sapins et d'épinettes blanches la régénération dans les trouées est davantage dominée par le sapin. Dans les sapinières pures, le bouleau blanc devient plus abondant à la suite des perturbations, mais seulement temporairement. En général la tendance historique vers une plus forte abondance de sapins est soutenue par un régime de perturbation par petites trouées, et continuera pour atteindre graduellement un équilibre lorsque les peuplements deviendraient des sapinières pures. Contrairement à ce qu'on s'attendait, ni l'activité de la Tbe ni la petite dimension des trouées sont déterminantes pour le recrutement du sapin.

Nos résultats suggèrent qu'un programme d'aménagement forestier écosystémique, basé sur des coupes partielles imitant les petites trouées naturellement produites, devra considérer une grande variabilité de dimensions de trouées. Parmi les dimensions de trouées considérées dans cette étude (<0.1ha), la plupart sont très petites. Un certain nombre de trouées plus grandes seront nécessaires afin de maintenir des arbres d'essences héliophiles dans le couvert. En termes de caractéristiques de trouées individuelles, la dimension, la forme et l'orientation des trouées varient peu parmi les différents types

de forêt et d'environnements. La cause mortalité des arbres a un effet sur la composition des arbres recrus, mais pas toujours de façon attendue. La vitesse de rotation des peuplements purs de sapins est plus lente que pour les autres types de peuplements. Selon les méthodes de récolte de bois utilisées, il pourrait être intéressant de s'inspirer du regroupement spatial de sapins dans les peuplements d'épinettes noires ou d'arbres décidus qui subissent une révolution plus rapide que dans le reste du peuplement.

INTRODUCTION GÉNÉRALE

Cette étude est le fruit de plus de deux ans de travail (2001-2003) visant à décrire et à évaluer les régimes naturels de perturbations par petites trouées dans la région de Baie-des-Chaleurs en Gaspésie, dans l'Est du Canada. On a voulu premièrement vérifier s'il est raisonnable de tenir compte des trouées individuelles pour expliquer le fonctionnement de ces forêts, deuxièmement identifier les facteurs associés à la variabilité spatiale du régime des trouées, et troisièmement décrire la variabilité temporelle récente du régime de perturbations et aborder quelques explications sur son impact sur l'évolution de la forêt.

Le contexte et la justification de l'étude

La majorité de la forêt boréale naturelle a comme origine immédiate une perturbation sévère, principalement des feux, des épidémies d'insectes et des chablis. Ces perturbations créent une certaine homogénéité structurelle et de composition sur des étendues plus ou moins grandes (Bergeron *et al.* 2002). Lorsque ces perturbations sévères occupent de plus petites superficies ou sont moins fréquentes, le renouvellement du couvert forestier se fait plutôt par des perturbations de petites échelles, où la mortalité des arbres se fait individuellement ou par petits groupes. Il se crée alors une hétérogénéité de la canopée forestière à l'intérieur d'un même peuplement forestier, prenant la forme d'une mosaïque constituée d'unités de forêt rendues à des stades de développement variables (White et Pickett 1985). Cette conception d'une dynamique de trouées ("gap dynamics" en anglais) a été présentée par Alex S.Watt (1947), qui utilisa le terme "patch" pour désigner ces unités de la mosaïque. Depuis ce temps, les termes "patch" et "gaps" sont utilisés, parfois de façon interchangeable, mais le plus souvent "patch" se réfère plutôt à de très grandes ouvertures de la forêt. Nous appelons "trouées" les ouvertures dans la canopée forestière, ce qui correspond généralement au terme "canopy gaps" utilisé dans la littérature scientifique anglophone. Ces trouées sont en fait des portions de la forêt qui n'ont pas encore atteint la maturité, soit le sommet de la canopée. Les petites ouvertures dans la canopée produisent des conditions de régénération différentes de ce qui existe lorsque presque tout le couvert forestier est éliminé simultanément, puisque la disponibilité de la lumière est un élément critique pour le développement de l'arbre (Canham *et al.* 1990; Leemans 1990; Gilbert *et al.* 2001). Pour cette raison, et par le fait qu'il s'agit souvent d'un assemblage de plusieurs types de perturbations dans un même

peuplement, une dynamique de petites trouées doit être considérée séparément d'une dynamique de "patch". Depuis au moins un siècle on étudie ce type de régime de perturbation en forêt tempérée (Pinchot 1905; Cooper 1913 dans Sprugel 1991; Aubréville 1938) et surtout, depuis quelques décennies, en forêt tropicale (Attiwill 1994). En ce qui concerne la forêt boréale (ou alpine), la part affectée par les grandes perturbations fait en sorte que la reconnaissance du rôle de régimes de petites trouées a été plus tardive (Battles et Fahey 1996; Kneeshaw et Bergeron 1998). Il y a eu toutefois certaines études précoces (Iwaschkewitsh dans Jones 1945; Sernander 1936 dans Liu et Hytteborn 1991). Une conscientisation des formes variées de la forêt boréale (et alpine), l'allongement du cycle des feux, et une meilleure compréhension de la dynamique de trouées ont mené plusieurs à s'y intéresser (MacCarthy 2001) en Europe (Kuuluvainen 1994; Holeksa et Cybulski 2001), en Asie (Yamamoto 1995; Taylor et Zisheng 1988) et en Amérique du Nord (White *et al.* 1985; Battles *et al.* 1995; Worrall et Harrington 1988; Foster et Reiners 1986).

Dans la forêt boréale de l'Est du Canada, plusieurs études ont été réalisées sur l'impact des épidémies de la Tordeuse des bourgeons de l'épinette (Tbe) (*Choristoneura fumiferana* Lem.), notamment en Gaspésie (Blais 1983) et au nord du Nouveau Brunswick (MacLean 1980), mais relativement peu d'études décrivent l'impact des vents (Ruel et Benoit 1999). Souvent l'évaluation concerne surtout les grandes ouvertures produites dans la forêt (ex.: Furayev *et al.* 1983). Certaines mémoires de maîtrise ont eu comme objectifs d'évaluer certains aspects de régimes de perturbations par petites trouées, notamment sur des forêts dans le Parc de la Gaspésie à plus de 650m d'altitude (en dehors de l'aire des épidémies de la Tbe) (Dansereau 1999), et dans le Parc Forillon (mais avec un aperçu sur toute la péninsule) (Lévesque 1997). D'autres études se concentrent sur les conditions de régénération produites par des petites trouées, afin d'améliorer le rendement des coupes de jardinage par exemple, mais peu cherchent à évaluer globalement les régimes naturels de perturbation malgré le fait que le concept de l'aménagement écosystémique soit répandu (Coates et Burton 1997; Lähde *et al.* 1999). L'étude de Kneeshaw et Bergeron (1998), qui porte sur la variabilité des régimes de petites trouées selon l'âge depuis feu des peuplements en Abitibi, est exceptionnelle par son traitement global du sujet et fut une inspiration lors de la conception de notre étude. Plusieurs études de régimes de petites trouées dans les forêts alpines et sub-alpines de la chaîne de montagnes des Appalaches aux Etats-Unis nous ont aussi été utiles, malgré l'absence d'épidémies de la Tbe et la présence d'espèces d'arbres légèrement différentes (ex.: Foster et Reiners 1986).

Faire une évaluation du régime de perturbations en Gaspésie est important et avantageux pour plusieurs raisons. Malgré les coupes forestières pratiquées sur une large portion du territoire, la forêt

couvre toujours plus de 95% du territoire et il subsiste encore des endroits peu ou jamais aménagés de façon industrielle à partir desquels il est envisageable de développer des méthodes d'aménagement écosystématique (CDDFG 2004). L'intervalle entre feux est plus long et les dimensions de brûlis sont plus petites dans cette partie de l'Est du Québec, en raison du relief relativement accidenté et du climat influencé par la proximité de la mer, ce qui a comme conséquence qu'une part particulièrement grande de la forêt est régie par des perturbations secondaires (Gauthier *et al.* 2001; Dansereau et Bergeron 1993; Bergeron et Leduc 1998; Bergeron 2000; Furayev *et al.* 1983; Kneeshaw 2001). L'étendue de ces régimes de perturbations va sans doute s'accroître avec le temps en raison des activités de protection contre le feu et du réchauffement climatique (Bergeron et Archambault 1993; Bergeron et Leduc 1998; Flannigan et Bergeron 1998; Lauzon *et al.* 2005). Malgré la plus faible diversité spécifique des sapinières comparé à celles dans l'Ouest du Québec, en Gaspésie le fort gradient environnemental, surtout à cause du dénivelé topographique, suggère qu'il y a une grande variabilité de régimes de perturbations (Battles *et al.* 1995).

Les aspects du régime de perturbations qui sont évalués

Il est largement reconnu que des perturbations dans la canopée provoquent des changements dans le sous-bois, et par conséquent influencent le processus de remplacement des arbres, mais certains chercheurs préfèrent étudier ces processus au niveau du peuplement et non pas à l'échelle de la trouée individuelle (ex: Veblen *et al.* 1991; Frelich et Reich 1995). Les plantes en régénération dans la trouée ("gap fillers") réagissent aux trouées (ex: Frelich et Lorimer 1991; Cumming *et al.* 2000; Hatcher 1964), mais les plantes en dehors de la surface délimitée par la projection verticale de la trouée sont aussi jusqu'à une certaine mesure affectées, et certains auteurs pensent qu'il est maladroit de décrire le processus de rotation du peuplement uniquement à partir des caractéristiques des trouées (Lieberman *et al.* 1989). Un échantillonnage adapté pour inclure des surfaces en dehors de la trouée («expanded gaps» de Runkle 1982) ne peut être que partiellement efficace parce que l'effet n'est pas symétrique autour de la trouée, et parce que peu importe l'agrandissement de l'aire évaluée jamais la portée de lumière au sol sera entièrement représentée (Canham *et al.* 1990). En forêt boréale, la morphologie des arbres et parfois une régénération défailante font en sorte que la canopée est parfois moins densément fermée. Ceci facilite la pénétration de rayons lumineux sur des axes inclinés, et la mesure de l'impact en dessous des ouvertures est donc davantage problématique et mise en doute (Bartemucci *et al.* 2002; Palik *et al.* 1997; Liu et Hytteborn 1991). Quelques chercheurs viennent même à se demander si les ouvertures dans la canopée ont un effet significatif sur la dynamique du peuplement, en forêt boréale et ailleurs (Barden 1989; Webb et Scanga 2001; Nowacki et Abrams 1997). Il est néanmoins probablement important d'évaluer les trouées individuellement (Gagnon *et al.* 2004) parce qu'elles

sont un aspect traditionnellement utilisé par les forestiers pour distinguer les peuplements, et aussi parce que l'hétérogénéité de la régénération en sous bois est au moins en partie conditionnée par l'emplacement des trouées. Le premier volet de notre étude a donc consisté à vérifier si il est raisonnable d'étudier le régime de trouées dans ces forêts, en cherchant un réel et quantifiable impact des trouées. Pour ce faire nous avons évalué la densité, la composition, la date d'établissement et le patron de croissance des arbres en régénération.

Le second volet de l'étude a consisté à identifier les caractéristiques de peuplement, les types de perturbations, et les facteurs environnementaux qui sont associés à la variabilité du régime des trouées. Si les causes de mortalité des arbres ne sont pas considérées assez en détail le régime de trouées peut paraître homogène sur un territoire lorsqu'il ne l'est pas, et il est préférable d'essayer de concevoir individuellement les couches de perturbations pour bien comprendre le fonctionnement (Rykeil 1985; Frelich 2002; Worrall et Harrington 1988). C'est sans doute particulièrement important dans le cas de la Gaspésie en raison de l'hétérogénéité du relief et des changements historiques de l'importance des agents de perturbation (CDDFG 2004).

Le troisième volet de l'étude a consisté à décrire la périodicité des perturbations, selon les causes de mortalité des arbres et le type de peuplement. Des connaissances sur l'étalement des perturbations permet d'entrevoir un autre aspect de la variabilité du régime, et peut servir de modèle pour planifier la périodicité des interventions dans un système de coupes partielles par l'industrie forestière. La période évaluée s'étend sur 24 années (1978-2001), et comprend les années qui ont subi le principal impact de la plus récente épidémie de la tordeuse des bourgeons de l'épinette (1973-1991). Un effort est par ailleurs fait pour comprendre comment la variabilité des dimensions et de l'origine des trouées détermine l'évolution de la forêt.

STUDY AREA AND FIELD METHODS

Study area

The Gaspésie peninsula is the northeastern extremity of the Appalachian Mountain Chain, and reaches a maximum elevation of 1268m. It is located in the boreal zone, has a continental humid climate despite its proximity to the sea, and 95% of its area is covered by forest (Thibault 1987). The topography is rugged, but slopes are rarely inclined more than 20% (Robitaille and Saucier 1998). Lakes are rare, and over 90% of the area has mesic hydrological conditions (Robitaille and Saucier 1998). Rapid rivers and streams flowing towards the Chaleurs Bay to the south have cut deep V-shaped valleys through the sedimentary formations. The soil is underlain by deformed Paleozoic sedimentary and metamorphic rocks, and lesser amounts of volcanic and intrusive rocks (Charbonneau and David 1993). On top are moderately folded sediments of Silurian to Devonian age, including sandstones, limestones and siltstones, and a variety of mafic and felsic volcanic rocks (Charbonneau and David 1993). Unconsolidated sediments include till (average thickness of 45cm), glaciofluvial deposits and a surficial boulder mantle, with accumulations of colluvions downslope (Charbonneau and David 1993; Thibault *et al.* 1995). The climate is characterized by cold and long winters with a heavy snowfall, and by short, hot and moderately humid summers (Landry *et al.* 2002). The altitudinal gradient creates much variability of temperatures and precipitation rates (Table A), as well as a corresponding diversity of forest types (Thibault 1987). Deciduous and mixed forests are limited to the 20-30km wide fringe of Coastal Lowlands, at higher elevations stands are composed of balsam fir (*Abies balsamea* (L.) Mill.) or spruce (*Picea* spp.) or a combination of these species, and close to the summits tundra conditions prevail (Saucier *et al.* 1998; Charbonneau and David 1993).

Table A
The climatic normals within the studied area (Environment Canada)

			Mean daily temperature (°C)			Precipitation (mm)			Number of days		Degree-days
station	period	alt.(m)	jan.	july	annual	rain	snow	total	temp. >0°C	with snow	>5°C
New Richmond	1964-90	47	-11.3	17.9	3.7	766	253	1019	272	43	1461
Saint-Elzéar	1949-90	229	-12.5	16.6	2.6	866	318	1186	263	49	1286
Murdochville	1952-90	575	-13.3	16.2	1.6	572	487	1059	-	79	-

Historical disturbances by natural and anthropomorphic agents have had important consequences on the forest and its disturbance regime. Widespread killing of spruce trees by indigenous and introduced insects in the 1930s, and severe climatically induced dieback on birches in the 1940s, has dramatically augmented the proportion of fir in the region (Lévesque 1997). Probably as a consequence of this, Spruce budworm (Sbw) (*Choristoneura fumiferana* Lem.) epidemics appeared for the first time in 1911, and have since increased in intensity and severity, and the interval between episodes has shortened (Blais 1983). In the study area the most recent Sbw epidemic occurred from 1973 to 1991, according to the Ministry of Natural Resources of Québec map surveys (1:250 000 scale) of moderately-to-severely defoliated areas. The rarity of stands composed of species adapted to fire disturbances (Baskerville 1975; McLean 1984; Morin *et al.* 1993; Bergeron and Leduc 1998; Furayev *et al.* 1983; Flannigan and Bergeron 1998), the irregularity of the relief (Dansereau and Bergeron 1993), and the maritime climate (Baskerville 1975; McLean 1984; Morin *et al.* 1993; Bergeron and Leduc 1998; Pominville *et al.* 1999; Bertrand *et al.* 1992) all suggest a longer fire cycle than in the western part of the Québec boreal forest (Furayev *et al.* 1983; Bergeron and Dansereau 1993). A recent study suggests that the fire cycle in the Chaleurs Bay area is approximately 200 years (Lauzon *et al.* 2005). Windthrow also can occasionally cause important disturbances (Ruel *et al.* 1999). The Balsam fir-yellow birch forest located along the coast has been inhabited by Europeans since the 17th century (Wein and Moore 1977), but the forest has been exploited on an industrial scale only since the 1940s (Lévesque 1997).

The aim was to describe and evaluate the variability of small gap regimes in the Chaleurs Bay area (north of the towns of Nouvelle-Ouest and New Richmond), at low- and mid-level altitude (south of the Murdochville highway), in public lands under lease (CAAF) to the Temrex forest company. In our choice of sites we strove to represent the major types of forest stands present in the region.

Twenty-seven sites with altitudes from 139m to 770m were investigated, approximately equally distributed in three localities about 50 km distant from one another (fig. A and appendix A). One third of the sites are located in the Fir-Yellow birch bioclimatic domain (4c), or the Temiscouata-Restigouche section (L.6) of the Great Lakes-St.Lawrence Forest Region according to Rowe (1972), on the Coastal Lowlands (MRNQ 2000). The other sites are located in the Fir-White birch bioclimatic domain (8b and 9b), corresponding to Rowe's (1972) Gaspé forest region (B.2). The most common tree species encountered are balsam fir, white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) B.S.P.), eastern white cedar (*Thuja occidentalis* L.), white birch (*Betula papyrifera* Marsh.), yellow birch (*Betula alleghaniensis* Britton.), mountain ash (*Sorbus Americana* Marsh.), pin cherry (*Prunus pensylvanica* L.f.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.). Trembling aspen (*Populus tremuloides* Michx.) are mostly only found in close proximity to roads or burnt areas. No red spruce (*Picea rubens* Sarg.) were encountered.

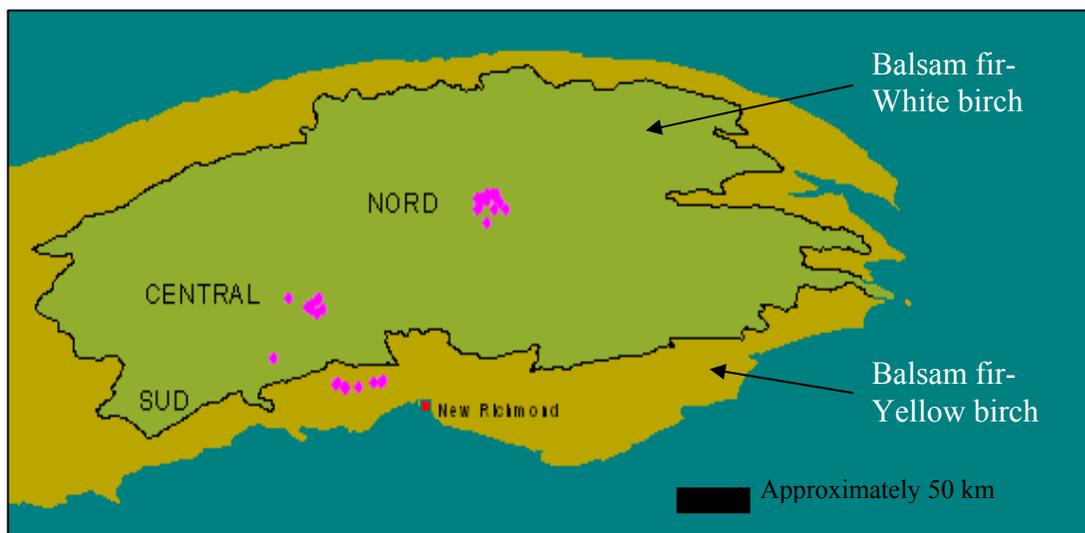


Figure A. Localization of the 29 sites, within northern (Nord), central (Central) and southern (Sud) groups. The demarcation between both bioclimatic domains is shown: Fir-Yellow birch along the coast and Fir-White birch in the interior.

Chosen sites had not burned for more than a 100 years (Lauzon *et al.* 2005) and had old-growth attributes such as the presence of old trees, no evidence of recent tree cutting, fallen trees at different stages of decomposition and an irregular stand structure (Kneeshaw and Burton 1997; White *et al.* 1985). Transects were located at least 20m from managed or more severely disturbed stands, so that a certain structural and compositional homogeneity exists throughout the site. Only parts of the stand

with small canopy gaps are considered. Soil conditions of the sites were generally mesic, but some sites were located on very steep inclines.

Gap fraction and gap characteristics

Canopy gaps in each site were sampled using a single linear transect, of a length varying from 150m to 500m depending on the maximum distance available. Many gap studies like us have used the Line Intersect Sampling method (LIS) to calculate gap fraction by the ratio of transect length in gaps over transect length under forest cover (Runkle 1992; Battles *et al.* 1996; Kneeshaw and Bergeron 1998; Worrall and Harrington 1988; Lertzman and Krebs 1991; Liu and Hytteborn 1991; Cho and Boerner 1991; Cumming *et al.* 2000; Reiners and Lang 1979; Krasny and DiGregorio 2001; Perkins *et al.* 1992). The method is also used to evaluate the distribution of gap characteristics (e.g.: gap size) from a sub-population of gaps, but, unlike for the gap fraction calculation (Battles *et al.* 1996), in this case the higher probability of larger gaps being intercepted creates a source of error (de Vries 1986). Some authors choose to ignore this bias (Bartemucci *et al.* 2002), probably because no correcting device seems entirely satisfactory (Runkle 1982) and because taking gap shape into account is perhaps ultimately necessary (Battles *et al.* 1996). Like Runkle (1982: 2nd method) we applied a partial correction of the size frequency by dividing each gap area by its square root, the radius of the gap (considered as a circle) being directly proportional to the probability of interception (Foster and Reiners 1986). The resulting increased ratio of small sizes relative to large sizes is striking (fig.B), and because of the skewed distribution the mean gap size value finds itself much altered (from 68m² to 28m²). In view of this, we did not attempt to estimate a gap density (number of gaps per surface area).

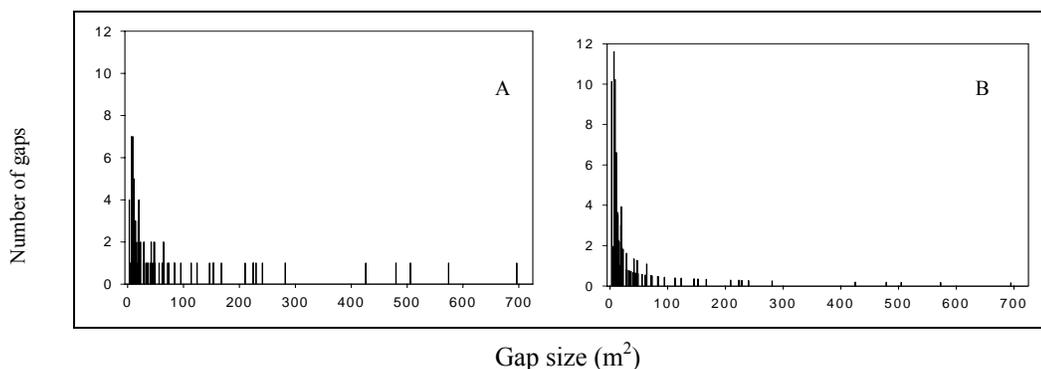


Figure B. The uncorrected (A) and corrected (B) frequency of gap sizes.

Distances along the transect were measured at every canopy gap border to a precision of 0.1m. Only gaps caused by the death of a canopy tree were considered in our census, which was nearly always the

case because edaphic gaps were very rare and few streams were crossed. Because in some cases gap fillers were quite tall, we considered, as others have done (Battles and Fahey 2000; Liu and Hytteborn 1991; Hunter *et al.* 1993; Bartemucci *et al.* 2002), that the gap was closed when gap fillers had reached at least 2/3 of the height of the lowest canopy trees. Using a strict definition of what constitutes a canopy tree (e.g.: minimum dbh or tree height) was impractical and unnecessary. There was no lower limit of gap size, but no gaps were smaller than 3m². Only "actual gaps" (as opposed to "extended gaps") were measured (Runkle 1982), their area determined by the vertical projection on the ground of the canopy-tree crown extremities (Brokaw 1982). A conversion from "actual" to "extended" gap sizes could eventually be done if it is found to be useful, since in our sites there are relatively few tree species.

For all gaps the cause of tree mortality was attributed to either defoliation by the Sbw, windthrow (excluding Spruce budworm origin) or senescence. We functioned by deduction: a senescence origin was assigned when neither wind (whose impact is usually quite evident given the slow rate of decomposition) nor the Sbw were responsible. Mortality by the Sbw typically results in fir snags remaining standing for many years (most of the observed trees killed by the insect were still standing), with twigs absent because of defoliation (unlike snags dead by senescence). Sbw-killed trees also usually have particular bark retention characteristics, still clinging to the trunk for at least 27 years (Dansereau 1999).

Of the 685 gaps sampled, 101 gaps from 8 transects were used to evaluate the size, shape, and orientation of gaps, as well as characteristics of the gap filler community. These gaps were randomly chosen in order to know the size distribution, but with the intention of having all three the stand types and environmental factors more or less equally represented. Considering gap shape and orientation is important because the compass direction (Canham *et al.* 1990) and the distance from gap center (Battles *et al.* 1996) often affect the plant regeneration within the gap, especially at high latitudes where the arc of the sun's trajectory is further from the equator. The orientation of gaps was roughly determined by the azimuth of the longest possible axis (major) traversing the gap. Gap size (i.e.: surface area) was determined by measuring the length of a number of lateral axes perpendicular to the major axis, which gives a more precise estimation than measuring only two perpendicular axes and considering the gap shape as elliptic as is often done (e.g.: Runkle 1992). Depending on the size of the gap, the distance between the lateral axes varied from 1m to 10m, but most intervals were 1m long and very rarely surpassed 2m. Gap area was calculated by summing the area of polygons delimited by the major axis, two lateral axes, and the approximate length of the gap border segment. Gap perimeter was

estimated by adding the lengths of these gap border segments (i.e.: the connecting lines between endpoints of the lateral axes). The shape of gaps was assessed by the ratio of gap perimeter to gap area, a more irregular shape (i.e.: more different than a circle) having a longer perimeter for a given gap size (Lertzman *et al.* 1991; Gagnon *et al.* 2003). In most gap studies, however, gap shapes are likened to ellipses and the eccentricity is measured as the ratio of the lengths of the major axis and its perpendicular axis, with the circle (axes of equal lengths) once again used as the benchmark (Runkle 1990; Perkins *et al.* 1992; Battles and Fahey 1996; Hunter and Parker 1993; Holeska and Cybulski 2001). We therefore also calculated the approximate lengths of major (2a) and lateral (2b) axes in an ellipse for a given perimeter (P), using the formula developed by S. Ramanujan (1887-1920): $P \approx \pi[3(a+b) - ((3a+b)(a+3b))^{0.5}]$. As others have done (Kneeshaw and Bergeron 1998; Hunter and Parker 1993), when occasionally a major axis could not cover adequately the length of the gap because of its very irregular shape, different parts of the gap were measured separately in the field.

The density, height and composition of trees in gaps were measured along four perpendicular axes oriented in each cardinal direction from the gap center. In bands running the length of each axis, measuring 1m wide and for a maximum length of 7m, seedlings (diameter at ground level <1cm) and saplings (diameter at ground level \geq 1cm) were counted and their species noted. The axes were divided lengthwise in three sections (near the gap center, at midway, and at the extremity of the axis). In each section only the presence of opportunist shrubs and tree species was recorded, including mountain maple (*Acer spicatum* Lam.), striped maple (*Acer pensylvanicum* L.), beaked hazelnut (*Corylus cornuta* Marsh.), Saskatoon berry (*Amelanchier canadensis* (L.) Med.) and mountain ash (*Sorbus americana* Marsh.).

Calculation of the period of return of disturbances

The date of disturbance events was determined from growth responses among gap fillers, since it is presumed that the greater amount of solar radiation made available by the opening of the canopy accelerates the accumulation of biomass (Foster and Reiners 1986). We evaluated the response by measuring the radial growth of stems (Coates 2000), in terms of the differential width of concentric growth rings apparent on a transversal section of the stem. Sections at ground level were collected from three of the tallest saplings in each gap, 85% of which were fir. In the second field season (2003), 322 additional samples were taken to improve the confidence level of interpretations, bringing the total amount to 598 samples (not counting samples taken in one gap analyzed in more detail, and not presented in this report). Of the 101 gaps (from 8 sites) earmarked for estimating the temporal distribution of gap events, 79 were successfully dated, in 11 gaps no clear result was obtainable, 4 gaps

were aged >30 years, and 7 gaps had more than one date (table B). The few recordings of relatively old disturbance events, which are perhaps a consequence of repeated disturbances on developing trees or a retarded regeneration, have been left out of our analysis because they would cause an under-evaluation of the annual rate of disturbance since most gaps dating that far back would have disappeared (White *et al.* 1985; Cho and Boerner 1991; Dahir and Lorimer 1996), and it may also give the impression that the rate of gap creation is augmenting.

Table B

The number and provenance of gaps used for dating disturbance events
(and those that were not considered)

Transect name	A1	A3	A7	A6	A21	A2	A20	A31	total
stand type	Fir	Fir	Fir	Fir-Sw	Fir-Sw	Low-Fir	Low-Fir	Low-Fir	
initial number of gaps (with gap size data)	11	12	12	3	22	15	8	18	101
(-) gaps with no samples	3	1	1			8	1		14
(-) gaps with no dates		1	5		2	1	1	1	11
(-) gaps too old			4						4
(+) more than one date per gap		2			1	1	1	2	7
net number of gaps	8	12	2	3	21	7	7	19	79
% of the total area in gaps	13	24	1	7	25	4	9	18	

Identification of a growth release date requires distinguishing at least two periods in the plants' lifetime, one of slow growth followed by one of faster growth (i.e.: wider growth rings), and then identifying the year when such a change occurred. Annual tree ring width measurements were read to a precision of 0.01mm, with a Measure J2X (2001) apparatus and a binocular microscope with magnification up to 50x. Mean values were obtained from two readings on each sample, along the shortest and longest radii, in order to reduce the possibility of error occurring when the growth around the stem is asymmetrical and when the transversal slice is not perpendicular. We didn't check for absent or superfluous rings, but both ring counts had to have the same total number of rings. Numerous types of criteria are used in gap studies to systematically detect such release dates, probably because the environmental circumstances and the objectives of research are so diverse. For example, in the context of a tree plantation where growing conditions are uniform, a growth rate above a minimal benchmark rate can be used to signal a canopy disturbance (Ishikawa *et al.* 1999). Given the local and regional variability of our sites, the use of such a straightforward approach would be ineffective. We

chose a technique inspired from that used by Orwig and Adams (1995) and others (Nowacki and Abrams 1997, Rensch *et al.* 2002 and 2003), which is robust enough to allow for the varied environmental and tree mortality patterns in our sites. The method consists of calculating an annual percent growth change value (%GC) based on the mean rate of 10-year sequences before and after the point year, with a one-year shift to take into account the delay of response (Parish *et al.* 1999) (see appendix B for details and examples). Some uncontrolled factors could have affected the growth pattern by creating an unrelated response, a delayed response, or could have reduced our ability to detect a response: partial canopy openings due to persistent snags, climatic variability, heterogeneous soil conditions, encroachment by competing shrubs, and herbivory by mammals or insects such as the Sbw or deer. An analogous response in all three samples does not guarantee that these factors were not at play, but the high number of samples and the fact that most samples came from fir trees (a widespread species that reacts forcefully to gaps and whose ring pattern is easy to discern) decreases the potential for error.

An estimation of the duration of gaps, or the least amount of time required for gap fillers to reach the level of canopy, is necessary to know the period on which to base the calculation of the period of return of disturbances. If the considered period of time is too long there will be an underestimation of the disturbance rate (i.e.: some of the gaps will have been closed), and if it is too short there is a risk that the calculation will not have taken into account enough variability. Dividing the height of gap fillers by their age gave various mean growth rates according to tree species: white birch the fastest rate (43 cm/year), and balsam fir had intermediary values (29cm/year). Since the lower level of the canopy is approximately at 10m height, the fir and birch trees could on average close the gap in 23 and 34 years respectively. This result is questionable, however, because the period of growth under closed canopy conditions (for pre-established individuals) is included in the calculation, and also because the different stem heights of gap fillers (and the differential rates associated with them) are not taken into account. To have a better estimate we did a stem analysis (taking transversal sections of the stem at ground level, at 50cm height, at 1m height, and at every meter afterwards) on a total of four trees at least 7m tall within middle-sized gaps. Trees of different species had during the post-disturbance period all approximately a maximum rate of growth of 33cm/year (see appendix C), suggesting it takes about 30 years for the gap to be closed at a height of 10m. The actual duration of gaps is probably even shorter, perhaps between 25 and 30 years, because the vertical distance to be covered is not from ground up, but from the top of pre-established saplings that are often already 1m tall. Our dating of disturbance events shows an absence of disturbances before 1978 (fig.C2), thus 24 years may represent the maximum duration of gaps. Another method to determine gap duration is to date gap filler growth

release episodes that did not persist until the canopy is attained, in other words when such episodes are followed by a period of resumed slow growth. Ten confined growth release episodes were noted (table C), with an average duration of 31 years, but because of the time lag and the improbability of multiple canopy openings in the same place, these results may not merit much confidence. This method should probably only be used when reconstructing the disturbance history from growth patterns in mature trees or to confirm results obtained through other methods.

Table C

The duration and date of ten confined growth release episodes

Dates	1939 -1974	1941 -1980	1944 -1963	1944 -1991	1947 -1964	1947 -1975	1949 -1975	1961 -1994	1967 -1985
Duration (years)	35	39	19	47	17	28	26	33	18

No account was taken of the possibility that gap closure could occur partially through the extension of branches from trees bordering the gap, which could imply that more than one opening in the canopy would be necessary for gap fillers to form part of the canopy. Some studies report that most gaps close through the lateral extension of bordering trees in temperate and tropical forests (Hibbs 1982; Runkle 1990; Payette 1990) and even in a west coast (Oregon) conifer forest (Spies and Franklin 1989, but for opposite results see Bartemucci *et al.* 2002). Lateral closure is taken into account, or at least measured, in some studies involving forest types similar to ours (White *et al.* 1985; Holeksa and Cybulski 2001), but other authors ignore it or believe that it has an insignificant impact (Perkins *et al.* 1992; Foster and Reiners 1986). Conifers, compared to deciduous trees, have a monopodial growth form which restricts their ability to forage for light (Lertzman and Krebs 1991; Kuulavainen 1994). Given the great abundance of conifers in most of our stands and the low canopy height we assumed that lateral closure had a negligible effect on gap sizes and gap ages.

The period of return of disturbances is the average number of years required for an equivalent surface area as that evaluated to be disturbed (Heinselman 1973). In our case, the annual net amount of disturbance was evaluated as the proportion of the total transect (1122m) disturbed in a year, and the period of return as the reciprocal of its mean value (Runkle 1982; Lawton and Putz 1988; Spies and Franklin 1989; Barden 1989; Dahir and Lorimer 1996; White *et al.* 1985). We found it better to directly calculate the disturbance rate rather than by using the mean gap size (van der Meer *et al.* 1994). The lower gap fraction in the transects used for the evaluation (34% compared to 43% for all

sites) may have led to an underestimation of the period of return. We rectify this by equally augmenting the rate of disturbance in all years. When occasionally two disturbance events were identified in one gap, the transect segment was divided in half and considered separately.

The species composition of stands

Stand characteristics (canopy height, basal area, stem density and composition of trees with dbh ≥ 10 cm) were measured approximately at every 100 meters along transects, for a total of 79 sample points. The values were averaged out per sample point and then per stand. Three types of stands were distinguished on the basis of their species composition, because this aspect best represents the considerable differences among sites and because it presumably most determines a stand's susceptibility and vulnerability to all three disturbance agents: pure fir stands (Fir), stands composed of fir and white spruce (Fir-Sw), and stands with a strong component of either hardwoods or black spruce (Low-Fir)(see appendix D). In the context of widespread and severe Sbw epidemics particularly, firs are the most exposed to mortality, followed by white spruce (Nealis and Regnière 2004). Black spruce are relatively less at risk, perhaps as much as deciduous trees are, which is the reason we grouped both these types of stands together even though they usually do not develop in very similar environments.

Table D

The species composition of the stands

Stand type	nb. sites	% fir	std	% fir+w.spruce	std	% hardwoods	std	criteria
Fir	8	78	7	87	10	0	0	$\geq 70\%$ fir
Fir-Sw	10	63	6	79	14	1	4	$>60\%$ (fir + w.spruce)
Low-Fir	9	31	15	36	16	15	25	$\leq 60\%$ (fir + w.spruce)
All	27	57	22	67	26	5	15	

(hardwoods include yellow birch, sugar maple, and red maple)

Many of our conclusions are based on the species composition of the forest before disturbances. Our assessment of past stand characteristics is based only on an estimation of the species proportions among gap makers. The presence of gap-maker species was recorded in each gap, but no counting of trees or precise proportion of each species was attempted. Since most gaps are relatively small, the potential error is not as great as it could otherwise be. We propose that if the amount of fir in the actual canopy is directly proportional to the amount of fir as gap makers, then the actual stand composition is a faithful reflection of the prior stand composition. Although there is no reason to believe that this doesn't apply to all species, strictly speaking it concerns only the fir (i.e.: stands presently containing

more fir formerly also contained more fir), which is the element most critical for the evaluation of the disturbance regime. We use two ways to estimate the proportion of fir among gap makers: first, the percent of gaps in a stand type which have at least one fir gap maker; and second, considering each species presence as one count, the percent of fir counted in a stand type. Both these approaches show that the amount of fir in the canopy is proportional to the amount of fir dead (table E). This conclusion is valid when comparing stand types with varying amounts of fir, and in general for all sites (fig. C).

Table E

The % of fir in the present-day canopy, the % of gaps with fir gap makers, and the % of fir gap makers (with standard deviations)

stand type	canopy		gap makers			
	mean % fir	std	mean % gaps	std	mean % fir	std
Low-Fir	30	5.0	86	5.6	66	5.6
Fir-Sw	61	1.7	90	2.8	75	5.3
Fir	78	2.1	98	12.4	89	11.7
all	57	4.1	90	4.1	74	4.3

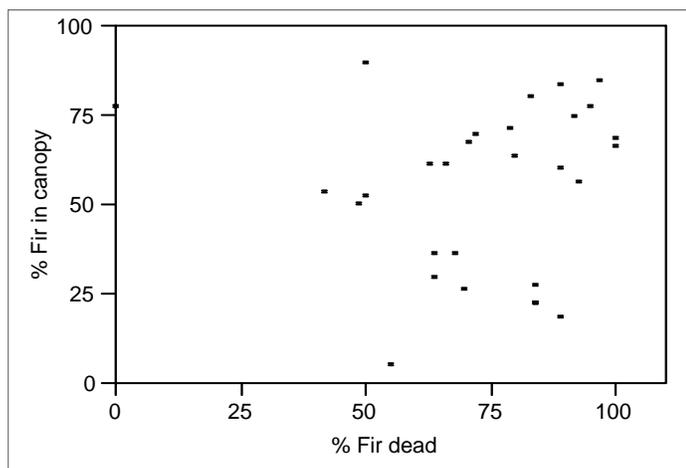


Figure C. The amount of Fir in the canopy as a function of the amount of dead fir in each site.

The statistical analyses

All statistical analyses are performed with the JMP computer program (version 4), which is a recent version of the SAS system. One-way ANOVAs are used to judge the similarity between values in more than two groups, such as when comparing gap sizes from different sites. Student T and Tukey HSD tests are used to identify which groups are different. When only two groups are involved a T test is utilized instead. Simple regressions are used to determine whether the variability of a regime

parameter, such as gap fraction, is related to the variability of an independent variable, such as the altitude of sites. A stepwise multiple regression analysis is used to find out if the significant independent variables can together better explain the gap fraction variability, and if so which ones in particular and in what order. For all these statistical exercises the normal distribution of values and the homoscedacity (through the Brown-Forsythe test) are verified. When the distribution of values is found not to be normal, through the Goodness-of-fit test of Shapiro-Wilk, the values are transformed, usually by natural logarithm, and when this is not practical a non-parametric Wilcoxon test is used. In all cases, the probability of rejection of the Null hypothesis is determined with an α of 0.05.

CHAPITRE I

DO SMALL GAPS IN THE CANOPY INFLUENCE STAND DYNAMICS IN SOUTHERN BOREAL FORESTS OF EASTERN CANADA?

Abstract

Although the role of small canopy gaps in tree replacement dynamics has generally been recognized, their actual impact has sometimes been put into doubt, particularly as regards boreal forests. We hypothesized that gaps in the tree canopy quicken the development of understory trees and increase the density of saplings. A greater impact should occur during periods of particularly intense canopy disturbances. Shade-intolerant tree species, such as white birch (*Betula papyrifera* Marsh.), should be particularly affected.

There is a greater number of gap fillers generally, and white birch specifically, per unit area in larger gaps. Over a 70-year period the rate of establishment of fir (*Abies balsamea* (L.) Mill.) was continuous, while the rate of establishment of white birch surged during periods of major canopy disturbances created by eastern spruce budworm (*Choristoneura fumiferana* (Clem.)) epidemics. Gap filler growth rate accelerated noticeably after gap formations. However, stem abundance at the sapling level does not necessarily imply a lasting gap impact. Because white birch are present in all gap sizes and can survive well after gap closure, we conclude that gaps are not necessary for tree recruitment to the canopy and possibly not for seedling establishment either. Gaps are influential but probably not a critical aspect of tree replacement dynamics.

1.1 Introduction

The role of small-scale canopy disturbances in forest dynamics has been recognized in many types of forest for at least a century (Pinchot 1905; Cooper 1913 in Sprugel 1991; Aubréville 1938; Sernander 1936 in Liu and Hytteborn 1991; Iwaschkewitsh in Jones 1945). Regenerating trees react to the elimination of canopy trees in a number of ways (Narukawa and Yamamoto 2001; McCarthy 2001; Drobyshev *et al.* 2000), but usually it is the increased amount of light penetrating into the understory that is the most important stimulus (Denslow 1987; Oliver and Larson 1990). The variable capacity of tree species to tolerate shady conditions plays a crucial role in the dynamics of most forests, especially in small gap regimes where light is available in limited quantities (Whitmore 1989). Two main

assumptions are commonly used in studies on gap dynamics: 1) disruptions in the canopy have an effect on tree development in the understory and 2) gap characteristics, especially gap size, determine to a large extent the structure and the composition of tree development in the understory within and in proximity to gap areas. For a number of reasons these assumptions have come into doubt in recent decades (Barden 1989; Webb and Scanga 2001; Nowacki and Abrams 1997). The objective of this study is to verify if gap size and the intensity of canopy disturbance have an impact on the stand development in fir-dominated boreal forests in southeastern Canada. Understanding the link between canopy disturbances and stand development is important to further our knowledge of gap dynamic processes, as well as for the development of partial wood cutting systems based on the size of forest gaps of natural origin (Gagnon *et al.* 2004).

The dichotomous conception of the forest as an amalgam of disturbed (i.e.: in gap phase) areas and intact areas can be misleading (Lieberman *et al.* 1989). Plants growing directly beneath are usually found to react to disturbances in the overstory (e.g.: Frelich and Lorimer 1991; Cumming *et al.* 2000; Hatcher 1964), but the impact of a gap is not limited to that area because solar rays also penetrate diagonally into the understory (Ban *et al.* 1998). The area affected outside the "actual" gap (delimited by the vertical projection of the contour of the opening in the canopy) depends upon the species and height of the trees bordering the actual gap (Runkle 1982), and upon the latitude of the site, with increasingly deformed extensions of affected area in more northern sites (Canham *et al.* 1990). Considering a larger or "extended" gap area (*sensu* Runkle 1992), meaning an area delimited by the stems of adjacent canopy trees, only gives a potentially more accurate estimate of the gap impact. Apart from this difficulty in considering the surface area in the understory affected by a gap in the canopy, forests with a sparse tree cover or a low canopy height apparently allow light to penetrate into the understory regardless of the dimension or amount of openings in the canopy, rendering relatively insignificant the impact of new gaps on tree replacement processes. It is particularly in boreal forests that the importance of small gap dynamics and gap size has been brought into doubt (Bartemucci *et al.* 2002; Palik *et al.* 1997; Liu and Hytteborn 1991).

Among the known quantifiable effects of gaps is the influence of gap size on seedling or sapling density (i.e.: the number of plants per surface area in the understory). Larger gaps usually bring about a greater density of saplings in boreal (Kneeshaw and Bergeron 1998; Liu and Hytteborn 1991) as well as in other (Brokaw 1985; Lawton and Putz 1988) types of forest, but not in all cases (Runkle 1982; Lertzman 1992; Gagnon *et al.* 2004; Coates 2002; Abe *et al.* 1995). The greater amount of light introduced through larger gaps benefits all regenerating plants, but it is to be expected that larger gaps

are particularly advantageous for species which are less shade-tolerant (Ghent 1958; Brokaw 1987; Runkle 1981 and 1990). Although such "opportunist" tree species may be present in gaps of all sizes (Brokaw and Schreiner 1989; Kneeshaw and Bergeron 1998; Hytteborn *et al.* 1991), they are more numerous (Runkle 1982), or sometimes only begin to appear (Hytteborn *et al.* 1991), where larger gaps are present because they require or are better adapted to the increased light conditions.

Shade-intolerant species should also be particularly advantaged during periods of more intense canopy disturbances, either because of the greater number or the larger size of gaps. Aside from favoring the growth rate of these trees, the number of seedlings becoming established should also be exceptionally high during this time, despite the possible lack of synchronism with seed years and despite the occasional presence of a dense cover of pre-established shade-tolerant saplings. Because of the importance of disturbances produced by the spruce budworm (Sbw), the recruitment of shade-intolerant trees should presumably take the form of cohorts timed to the pulses of massive tree mortality produced by the insect.

Another evidence of the importance of gaps is the sudden accelerated growth of understory trees following the canopy disturbance. The quickened development of the portion of forest in gap phase, which represents a temporary local disequilibrium of the forest system, is at the basis of the shifting state mosaic concept of gap or patch dynamics (Watt 1947; Remmert 1991), and many studies have evaluated such responses (Brokaw 1985 and 1987; Battles and Fahey 2000; Canham 1988; Fye and Thomas 1963; White *et al.* 1985; Hibbs 1982; Runkle and Yetter 1987; Hatcher 1964). Among the numerous methods devised to gauge the impact of canopy disturbances, often in order to date the disturbance event, one of them aims at measuring the growth rate change in gap fillers (i.e.: young trees growing directly within the "actual" gap area) which are expected to eventually close the gap. Tree species most appropriate for this evaluation are pre-established, have growth rings which are easy to read, and while inevitably being to a certain extent shade-tolerant are able as well to respond vigorously to a light stimulus. In the region under study, the omnipresent balsam fir satisfies well these conditions (Webb 1957; Baskerville 1975; Zarnovican 1983).

In this study our objective was to determine if small canopy gaps have an impact on regenerating trees in fir-dominated boreal forests, and we verified this in four ways (listed below) by evaluating the impact of gap size and disturbance intensity. We hypothesized that gaps of larger size bring about a higher density of saplings, both when considering all species together, and when considering specifically white birch, which is the most widely distributed shade-intolerant tree species in the

region. We hypothesized as well that during periods of intense canopy disturbance there results a pulse of seedling establishment within the white birch population. Finally, we verified whether the increase in resources which results from the creation of a gap induces a sudden growth impulse among tree gap fillers situated within the actual gaps.

1.2 Study area

Gaps were surveyed in eight sites in the Bay-of-Chaleurs region of the Gaspésie peninsula, which is the northeastern extension of the Appalachian Mountain Chain located in the eastern part of the province of Québec, Canada (see figure A). The sites are spread out on the southeast aspect, separated by as much as 100km from each other and at a maximum elevation of 770m. The region, at the southern limit of the boreal zone, is part of both the Balsam fir-white birch and Balsam fir-yellow birch bioclimatic domains according to the Québec government classification (MRNQ 2000), or part of the Great Lakes-St. Lawrence (L.6) and Gaspé (B.2) Forests Regions according to Rowe (1972). The region has a continental humid climate (Thibault 1987), with mean daily temperatures from 1.6 to 3.7°C and mean annual precipitation from 1019mm to 1059mm (of which between 253mm and 457mm as snow), according to Environment Canada records taken at meteorological centers in New Richmond (1964-1990), Saint-Élzéar (1949-1990) and Murdochville (1952-1990). All sites are on mesic soils, which are mainly composed of tills usually less than 1m thick, glaciofluvial deposits, and accumulations of colluviums downslope (Charbonneau and David 1993; Thibault *et al.* 1995).

In the region the fire cycle is approximately 200 years long (Lauzon *et al.* 2005), and the investigated sites showed no signs of recent major human or natural disturbances. The existence of old-growth characteristics was a condition for selecting sites, such as an irregular stand structure, and abundant coarse woody debris and snags of variously aged trees. A range of forest types are included, including fir-dominated and spruce-dominated stands, as well as mixed fir-spruce and fir-hardwoods stands. As in other regions in Eastern Canada where balsam fir trees are ubiquitous in the canopy and in the understory, defoliation by the Sbw represents the main cause of tree mortality apart from fire (Furayev *et al.* 1983). Epidemics of this insect recur every couple of decades, but in Gaspésie the infestations only began in 1911 (Blais 1983), probably as a result of an increased abundance of balsam fir in the region, due to human harvesting practices as well as to some severe natural disturbances by other insects and climate-induced dieback earlier this century (Lévesque 1997). Near the coast some spruce (*Picea* spp.) and eastern white cedar (*Thuja occidentalis* L.) are present, but the fir is mostly

accompanied by hardwoods such as yellow birch (*Betula alleghaniensis* Britton.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white birch, mountain ash (*Sorbus Americana* Marsh.), pin cherry (*Prunus pensylvanica* L.f.), and more rarely with white pine (*Pinus strobes* L.). Further up in altitude, stands are composed mostly of only fir or a spruce, including black spruce (*Picea mariana* (Mill.) B.S.P.) or white spruce (*Picea glauca* (Moench) Voss), or a combination of them, often with a presence of white birch. Trembling aspen (*Populus tremuloides* Michx.) are mostly found only in close proximity to roads or burnt areas, and no red spruce (*Picea rubens* Sarg.) were encountered.

1.3 Methods

Gaps were surveyed by the Line Intersect Sampling (LIS) method (Runkle 1992), with a single transect between 150m and 500m in length at each site. Beginning and end points of transects were distanced at least 20m from areas modified by humans or by a severe natural disturbance, so that the stand structure and composition was relatively homogeneous. Rather than aiming to have a same number of gaps in each size class, series of gaps were chosen randomly along the 8 transects in order to estimate the natural distribution of gap sizes. Gaps smaller than 1000m² were considered in the analyses; only a few gaps were found to be larger, and these were measured for comparison purposes and are referred to as "patches". To be considered a gap (Runkle 1982) the forest canopy opening had to have been caused by the apparent death of a canopy tree, and gap filling trees had to be not taller than 2/3 the canopy height. One hundred and one gaps were used to evaluate cause of tree mortality, gap size and tree regeneration within the actual gap. Seventy nine of these gaps were dated.

The cause of tree death was determined as being either defoliation by the Sbw, windthrow, or senescence, the last category made up of cases not covered by the other two. Government (MRNQ, Québec) aerial surveys of areas experiencing moderate-to- severe levels of defoliation by the Sbw, recorded on maps (1:250 000), show that the epidemic in our sites occurred from 1973 to 1991 inclusively. Most of the impact of the recent Sbw epidemic is therefore included in our analysis (see appendix C). In each gap the causes of disturbance were differentiated visually on the basis of the physical condition of gap makers, including the presence of bark, broken tops, and the presence of twigs and branches (Dansereau 1999). Trees killed by wind nearly always snapped rather than upended. Although it is possible that some trees dead by senescence a long time ago may have been counted wrongly, Sbw-killed trees were generally easily distinguished. If a tree killed by the Sbw was

thereafter thrown by the wind, the gap was considered to have a Sbw origin. When more than one agent was responsible for creating the gap, which occurred very rarely, that gap was not used when comparing relative frequencies of gap origins.

Gap size (i.e.: surface area of actual gaps) was estimated by measuring the length of the longest possible axis within the gap, and a various number of lateral axes perpendicular to it; the total area was calculated by adding up the area of polygons thereby obtained. When the shape of a gap was too irregular to use a single main axis, parts of the gap were measured separately in the field (Kneeshaw and Bergeron 1998). Depending on the size of the gap the distance between the lateral axes varied from 1m to 10m, but most intervals were 1 meter long and very rarely more than 2 meters. Gap extremities were identified as the vertical projection at ground level of the canopy tree edges.

To evaluate whether gaps have an impact we compared tree regeneration characteristics along a gradient of gap size (e.g.: Coates 2002), rather than by comparing tree regeneration characteristics inside the gap from that outside the gap (e.g.: White *et al.* 1985). This is a more certain way to determine the influence of gaps because, as mentioned above, the identification of a supposedly intact part of the stand is problematic. The number and species of trees regenerating within gaps was estimated by sampling a variable portion of the area, within 1m wide axes running towards the four cardinal directions from the center of the gap. If axes were longer than 7m long, sampling areas were divided into central, mid-point and endpoint of axes. Two tree size categories were distinguished, seedlings (stems with ≤ 1.0 cm diameter at ground level) and saplings (> 1.0 cm diameter at ground level). The presence of herbaceous species was noted, but no measure of their abundance was made because they were relatively rare. Two methods were used to estimate if gap size is a significant factor affecting sapling density in gaps because of the uneven and low numbers of gap size samples in sites. A non-parametric Kruskal-Wallis test was used to compare the stem density among gap size classes. When only two gap sizes were compared a T test was used. The effect of gap size on stem density was evaluated by using a linear regression as well. We also verified if there was a relationship between gap size and gap age, in order to exclude the possibility that the variability of sapling density was a function of the latter.

The dating of small-scale disturbance events in the best of situations comprises difficulties and inevitably is sometimes impracticable (Foster and Reiners 1986). We aged gaps by identifying sudden radial growth releases among the tallest gap filler stems inside actual gap areas. At least three and often considerably more gap fillers were used per gap, usually balsam fir (279 stems, or 85%) but

sometimes also white birch (44 stems). Stem sections at ground level were sanded and the width of rings measured to a precision of 0.01mm with a Measure J2X (2001) apparatus and a binocular microscope with magnification up to 50x. Mean values were obtained from two readings on each sample, along the shortest and longest radii, in order to reduce the effect of asymmetrical growth around the stem and of a transversal slice not quite perpendicular. We didn't check for absent or superfluous rings, but both ring counts had to have the same total number of rings. We defined a significant growth response, like Orwig and Abrams (1995) and others (Nowacki and Abrams 1997, Rensch *et al.* 2002 and 2003) have done, as at least a 100% Growth Change (%GC) between the mean growth rates during the 10 years following a year from that of the 10 years preceding it (see appendix B):

$$\%GC = \frac{100(M_2 - M_1)}{M_1}$$

Where: M_1 = the sequence of the 10 preceding years

M_2 = the sequence of the 10 following years

[For example: For the %GC of the year 1950, M_1 =1941-1950, and M_2 =1951-1960]

A one-year delay is integrated in the equation to account for the delayed response of the plant. The 10 year period is long enough not to be overly influenced by short term climatic artefacts (Lorimer and Frelich 1989), and should reflect most of the growth change (Orwig and Abrams 1995). The ground level ring count also provided us with an approximate total age of the tree, and thus its year of establishment. Some of the 101 gaps were not used for dating disturbances because either no samples were collected (14 gaps), no date was able to be assigned (11 gaps), or because the gap was older than 25 years (4 gaps), which we estimate to be the maximum gap age (see appendix C). In 7 cases at least two disturbance events are distinguished within the same gap. The dating of events and the change in seedling establishment rates through time are only appraised qualitatively.

1.4 Results

Gaps of larger size have on average a greater density of saplings (fig. 1.1a). A linear regression (excluding patches, or gaps larger than 1000m²) shows a weak relationship ($R^2=0.16$), but an analysis of variance suggests that the fit is statistically different from a horizontal line at the mean ($P < 0.001$). The differences are particularly noticeable when considering only two gap size classes: gaps >40m² and ≤ 40m² (fig. 1.1b). A non-parametric Kruskal-Wallis test shows there is a difference among gap

size classes ($\text{Prob} > \text{Chi Sq} = 0.0028$), and the difference becomes strongly significant when only these two size classes are considered and evaluated by a T-test ($\text{Prob} > 0.001$). In gaps larger than 150m^2 the rate increase in sapling density levels off. Gap size and gap age are not correlated, implying that the greater sapling density in larger gaps is not because these gaps are older.

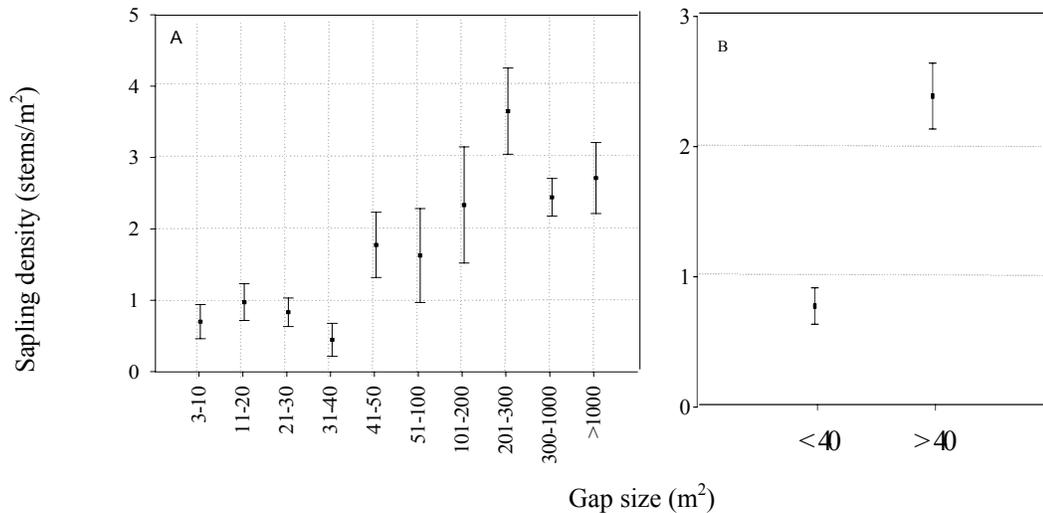


Figure 1.1. The density of saplings as a function of gap size (with standard errors), according to numerous (a) and two (b) gap size categories.

[The number of gaps sampled in each gap size class is: 3-10= 24; 11-20= 23; 21-30= 10; 31-40= 3; 41-50= 10; 51-100= 5; 101-200= 4; 201-300= 5; 300-1000= 4; and >1000= 17].

The density of white birch saplings is also greater in larger gaps (fig. 1.2). A linear regression shows the relationship to be stronger ($R^2=0.38$; $P<0.001$) than when all species are considered together. The increasing stem density levels off in gaps larger than 150m^2 or 200m^2 .

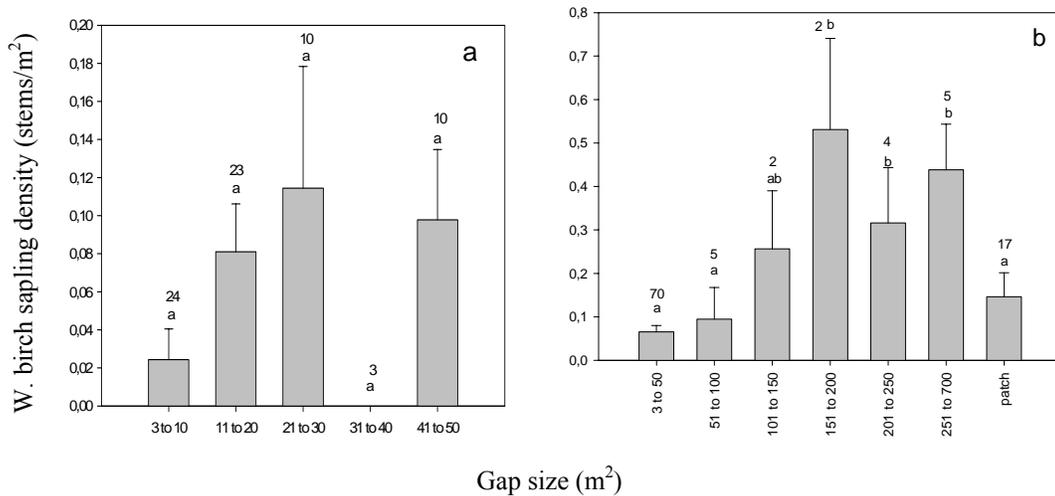


Figure 1.2. The density of white birch saplings as a function of gap size, among gaps $\leq 50\text{m}^2$ (a) and overall (b). Boxes represent mean values, lines are standard errors around the means, similar letters indicate that the groups are not significantly different according to a Student multiple comparison test, and the number of gaps in each class are shown. [patch=gaps $>1000\text{m}^2$].

As expected, Sbw was the main cause of canopy tree mortality and is responsible for creating a disproportionate amount of disturbance during epidemic periods. The extraordinary opening up of the canopy during the most recent Sbw epidemic, occurring from 10 to 28 years beforehand (1973-1991), led to a sudden increase of the rate of establishment of white birch (fig. 1.3). At the same time, the rate of establishment of fir, in contrast, was gradual and unaffected by the recent or the former epidemic, the latter occurring 43 to 51 years beforehand (1950-1958). No clear increased rate of establishment of white birch is detected during the former epidemic period. During the latest 15 years fewer trees became established because only saplings were used in this analysis.

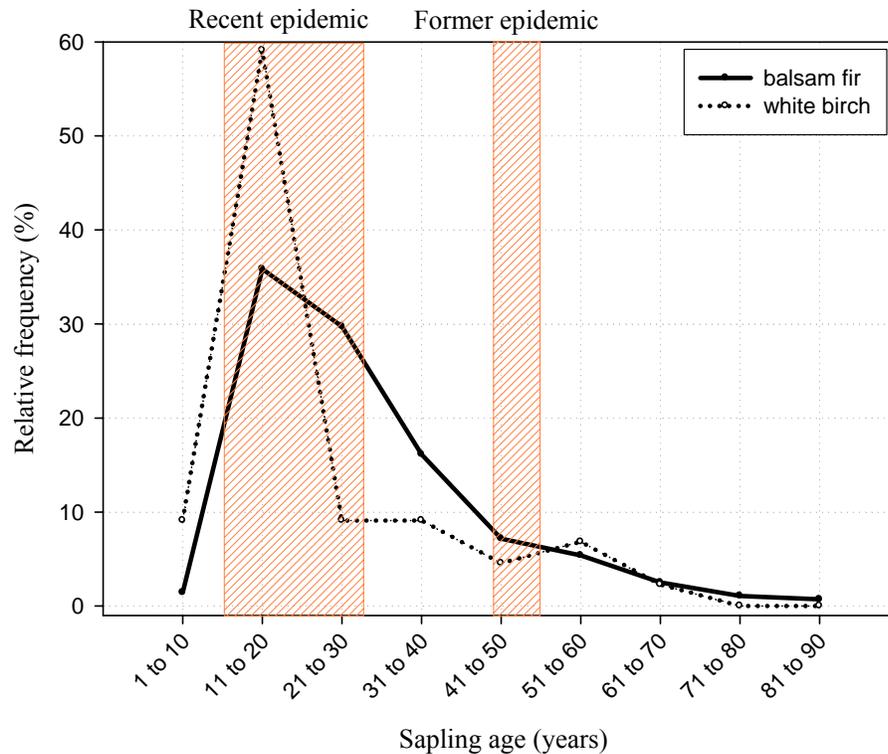


Figure 1.3. Establishment dates of balsam fir and white birch saplings presently growing in gaps, with respect to recent and former Sbw epidemic periods (the frequencies are based on 279 fir and 44 birch samples).

Eighty nine percent of surveyed gaps could be dated because gap fillers showed a sudden and sustained growth response to openings in the canopy. On average radial growth increased by a factor from 2.5 to 40, with a mean value of 8. The mean tree ring width changed from 0.1mm to 0.8mm following the canopy disturbance.

1.5 Discussion

In other forests, changes in sapling density and composition along the gap size gradient do not always occur (see Whitmore 1978 versus Grubb 1977) because of a variety of factors (Brokaw 1987). That these changes do occur in our sites, also when white birch are considered separately, suggests that the existence of gaps has an impact. Gaps which are older have sometimes been found to have a greater amount of saplings (Vincent 1962; Runkle 1990; Brokaw 1985), but this was not a factor in our case.

Self-thinning within the gap filler community may eventually affect the trend of more saplings existing in larger gaps (Bégin *et al.* 2001; Hubbell *et al.* 1999), but white birch will nonetheless probably survive and reach the canopy. The density of saplings, even of shade-intolerant species, does not increase past a certain gap size probably because they are then outcompeted by more opportunistic plant species (Aubin *et al.* 2000). A number of other studies have also noted that the effect is only apparent among smaller gap sizes (Kneeshaw and Bergeron 1998; Coates 2002; Osawa 1994).

A higher disturbance intensity, in terms of greater gap fraction and larger gaps, resulted in a greater presence of shade-intolerant species such as white birch. Some white birch saplings were as much as 70 years old (fig.1.2), even though we estimate gaps to last no more than 25 to 30 years, suggesting that disturbance intensity was more important for the establishment than for the subsequent development of understory trees. Others (Coates 2002; Brokaw 1987) have on the contrary found that disturbance intensity has relatively little impact on seedling establishment. However, the establishment of white birch does not absolutely require unusually intense disturbances since the rate of establishment does not drop to zero between Sbw epidemic periods (fig.1.2). This capacity of white birch to grow under apparently suppressed conditions, or in very small gaps (3-10m²), is also surprising given that species' reputed intolerance to shade. White birch are found to be unable to survive under an intact canopy (Hytteborn *et al.* 1987; Battles and Fahey 2000), for rarely more than one (Bergeron 2000), two (Osawa 1994) or five (Perkins *et al.* 1992) years.

Our results show that the rate of white birch seedling establishment concords with stand disturbance intensity, with that species becoming particularly abundant during the latest Sbw epidemic. There are several possible reasons why the previous epidemic did not bring about a similar response. It is known that not all Sbw epidemics occur with the same severity, and that massive tree mortality results usually after every second episode (Bouchard 2005). Thus it could be that the former epidemic was less severe and had less impact on the rate of birch recruitment. The absence of an impact during the former epidemic might also be due to our method of aging saplings (Parent *et al.* 2001), which could be less precise for older or suppressed saplings. Even though all species were treated similarly, the gradual recruitment of fir trees could have made differences due to sapling age undetectable. It also could be that in the long run only a small proportion of birch will survive in any case, which would imply that the impact of varying disturbance intensity is only temporary as regards that species.

Despite the capacity of fir to respond vigorously to increased amounts of light (Zarnovican 1983), its rate of establishment is remarkably gradual, as has been noted elsewhere in various stand types (Morin

2003), including in Gaspesian forests (Webb 1957). Other factors not controlled for in our study could have contributed to this fir recruitment pattern. The killing of seedlings by the Sbw could have masked an increased rate of fir establishment during the epidemic (Ruel and Huot 1993), although Sbw activity is also known to limit the amount of seeds produced by fir trees (Vincent 1962; Osawa 1994; Pominville *et al.* 1999). The relatively low intensity of Sbw infestations in our sites, however, makes these scenarios improbable.

Without following the growth pattern of gap fillers through time, from before to after the canopy disturbance, identifying a release date remains essentially an extrapolation. Although one can't be certain that the sudden increased stem growth is a response to an opening in the canopy, it is probable given the large amount of samples we used, as well as the relatively high growth rate (some fir attained a 4mm/year rate comparable to that of a free-to-grow w. birch) indicative of optimum growing conditions. Considering the growth rate within 10-year periods before and after, while it reduces the influence of short lasting anomalies, does not eliminate false indications resulting from sustained occurrences such as repeated animal browsing. Other uncontrolled factors could have influenced the growth response, such as gap filler stem density (Vincent 1962), species (White *et al.* 1985), height (Fye and Thomas 1963), vigor (Hatcher 1964), age (Brokaw 1985 and 1987), position within the gap (Liu and Hytteborn 1991), microsite conditions (Narukawa and Yamamoto 2001) and gap size (Brokaw 1987). Others (Fye and Thomas 1963; Ghent 1958) have found that balsam fir and spruce saplings increase their height growth rate by a mean factor of five following an opening up of the canopy by Sbw disturbances. This is less than the average of eightfold factor that we found in increased diameter growth.

It is generally taken for granted that at least some canopy disturbance is required in temperate deciduous (Runkle 1982) and coniferous (White *et al.* 1985) forests for all species, especially shade-intolerant species, to be recruited to the canopy. In the southern boreal forests of Gaspésie, in stands of mixed and coniferous compositions and which have a relatively low canopy, gaps do influence understory tree establishment and development patterns, but not to the extent of completely determining these processes. The contradictory evidence regarding w. birch establishment and survival together with the unmistakable impact of gaps on understory tree growth lead us to conclude, as Runkle (1982) did, that gaps are influential but do not play a critical role in the forest dynamic, at least as regards stand composition.

CHAPITRE II

VARIABILITY OF GAP REGIMES IN SOUTHERN BOREAL FORESTS ACCORDING TO DISTURBANCE AGENT, STAND TYPE, AND ENVIRONMENTAL FACTORS

Abstract

To increase our understanding of the origin and variability of small-scale natural disturbances in southern boreal forests, three aspects of canopy gap ($\leq 1000\text{m}^2$) regimes were investigated. First, we hypothesized that defoliation by the eastern spruce budworm (*Choristoneura fumiferana* Clem.) is the main secondary disturbance agent in the region not only because it produces large open patches, but also because it is responsible for creating most small gaps. For 665 gaps in 30 sites we identified the causes of tree mortality as defoliation by the budworm (Sbw), windthrow or senescence. Second, supposing that the Sbw is the main agent, we expected that stands composed of host-species were most disturbed (i.e.: they have the greatest amount of forest in gap phase). In this way, fir-dominated stands (Fir), stands composed of fir with white spruce (Fir-Sw) and stands composed mostly of black spruce or hardwoods (Low-Fir) should be respectively most, moderately and least disturbed. Third, we hypothesized that the altitude, slope and aspect of a site influences gap regime characteristics such as gap fraction and gap size. Because of the effect of climate on Sbw activity, sites at lower elevation and on southern aspects should be more impacted by the insect. Wind damage is known to be greater at higher altitude, on steeper slopes and on certain aspects because of local wind currents. Gaps should also be on average larger on steeper slopes because in such circumstances treefalls are known to bring about the fall of other trees.

Gap size distributions are similar among sites, and the mean gap size does not augment with gap fraction. The gap fraction is very variable. Although Sbw activity was responsible for most tree mortality, more open forests tend to be composed more of black spruce, are more disturbed by wind and less by the Sbw, and are located on western slopes. The Sbw created as much disturbance in Fir-Sw as in Low-Fir stands. Neither the altitudinal gradient nor the slope inclination have any effect, although very open stands ($>50\%$ gap fraction) are on average on steeper slopes. It was not possible to link together the factors found to influence the gap fraction variability.

2.1 Introduction

The Sbw is the main natural disturbance agent in the Gaspésie region apart from fire (Blais 1983). The insect population reaches epidemic proportions simultaneously in a number of areas, and then displaces itself aerially to other areas (Blais 1983; Morin 1998; Royama 1984; Webb and Irving 1983), creating massive amounts of tree deaths every couple of decades. Winds also cause much canopy disturbance in the region, presumably because of the irregular physiography of the peninsula and its proximity to the open sea (Holt *et al.* 1965). These secondary disturbances have received some attention from scientists, especially Sbw infestations, but often only relatively large scale events are considered and there exists little information on how these agents create small gap disturbance regimes. This is understandable given the large average size of disturbances occurring in the boreal zone generally, but in southern parts of the boreal forest, and especially in eastern Atlantic Canada, the longer fire cycle means that small gap dynamics play a more important part in stand replacement. Identification of the origin of gaps and of the spatial variability of gap regimes will improve our knowledge of how natural ecosystems function, can be useful to produce more accurate natural-based partial wood cutting systems.

The most apparent effect of Sbw epidemics is large patches of open forest which result from the intense defoliation and killing of most trees in some locality. A number of factors are known to render an area particularly susceptible to a Sbw attack, such as the presence of host tree species at the stand and landscape levels (Webb 1957; Bergeron *et al.* 1995; Sue *et al.* 1996), and stand characteristics such as a high tree stem density (MacLean 1980) and trees lacking in vigor (Thibault *et al.* 1995) because they are suppressed (Blais 1958; Webb and Irving 1983), old (MacLean 1980) or growing on infertile (MacLean 1980) or non-mesic (Dupont *et al.* 1991) soils. Balsam fir (*Abies balsamea* (L.) Mill.) is the favorite host tree species, followed by white spruce (*Picea glauca* (Moench) Voss), while black spruce (*Picea mariana* (Mill.) B.S.P.) is much less sought after (Morin *et al.* 1990; MacLean 1980). The spatial arrangement of severely infested areas may also be a function of the distance of the area from epicenters of the Sbw population, or to environmental characteristics making the insect's displacement difficult, such as sites upslope, sites not located in the trajectory of wind currents, and sites which have a colder climate.

It is not known if the Sbw is the predominant disturbance agent in forests characterized by small gaps in the canopy, or if it has this status only in areas of the forest where it creates large patches of open forest. The disturbance history of the region gives reason to believe that the role of Sbw infestations

may be more superficial, or limited to hot spots, than in other regions. In all regions of northeastern North America presently experiencing Sbw epidemics, except the Gaspésie peninsula, these epidemics have apparently been recurring since at least 300 years and probably millennia (Furyaev *et al.* 1983). Only in Gaspésie have Sbw epidemics begun relatively recently, starting in 1911. Since then, episodes in this region have occurred more or less synchronously with those in other regions, and have increased in frequency, duration and severity. The development of Sbw epidemics in the region is due to changes in the forest composition, specifically a greater abundance of balsam fir, which came about through human management practices, as well as other insect epidemics and climatic events which decimated spruce and birch trees (Lévesque 1997). Prior to the emergence of Sbw epidemics, wind was the predominant disturbance agent (Blais 1961), and at present could possibly be the agent mainly responsible for creating small gaps (Webb 1957).

Results from other studies suggest that the physical environment and climatic conditions can strongly influence the gap regime, in terms of the types of disturbance agent and how effective they are (Worrall and Harrington 1988; Foster and Reiners 1983). It is reasonable to expect that in the mountainous terrain of Gaspésie the variability of environments brings about a variability of gap regimes, and along with it a more complex assemblage of disturbance processes. Gap regimes are known to be affected by an altitudinal gradient (Worrall and Harrington 1988; Jonsson 1989; Perkins *et al.* 1992; Battles *et al.* 1995), but not always (Foster and Reiners 1983). Trends, in terms of changing gap fraction and gap size, are not always continuous throughout the whole range of the gradient (Battles *et al.* 1995; Worrall and Harrington 1988). Like for other insects (Worrall and Harrington 1988) the ability of the Sbw to feed and reproduce is lessened in cold and humid weather, making infestations less severe or absent in sites located at higher elevations and on slope aspects towards the north (Craighead 1925; Blais and Martineau 1960; Blais 1961; Webb 1957). Elevations higher than 550m in Gaspésie have been found to be limit the insect's capacity to reproduce (Blais 1961). In some forests above 650m in elevation in Gaspésie, which would otherwise be susceptible to the Sbw, no evidence was found of an epidemic (Dansereau 1999).

Winds are known to create more disturbances at higher elevations (Hunter and Parker 1993; Battles and Fahey 1996; Worrall and Harrington 1988; Jonsson 1990; Geiger 1961; Ruel *et al.* 1998), on steeper slopes (Battles *et al.* 1995), and presumably on certain slope aspects according to the trajectory of local currents (Foster and Reiners 1983; Sprugel 1976; Hunter and Parker 1993). On steeper slopes gaps may also be larger, and the gap fraction higher, because treefalls in such circumstances tend to bring about the downfall of other trees (Hunter and Parker 1993; Battles and Fahey 1996). Increased

wind activity can reduce the development of Sbw populations because larvae are thrown off trees (Blais and Martineau 1960). The net sum of changes is hard to predict because of the conflicting forces at play; for example the amount of disturbances at higher altitude might be augmented because of wind but lessened because of the absence of the Sbw. In the terrain it is visually evident that certain slope aspects are more disturbed than others, but this might be caused by factors not directly related to our identified agents of disturbance (Brang 1998). The lack of information about wind trajectories makes predictions concerning that agent impossible, particularly in regards to which slope aspects would be more affected. Stand composition seems to be a useful factor upon which to base predictions of gap regime characteristics because fir trees are ubiquitous and are vulnerable to all three disturbance agents, being particularly important for the Sbw (Su *et al.* 1996), mechanically weak because of heart rot (Webb 1957; Morris 1948), and relatively short-lived (Morris 1948).

We verified if Sbw is the predominant cause of tree mortality for small canopy gaps, and we hypothesized if it is so then stands with a greater proportion of host species would be more disturbed than other stands. Based on the insect's preference for different species (fir > white spruce > black spruce), as well as on the general vulnerability of fir to windthrow, we expected that fir-dominated stands (Fir) would be much more disturbed than stands mostly composed of black spruce or hardwoods (Low-Fir), and that stands composed of fir and white spruce (Fir-Sw) would be moderately impacted. We also hypothesized that altitude, slope and aspects of sites (see below) would affect the gap regime, without being necessarily cumulative because of the different disturbance agents involved. At higher elevations and on steeper slopes wind disturbances should be more important relative to the Sbw. Gaps on steep slopes were expected to be on average larger. We also expected that south-facing aspects, being warmer, would on average be more affected by the Sbw, and that wind disturbances would be more abundant on some slope aspects (i.e. those affected most by wind currents).

2.2 Study area

Gaps were surveyed in 30 sites in the Bay-of-Chaleurs region of the Gaspésie peninsula, which is the northeastern extension of the Appalachian Mountain Chain located in the southeast of the province of Québec, Canada (see figure A). The sites are spread out on this south side of the mountain chain by as much as 100km distance from each other. Sites range from 139m to 770m (mean of 551m, mode of 533m) in altitude. Slopes range from 2% to 62% (mean of 28%, mode of 18%). The region, at the southern limit of the boreal zone, is part of both the Balsam fir-white birch and Balsam fir-yellow

birch bioclimatic domains according to the Québec government classification (MRNQ 2000), or part of the Great Lakes-St. Lawrence (L.6) and Gaspé (B.2) Forests Regions according to Rowe (1972). The region has a continental humid climate (Thibault 1987), with mean daily temperatures from 1.6 to 3.7°C and mean annual precipitation from 1019mm to 1059mm (with between 253mm and 457mm as snow), according to Environment Canada records taken at meteorological centers in New Richmond (1964-1990), Saint-Élzéar (1949-1990) and Murdochville (1952-1990). All sites are on mesic soils, which are mainly composed of tills usually less than 1m thick, glaciofluvial deposits, and accumulations of colluviums downslope (Charbonneau and David 1993; Thibault *et al.* 1995).

In the region the fire cycle is approximately 200 years long (Lauzon *et al.* 2005). Balsam fir trees dominate the landscape, both in the canopy and in the understory. Near the coast some spruce (*Picea* spp.) and eastern white cedar (*Thuja occidentalis* L.) are present, but the fir is mostly accompanied by hardwoods such as yellow birch (*Betula alleghaniensis* Britton.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white birch (*Betula papyrifera* Marsh), mountain ash (*Sorbus Americana* Marsh.), pin cherry (*Prunus pensylvanica* L.f.), and more rarely with white pine (*Pinus strobes* L). Further up in altitude, stands are composed mostly of only fir or a spruce, including black spruce or white spruce, or a combination of them, often with white birch present. Trembling aspen (*Populus tremuloides* Michx.) are mostly found only in close proximity to roads or burnt areas, and no red spruce (*Picea rubens* Sarg.) were encountered.

2.3 Methods

Investigated sites showed no signs of recent major human or natural disturbances. The existence of old-growth characteristics was a condition for site selection, such as an irregular stand structure, and abundant coarse woody debris and snags of variously aged trees. The more or less equal representation of three main stand types was also taken into consideration, including stands with at least 70% in fir (Fir), stands composed of at least 60% of fir and white spruce (Fir-Sw), and stands composed of other species (<60% of fir and white spruce), mainly black spruce or yellow birch (Low-Fir). This classification is based on the presence of host-species for the Sbw. A one-way Anova was used to evaluate if disturbance severity differed among the three stand types.

Gaps were surveyed by the Line Intersect Sampling (LIS) method (Runkle 1992), with a single transect between 150m and 500m in length in each site. Beginning and end points of transects were

distanced at least 20m from areas modified by humans or by a severe natural disturbance, so that the stand structure and composition was relatively homogeneous. To be considered a gap (Runkle 1982) the forest canopy opening had to have been caused by the apparent death of a canopy tree, and gap filling trees had to be not taller than 2/3 the canopy height, which was nearly always the case. Gaps larger than the maximum size used for this study (1000m²), river crossings and permanently denuded areas were very rarely encountered, and if so were discounted. The gap fraction, or percent of forest in gap phase, was calculated as the proportion of transect length without tree cover. The site altitude was measured with a GPS instrument, and computed from the average of values recorded at beginning and end points of the transect. The site aspect was estimated with a compass. Simple regressions were used to evaluate the relationship between the disturbance regime (gap fraction or gap size) and the altitude or slope of sites. The effect of slope aspect (direction of the slope) on gap fraction is graphically shown in a polar plot. Various categorizations of the aspect were used, including 2 groups (north versus south, or east versus west), 4 groups (north-east, south-east, south-west, and north-west), and 8 groups. A stepwise multiple regression was used to determine if all significant factors are interrelated.

At every 100m along transects an evaluation of stand characteristics, a measurement of slope (percent inclination measured with clinometer), and a verification of mesic soil conditions were made. A prism (grade 2) was used to estimate the tree (dbh \geq 10cm) surface area and stem density per species (see appendix D), as well as the diameter at breast height (dbh) of individual trees. As well, three co-dominants or dominants trees were used to evaluate the height of the canopy and the age (through analysis of cores removed at dbh) of dominant species.

For all 665 gaps surveyed the species of gap makers (i.e.: trees whose elimination originated the gap) and the agent of disturbance were identified. Neither the number nor the proportion of gap makers were recorded, but the species present were noted. The cause of tree death was determined as being either defoliation by the (Sbw), windthrow, or senescence, the last category made up of cases not covered by the other two. Government (MRNQ, Québec) aerial surveys of areas experiencing moderate-to-severe levels of defoliation by the Sbw, recorded on maps (1:250 000), show that the epidemic in our sites occurred from 1973 to 1991 inclusively. The epidemic episode should be completely included in our analysis, which covers the 24 years before the sampling date (2002). In each gap the causes of disturbance were differentiated visually on the basis of the physical condition of gap makers, including the presence of bark, broken tops, and the presence of twigs and branches (Dansereau 1999). Trees killed by wind nearly always snapped rather than upended. Although it is possible that some trees dead by senescence a long time ago may have been counted wrongly, Sbw-

killed trees were generally easily distinguished. When more than one agent was responsible for creating the gap, which occurred very rarely, that gap was not used when comparing relative frequencies of gap origins.

One hundred and one gaps from 8 sites were chosen for gap size measurements. Various numbers of gaps were chosen randomly along transects in order to estimate the natural distribution of gap sizes. Comparison of size distributions between sites was done using the non-parametric Wilcoxon test and a comparison-of-means test. A one-way Anova (with transformed values) was used to compare gap sizes among stand types, with 35 gaps coming from 3 Fir stands, 25 gaps from 2 Fir-Sw stands, and 41 gaps from 3 Low-Fir stands. Gap size (i.e.: surface area of actual gaps) was estimated by measuring the length of the longest possible axis within the gap, and a various number of lateral axes perpendicular to it; the total area was calculated by adding up the area of rectangles thereby obtained. When the shape of a gap was too irregular to use a single main axis, two sets of measurements were made in the field (Kneeshaw and Bergeron 1998). Depending on the size of the gap, the distance between the lateral axes varied from 1m to 10m, but most intervals were 1 meter long and very rarely more than 2 meters. Gap extremities were identified as the vertical projection at ground level of the canopy tree edges. In order to have a more accurate estimate of the frequency of gap sizes we applied the corrections to the LIS suggested by Runkle (1982: second method), whereby a value proportional to the probability of interception is used to transform the size frequencies (see general introduction).

We infer that the present proportion of tree species in a given stand is a good indication of the proportion of species prior to disturbances, in other words for each species the amount of trees eliminated was proportional to the amount of trees of that species that existed beforehand. Fir trees were killed more often than other species in all types of stands, but the amount of fir killed was proportional to the amount of fir originally present, so that the species proportions have remained similar. The relationship between the amount of fir killed and the amount of fir remaining in the stand is apparent whether one measures the amount killed in terms of the % of gaps with killed fir or in terms of the % fir killed at least once per gap, and either when considering stands individually or grouped according to the three stand types (table E and fig. C). The effect of stand composition, in terms of the presence of Sbw host species (% of fir, % of white spruce and % of black spruce) and other species groups (% of conifers, and % of deciduous), on overall disturbance severity (i.e.: gap fraction) was evaluated by calculating the coefficient of determination (r^2) and the statistical significance of the simple regressions.

2.4 Results

A negative exponential distribution of gap sizes is characteristic in all sites, with few large gaps and many small ones. Gaps at one site (the Fir stand no.A7) are significantly smaller than at other sites (non-parametric Wilcoxon test: $P=0.0028$). However, concluding from this that gap sizes are different between sites is probably not justified, given the great variability of sizes and the unequal and sometimes few number of replicates for each site (fig. 2.1). In any case, gap sizes in the three stand types are not statistically different (one-way Anova, with values transformed by their natural logarithm: $\text{Prob}>F = 0.4486$). Sizes range from 3m^2 to 698m^2 . The mean gap size is 68m^2 , but when corrections for the LIS bias are applied (Runkle 1982) the mean gap size is only 28m^2 , with half of the gaps measuring $<11\text{m}^2$ and half of the total gap area in gaps $<65\text{m}^2$. No trend in gap shape or gap orientation is apparent (see appendix E). In contrast, the gap fraction does varie much among the 30 sites (18% to 64%), and is on average high (42%) (fig. 2.2).

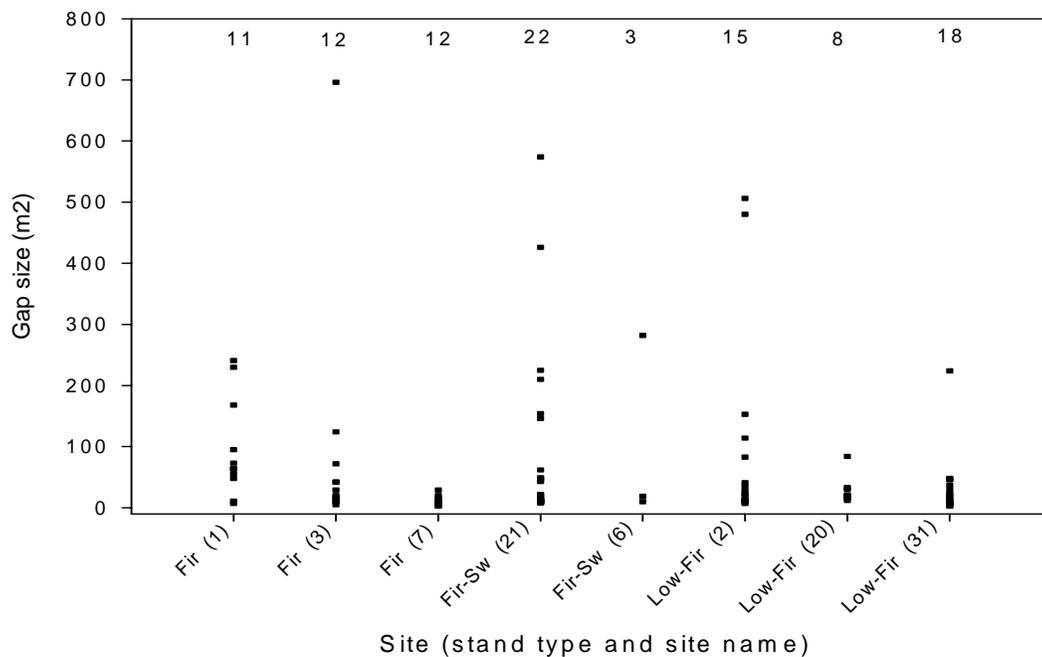


Figure 2.1. The size of 101 gaps from 8 sites (the number of gaps per site is shown in the top portion of the graphic).

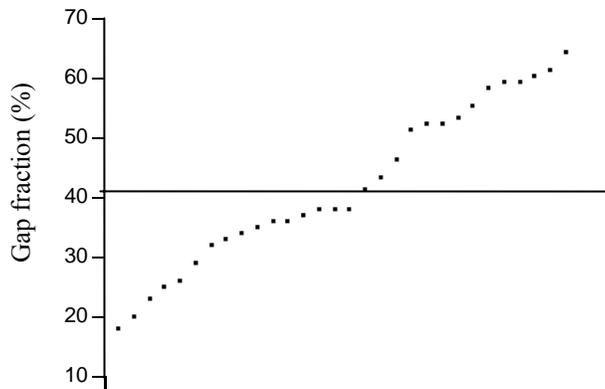


Figure 2.2. The distribution of gap fractions (with solid bar indicating mean value).

Altitude has no effect on the gap fraction ($P=0.3873$) (fig. 2.3), on the stand composition (in terms of species host to the Sbw), or on the cause of tree mortality. Linear regressions showed no significant change in the % of fir ($P=0.5582$), the % of white spruce ($P=0.7573$) or the % of black spruce ($P=0.1118$) in stands along the altitudinal gradient. The proportions of gaps created by Sbw ($P=0.1972$), wind ($P=0.3789$) or senescence ($P=0.2339$) were also not different.

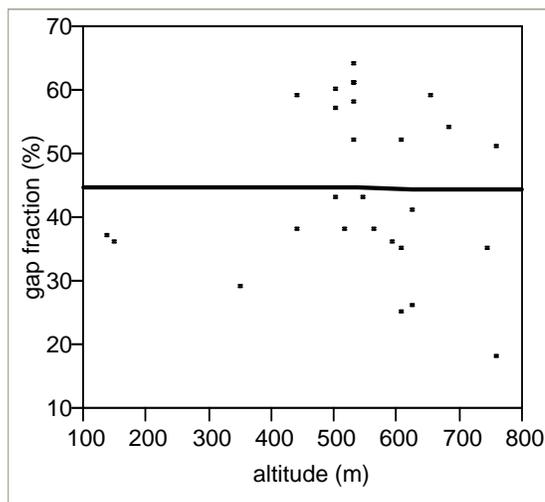


Figure 2.3. Linear regression of gap fraction with site altitude.

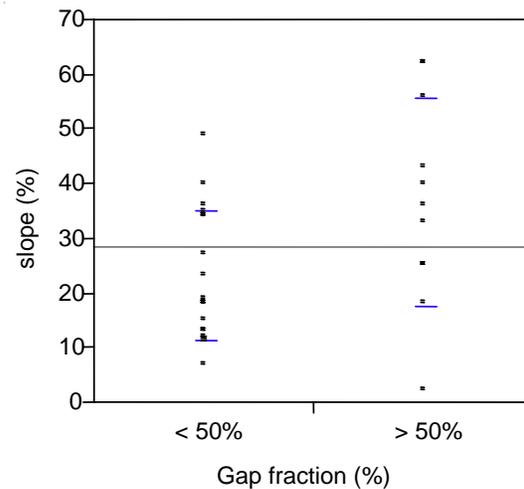


Figure 2.4. The slope of sites with gap fractions < 50% and in sites with gap fractions > 50% (with mean value line and one standard deviations).

The gap fraction is not greater on steeper slopes ($P=0.1122$), although sites that are exceptionally open (>50% compared to <50% gap fraction) tend to be located on steeper inclines when considered as a category (T test: $P=0.0291$ and $R^2=0.17$). Although the range of values used are not extensive, and therefore the conclusions are can only be tentative, simple regressions showed that there is no significant relationship between disturbance severity (gap fraction) and canopy height, mean dbh, mean stem density, and mean basal area in stands.

Table 2.1

The frequency of gaps according to stand type and disturbance origin
(% of gaps at least partly created by that agent)
(the number of gaps used for the calculation is provided in the last column).

	Sbw	windthrow	senescence	Nb. of gaps
Fir	73 (31) a	25 (21) d	34 (28) cd	130
Fir-Sw	59 (29) ab	40 (18) bcd	41 (25) bcd	253
Low-Fir	56 (40) abc	44 (25) bcd	40 (9) bcd	251
all stands	65 (32) a	37 (24) cd	36 (23) d	665

N.B. Standard deviations are in parentheses

N.B. letters show similar groups, according to Student T multiple comparison tests

Sbw defoliation is the main cause of tree mortality, being at least partially responsible for creating nearly twice as many gaps as either windthrow or senescence (table 2.1). Although globally important, Sbw activity is indirectly proportional to the gap fraction: forests are more open when there is proportionally less Sbw activity (linear regression: $P= 0.0191$) and more windthrow activity (linear regression: $P= 0.0205$) (fig. 2.5). The level of senescence mortality is not significantly associated with gap fraction.

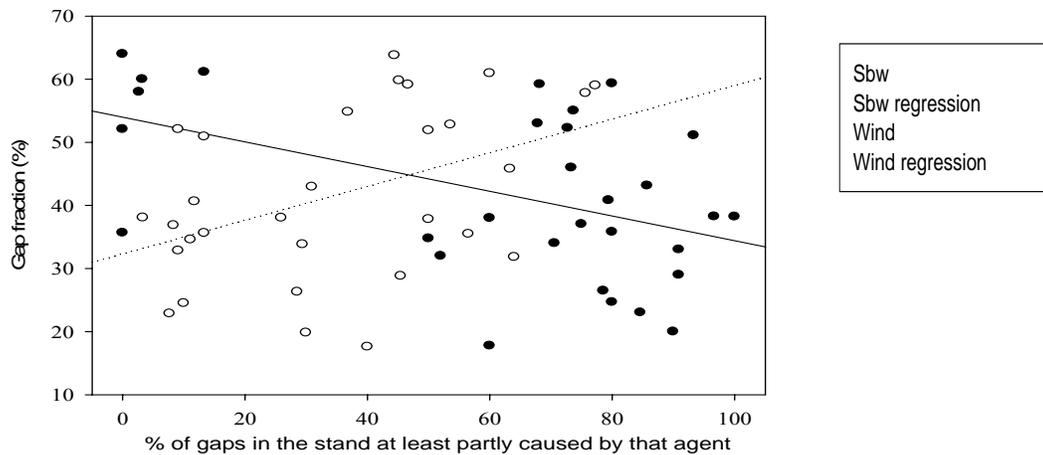


Figure 2.5. The relative importance of Sbw and Windthrow as a function of the gap fraction of the stand (Sbw: $b[1]=-0,196$) (Windthrow: $b[1]=0,269$).

Stands that are more severely disturbed do not tend to have a higher proportion of fir composition (or a combination of white spruce and fir). Rather, these stands tend to have more black spruce (polynomial 2nd degree regression including only the 21 out of 27 sites which have black spruce in the canopy: $P=0.0170$; $R^2=0.36$) (fig. 2.6). The gap fraction in Low-Fir stands, where black spruce in some cases forms an important component of the composition, is on average higher than in Fir stands (35%), but no different than in Fir-Sw stands (both have 45%).

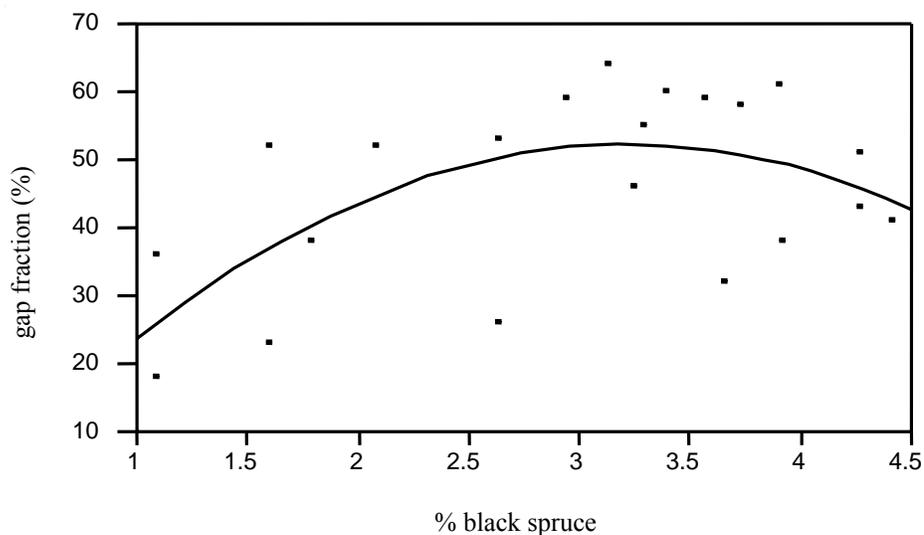


Figure 2.6. The gap fraction as a function of the % black spruce in the canopy (the values of the independent value have been transformed by natural logarithm in order to have a normal distribution).

More open forests also tend to be situated on western slope aspects (T test for East versus West: $P=0.0058$; $R^2=0.25$) (fig. 2.7). A simple regression using azimuth values independently (based on cardinal directions) suggested that the direction of the slope might have a significant impact ($P=0.0113$). Dividing the azimuthal projection into 8 parts was not effective (one-way Anova: $P=0.2430$), but it was when divided into 4 parts (North, East, West, and South) ($P=0.0459$; $R^2=0.27$), although not as significantly as when divided into 2 parts (East and West).

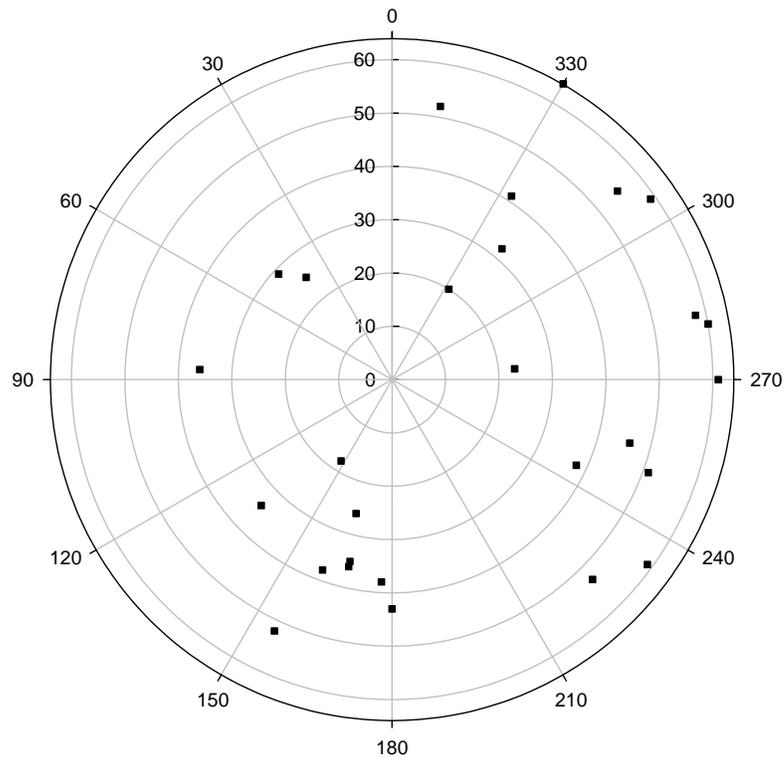


Figure 2.7. The gap fraction as a function of slope aspect.

No relationship was found between the factors that significantly influence gap fraction (% wind disturbance, % Sbw disturbance, % black spruce, site aspect, and slope) through any combination, and an attempt to use a stepwise multiple regression was unsuccessful.

2.5 Discussion

The results show that the Sbw is clearly the main cause of tree mortality, but also that increased disturbance severity is not simply the consequence of more Sbw activity or the amount of fir in the stand. Proportionally the Sbw created a lot more disturbance in Fir stands as expected, but unexpectedly Fir-Sw and Low-Fir stands were roughly equally affected by the insect (table 2.1). The reason that the Sbw was not more active in Fir-Sw than in Low-Fir stands is probably because the majority of gap makers in Fir-Sw stands were fir (85%), which means that white spruce was mostly spared in those stands. The fact that gap size does not vary with gap fraction could indicate that disturbance severity is not affected by the distance of sites to Sbw population epicenters, but the homogeneity of gap maker species can also have contributed to gap size uniformity. Arriving at such conclusions, however, would require information about Sbw activity in adjacent stands and the location of Sbw population epicenters, since the importance of stand characteristics depends on the intensity of Sbw infestations in the area (Craighead 1925; McLean 1980).

The abundance of fir in a stand canopy does not determine the gap size (see chapter 3), the gap fraction in the stand (Fir stands have a lower fraction than both other stands, and in Low-Fir stands the fraction is as high as in Fir-Sw stands), or the relative importance of Sbw activity (Fir-Sw stands are as much affected as Low-Fir stands). It is surprising that the amount of black spruce in stands determines gap fraction variability, given the lower vulnerability and longer lifespan generally associated with that species. The ubiquitous presence of fir among gap fillers, as well as the absence of a relationship between altitude and % black spruce among canopy trees, means that it is probably not a slower gap closure rate which is at cause.

A number of reasons may explain the absence of correlations of wind activity with altitude (positive), and of Sbw activity with altitude (negative). In some circumstances the Sbw is apparently able to reproduce at higher altitudes (Fillion *et al.* 1998). In our irregularly structured stands the level of wind damage may have more to do with the presence of tall (Hunter and Parker 1993; but see Hytteborne and Liu 1991) and old (Ruel 1995) veteran trees, wherever they may be, rather than the high exposure at high altitude, where trees may be better adapted to winds of regular intensity (Foster and Reiners 1983). Some authors have noted that small or oppressed trees are sometimes preferably attacked by the Sbw (Webb and Irwing 1983; Blais 1958; Sheedy 1980), especially during moderate invasions (Craighead 1925; Batzer 1973), which could mean that not all disturbance by Sbw was taken into

account in our study because only gap makers (i.e.: mature canopy trees) were considered. We don't have any reason to believe, however, that understory trees are more vulnerable at higher altitudes.

Gap size distributions are usually found to be similar in various forest types when the sample population is sufficiently large (e.g.: Runkle 1989; Liu and Hytteborn 1991). On the contrary, gap fractions have often been found to be variable, even within similar forest types (e.g.: Yamamoto (1995) compared to Foster and Reiners (1986)). The variability of gap fractions in our sites is not surprising, given the variable effect of disturbance agents (Worrall and Harrington 1988) and environmental conditions (Battles *et al.* 1995) typical of mountainous terrain such as exists in Gaspésie. Slope had no effect on gap size perhaps because the maximum slope among the 8 selected sites from which gap size data was collected is 35%, which is far below the 62% reached in some of our sites, and of course the effect of slope would be most apparent on steeper inclines.

CHAPITRE III

THE TEMPORAL PATTERN OF GAP DISTURBANCES BY VARIOUS AGENTS IN SOUTHERN BOREAL FORESTS IN EASTERN CANADA

Abstract

Apart from fire, defoliation by the eastern spruce budworm (*Choristoneura fumiferana* (Clem.) is the main cause of tree mortality in fir forests of the Gaspésie region, in southeastern Canada. Our investigation of 27 stands in the Baie-des-Chaleurs area, with compositions moderately to strongly dominated by host species, suggests that the budworm (Sbw) is the agent mainly responsible for creating small gaps in the canopy. The dating of gap formation during the past 24 years shows that a great increase of disturbances occurred during the Sbw epidemic period (1973-1991) in all stand types. There was also much annual variability of disturbance intensity within the Sbw epidemic period. Fewer gaps are created by wind or senescence, and their temporal distribution of disturbances does not seem to follow any pattern. The return interval of disturbances is on average approximately 50 years (or 2.0% area/year), but the time frame used in this study is too short to estimate if the gap regime is stable. All stand types experienced years of exceptionally high levels of disturbance, but the amplitude is greatest in fir-dominated stands (54% of actual gap area was created in only one year). In contrast, disturbance events in stands containing few Sbw-host species are more spread out throughout the period. Years of exceptionally high levels of disturbance do not occur simultaneously among stand types, not even Sbw disturbances. There is also no evidence that Sbw disturbances have led to a greater frequency of other types of disturbances.

The origin of disturbance (Sbw, wind or senescence) has no effect on the size of gaps, although this may be misleading because of the skewed distribution of values. But mean gap sizes are different: wind creates the largest and senescence the smallest gaps. Senescence gaps are particularly small in fir-dominated stands, and Sbw gaps are particularly small in stands with few Sbw-host species. Surprisingly, fir gap fillers are most abundant in wind gaps and least in senescence gaps, even though it is a shade-tolerant species. Generally a circular succession characterizes tree replacement processes (fir replacing fir), and shade-intolerant species (white birch) are maintained in the stand. Based on the relative amount of fir gap makers and survivors, proportionally more fir died in stands having low amounts of fir, suggesting that in this case patches of fir were rotating faster than other parts of the stand. In fir-dominated stands on the other hand, gap makers were proportionally more often white birch, but the contrast here with the residual stand composition is less great.

3.1 Introduction

Small gap disturbances are usually caused by a number of different agents (McCarthy 2001). Considering the effect of these agents separately is useful when evaluating disturbance patterns (Frelich 2002) and to understand how the various strata constitute a regime (White and Pickett 1985). In boreal fir forests in Eastern North America the main causes of tree mortality, apart from fire, are generally defoliation by the Sbw, winds and tree senescence in that order (Webb 1957; Furyaev *et al.* 1983; Kneeshaw and Bergeron 1998). Although most studies of natural disturbance systems in boreal forests evaluate large scale events, in some regions to the south and where much precipitation occurs, such as in the Gaspésie peninsula, the time interval between fires is long and gap dynamics play an important role. Better understanding the causes and patterns of the gap dynamics, as well as how these determine stand succession, will improve our knowledge of how the forest functions and allow us to develop silvicultural systems that emulate natural processes.

Sbw outbreaks generally occur every 20 to 30 years and cause massive tree mortality (MacLean 1980). Typically within a region, some areas are intensely disturbed by the insect, resulting in large patches of open forest, while in other areas tree mortality is dispersed and only small gaps are created in the canopy (MacLean *et al.* 2002). This however might not be the case in Gaspésie because Sbw epidemics are a recent development. In other regions of Eastern North America Sbw epidemics have been recurring since centuries and perhaps millennia (Furyaev *et al.* 1983), but in Gaspésie they began only in 1911, at first with moderate force, but with time the infestations have become increasingly severe and more frequent (Blais 1984). The cause for the emergence of Sbw epidemics has been attributed to an increased abundance of balsam fir (*Abies balsamea* (L.) Mill.) in the region, which came about as a consequence of forest management practices, spruce decline due to epidemics by other insects, and birch (*Betula* spp.) decline due to climatically induced dieback (Blais 1961; Lévesque 1999). Before the twentieth century wind was most probably the main agent of secondary disturbances (Lévesque (Lévesque 1999; Blais 1983), just as it is now the main agent in New England Appalachian mixed and coniferous forests where no Sbw epidemics occur (Worrall and Harrington 1988). Winds are particularly important in Gaspésie because of the irregular topography and the proximity to the sea (Holt *et al.* 1965). The increase of fir in the region presumably also brought about more wind disturbances, because heart rot and a superficial root system make that species especially vulnerable on an individual basis (Webb 1957). It may therefore be the case that, in Gaspésie, Sbw is today the main disturbance agent in some concentrated areas, where patches are produced, but that winds are still mainly responsible for creating small gaps. This remains a theory, however, because little is known

about the etiology of small canopy gaps in Gaspésie (Dansereau 1999), and there is no reason for thinking that the Sbw behaves any differently than in other regions. The fact that Sbw epidemics in Gaspésie occur in forests located in both the Fir-white birch and Fir-yellow birch bioclimatic domains (Thibault *et al.* 1995), and not just in stands mainly composed of fir, could imply for example that the Sbw is an important cause of disturbances at all spatial scales. Although senescence may be an important cause of death in other forests (Bartemucci *et al.* 2002), this is probably not the case in Gaspésie because of the short return interval of disturbances (Morris 1948; Webb 1957).

Historic changes to the disturbance regime, in terms of their etiology, can affect such aspects as gap size, the process of the canopy opening, soil disturbances, annual or periodic variability in the amount of disturbance, and the return interval of disturbances (Dahir and Lorimer 1996). Their effect on stand structure and composition can in turn influence stand succession. If Sbw is responsible for creating most gaps we would expect that the amount of disturbances greatly increases during the epidemic period, whose beginning and end dates are usually precisely known and synchronous at least throughout the landscape if not the region (MacLean 1980; Thibault *et al.* 1995; Lévesque 1999). In the same way, the return interval of disturbances during the epidemic period would also be a lot shorter. Even within the epidemic period the intensity of disturbances by the Sbw varies on an annual basis according to a recognizable pattern (MacLean 1980). In comparison, the amount of disturbances by wind would be much lower and their occurrence more irregular (Battles and Fahey 1996). Irrespective of which agent (Sbw or wind) is the main agent of disturbances, the amount of tree mortality by senescence should be the lowest of all, and events should be the most evenly distributed in time.

The recruitment of shade-tolerant tree species, such as balsam fir, tends to be more successful where the canopy is closer to being intact (Morin 1990), for example when canopy openings are smallest (Ghent 1958; Kneeshaw and Bergeron 1999) or partially formed (Kneeshaw *et al.* 1998), and when the soil substrate is undisturbed (Dahir and Lorimer 1996). Trees killed by Sbw defoliation commonly show a more complete branch structure (without twigs) than trees killed by senescence, resulting in gaps that are less fully open (Dansereau 1999). Gaps created by wind, in contrast, are suddenly and fully opened, and the topsoil may be disturbed. A circular stand succession of self-replacing fir is a typical consequence of Sbw epidemics in forests where pre-established fir are abundant and where herbaceous understory competition is weak, which is generally the case in Gaspésie (Hatcher 1964; Baskerville 1975; Morin 1994; Morin and Laprise 1997; Bergeron *et al.* 1995; MacLean 1988; Kneeshaw and Bergeron 1999; Vincent 1962; Fye and Thomas 1963). Fir regeneration is expected to

be abundant in canopy gaps created by trees killed by the Sbw (and by senescence) because these are usually formed gradually and soil conditions are maintained intact. The effect of these various disturbance types on gap regime characteristics and tree recruitment are different according to the composition and structure of stands, most notably in regards to gap size (Fye and Thomas 1963).

In this study we evaluated, over a period of 24 years, how Sbw defoliation, wind, and senescence have contributed towards the overall temporal pattern of disturbances and stand succession. We used three stand types to test our inferences, based on the presence of tree species which are host to the Sbw. We hypothesized that the Sbw is responsible for creating most canopy disturbances, and therefore that the overall disturbance pattern through time is a reflection of the varying intensity of Sbw activity. We hypothesized as well that Sbw outbreaks are particularly influential in stands having a greater host species component, and that overall they are responsible for an increasing abundance of fir in the region.

3.2 Study area

Gaps were surveyed in 27 sites in the Bay-of-Chaleurs region in the Gaspésie Peninsula, which is the northeastern extension of the Appalachian Mountain Chain located in the eastern part of the province of Québec (see figure A). The sites are spread out on this south side of the mountain chain, by as much as 100km distance from each other, at altitudes ranging from 139m to 770m (mean of 551 and mode of 533). The region, at the southern limit of the boreal zone, is part of both the Balsam fir-white birch and Balsam fir-yellow birch bioclimatic domains according to the Québec government classification (MRNQ 2000), or part of the Great Lakes-St. Lawrence (L.6) and Gaspé (B.2) Forests Regions according to Rowe (1972). The region has a continental humid climate (Thibault 1987), with mean daily temperatures from 1.6 to 3.7°C and mean annual precipitation from 1019mm to 1059mm (with between 253mm and 457mm as snow), according to Environment Canada records taken at meteorological centers in New Richmond (1964-1990), Saint-Élzéar (1949-1990) and Murdochville (1952-1990). All soils have mesic conditions, and are mainly composed of tills usually less than 1m thick, glaciofluvial deposits, and accumulations of colluviums downslope (Charbonneau and David 1993; Thibault *et al.* 1995).

The fire cycle in the region is approximately 200 years long (Lauzon *et al.* 2005). No recent major human or natural disturbances occurred at our sites. The existence of old-growth characteristics was a

condition for selecting sites, such as an irregular stand structure, and abundant coarse woody debris and snags of variously aged trees. Three main stand types was almost equally represented, including fir-dominated stands (Fir), stands composed of fir along with white spruce (Fir-Sw), and stands composed of other species, mainly black spruce or yellow birch (Low-Fir). Balsam fir is the favored host species of the Sbw, followed by white spruce (*Picea glauca* (Moench) Voss), while black spruce (*Picea mariana* (Mill.) B.S.P.) is much less attractive (Morin *et al.* 1990).

The forest composition in the region is dominated by balsam fir, both in the canopy and in the understory. Near the coast some spruce (*Picea* spp.) and eastern white cedar (*Thuja occidentalis* L.) are present, but the fir is mostly accompanied by hardwoods such as yellow birch (*Betula alleghaniensis* Britton.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white birch (*Betula papyrifera* Marsh), mountain ash (*Sorbus Americana* Marsh.), pin cherry (*Prunus pensylvanica* L.f.), and more rarely with white pine (*Pinus strobes* L). Further up in altitude, stands are composed mostly of only fir or a spruce, including black spruce (*Picea mariana* (Mill.) B.S.P.) or white spruce (*Picea glauca* (Moench) Voss), or a combination of them, often with a presence of white birch. Trembling aspen (*Populus tremuloides* Michx.) are mostly found only in close proximity to roads or burnt areas, and no red spruce (*Picea rubens* Sarg.) were encountered.

3.3 Methods

Gaps were surveyed by the Line Intersect Sampling (LIS) method (Runkle 1992), with a single transect between 150m and 500m in length in each site. Beginning and end points of transects were distanced at least 20m from areas modified by humans or by a severe natural disturbance, so that stands were structurally and compositionally homogeneous. To be considered a gap (Runkle 1982) the forest canopy opening had to have been caused by the apparent death of a canopy tree, and gap filling trees had to be not taller than 2/3 the canopy height, which was nearly always the case. Gap fraction was calculated as the proportion of the transect without forest cover (Runkle 1992).

The cause of tree death was determined as being either defoliation by the Sbw, windthrow, or senescence, the last category made up of cases not covered by the other two. The evaluation was visually done on the basis of the physical condition of gap makers, including the presence of bark, broken tops, and the presence of twigs and branches (Dansereau 1999). Trees killed by wind nearly always snapped rather than upended. Although it is possible that some trees dead by senescence a long

time ago may have been counted wrongly, Sbw-killed trees were generally easily distinguished. If a tree killed by the Sbw was thereafter thrown by the wind, the gap was considered to have a Sbw origin. Gaps originating from multiple events, which was rarely the case, were considered as part of one of four additional categories (3 double and 1 triple combinations) when evaluating the impact on sapling regeneration and mean gap size. Such gaps were however eliminated from the sample population when evaluating the relative importance of agents in the three stand types, and when evaluating the different gap size distributions (with a one-way ANOVA) produced by each agent.

The relative importance of disturbance agents was also evaluated by the extent to which each one contributed to setting the overall temporal pattern of disturbance intensity. Epidemics generally last between 10 and 26 years (Blais 1983; MacLean 1980). The Sbw population continually expands until no more food is available in the vicinity, after which it either moves on to other areas or returns to an endemic level (Blais 1983). Government (MRNQ, Québec) aerial surveys of areas experiencing moderate-to-severe levels of defoliation by the Sbw, recorded on maps (1:250 000), show that the epidemic in our sites occurred from 1973 to 1991 inclusively. The epidemic episode should be completely included in our analysis. Between the beginning of the epidemic (i.e.: intense defoliation of trees) and the beginning of massive tree mortality there is usually a delay of 3 to 7 years (Blais 1979; MacLean 1980), but it can be as much as 10 years (Nealis and Ortiz 1996). When the insect population is in its endemic phase defoliations do not generally lead to tree death (Su *et al.* 1996), but for a few years after the end of the epidemic period some amount of induced mortality can persist (Stillwell 1956 *in* Batzer 1973) because the infestation has rendered some trees moribund (Blais 1960) and because trees bordering gaps are more exposed to wind or other agents (Blais and Martineau 1960; Batzer 1973). In the midst of the epidemic period there often is a temporary (1-2 years) lull in the defoliation rate, and presumably in the mortality rate as well, but not always occurring during the same years (Morin *et al.* 1993; Simpson and Coy 1999).

One hundred and one gaps were used to evaluate gap size and tree regeneration within the actual gap, but only 99 gaps were used for evaluating the impact of gap origin and only 79 gaps were dated. These gaps were chosen in 8 sites, for reasons of fieldwork practicality and in order to have approximately the same number of gaps in each stand type. Rather than aiming to have a same number of gaps in each size class, series of gaps were chosen randomly along transects in order to estimate the natural distribution of gap sizes. Gap size (i.e.: surface area of actual gaps) was estimated by measuring the length of the longest possible axis within the gap, and a various number of lateral axes perpendicular to it; the total area was calculated by adding up the area of rectangles thereby obtained. When the shape

of a gap was too irregular to use a single main axis, parts of the gap were measured separately in the field (Kneeshaw and Bergeron 1998). Depending on the size of the gap the distance between the lateral axes varied from 1m to 10m, but most intervals were 1 meter long and very rarely more than 2 meters. Gap extremities were identified as the vertical projection at ground level of the canopy tree edges.

Stand and site attributes were evaluated at every 100 meters along the survey transects. The species composition of stands was estimated by considering tree stems with $dbh \geq 10\text{cm}$ with a prism (no.2). Because the amount of fir gap makers was proportional to the amount of fir trees presently in the canopy (see section Field Area and Study Methods), we assume that the present composition of stands adequately reflects the stand composition prior to the disturbances. For the analysis we grouped the 27 stands in three types, depending on the susceptibility of their tree species to the Sbw: stands that have a high proportion of fir ($\geq 70\%$) and therefore should be the most susceptible ("Fir"), stands that have a considerable amount of fir and white spruce ($\geq 60\%$ of fir and w.spruce) and should be moderately susceptible ("Fir-Sw"), and finally stands that have a low amount of fir and white spruce ($< 60\%$ of fir and w.spruce) and should be the least susceptible ("Low-Fir"). This last stand type (Low-Fir) includes stands having a number of intolerant deciduous trees, as well as stands having a relatively large number of black spruce (see appendix D). Of the 27 stands, 8, 10 and 9 were respectfully Fir, Fir-Sw and Low-Fir types. As regards the subgroup of gaps used to determine gap size, gap age (with slightly different proportions) and the sapling composition in gaps, 36%, 24% and 39% of them were respectively in Fir, Fir-Sw and Low-fir stand types.

The number and species of trees regenerating within gaps was estimated by sampling a variable portion of the area, alongside 1m. wide transects at the center, at mid point and at the extremity of axes running towards the four cardinal directions from the center of the gap. For each of the 4 axes the length of sampling transect never exceeded 7m, because in larger gaps this length (7m) was divided equally along the axis (center, midpoint and endpoint). Two tree size categories were distinguished, seedlings (stems with $\leq 1.0\text{cm}$ diameter at ground level) and saplings ($> 1.0\text{cm}$ diameter at ground level). Only the presence of invading herbaceous species was noted because their existence was usually relatively insignificant.

The dating of small-scale disturbance events in the best of situations comprises difficulties and inevitably is sometimes impracticable (Foster and Reiners 1986). We aged gaps by identifying sudden radial growth releases among the tallest gap filler stems inside actual gap areas, which it was inferred were caused by the likewise sudden availability of light in the understory. At least 3 and often

considerably more gap fillers were used per gap, usually balsam fir (279 stems, or 85%) but sometimes also white birch (44 stems). Stem sections at ground level were sanded and the width of rings measured to a precision of 0.01mm with a Measure J2X (2001) apparatus and a binocular microscope with magnification up to 50x. Mean values were obtained from two readings on each sample, along the shortest and longest radii, in order to reduce the effect of asymmetrical growth around the stem and of a transversal slice less than perpendicular. We didn't check for absent or superfluous rings, but both ring counts had to have the same total number of rings. We defined a significant growth response, like Orwig and Abrams (1995) and others (Nowacki and Abrams 1997, Rensch *et al.* 2002 and 2003) have done, as at least 100% Growth Change (%GC) between the mean growth rates during the 10 years following a year from that of the 10 years preceding it (see appendix B):

$$\%GC = \frac{100(M_2 - M_1)}{M_1}$$

Where: M_1 = the sequence of the 10 preceding years

M_2 = the sequence of the 10 following years

[For example: For the %GC of the year 1950, M_1 =1941-1950, and M_2 =1951-1960]

A one-year delay is integrated in the equation to account for the delayed response of the plant. The 10 year period is long enough not to be overly influenced by short term climatic artefacts (Lorimer and Frelich 1989), and should reflect most of the growth change thrust (Orwig and Abrams 1995). Some of the 101 gaps were not used for dating disturbances because either no samples were collected (14 gaps), no date was able to be assigned (11 gaps), or because the age of the gap was longer than 25 years (4 gaps), which we estimate to be the maximum gap age (see appendix C). In the rare instances (7) when two disturbance events were identified within the same gap, the area (or transect segment) was considered as two distinct gaps. The annual rate of disturbance was calculated as the proportion of the total transect length covered by gaps with the same age. The return interval of disturbances was calculated as the reciprocal of the rate (%) of area (here represented by the linear transect) disturbed during the period (Runkle 1982). Stem growth analysis on a number of fir and birch gap fillers suggest that it takes between 25 and 30 years for gap fillers to reach the canopy level, in other words for gaps to become closed, assuming that gaps are not closed laterally by bordering trees (see general introduction). This is therefore the maximum length of time that can be used to calculate the rate of return of disturbances, without risk of overlooking gaps which have closed.

3.4 Results

The Sbw is responsible for most disturbances: 65% of gaps are at least partly caused by that agent, compared to 37% and 36% respectfully caused by wind and senescence (table 2.1). Sbw appears predominant also when considering the percent of gap area (i.e.: transect length) affected (65% of area), while senescence (23%) disturbed more of the forest area than did wind (13%). The importance of the Sbw is also seen in the way the overall temporal pattern of disturbances obviously reflects the pattern of Sbw activity (fig. 3.2). Both the number of gaps created (table 2.1) and the Sbw-induced pattern (fig. 3.1) indicate that the impact of the insect was overwhelming in all three stand types, but that the effect was strongest in Fir stands.

None of the current gaps were created prior to 1978 (24 years before survey), which may mean that our dating technique is flawed (at least as regards old gaps), that we overestimated the minimum duration of gaps, or that there really weren't any disturbances back then. If the last option is correct, then Sbw activity created a sudden increase of tree mortality 5 years after the beginning of the epidemic period. As noted in other regions, the impact of Sbw activity was temporarily reduced for a short time (1987-1989). The amount of Sbw disturbances after 1992 strongly decreases, one year after the end of moderate-to-severe defoliation. During a few years at the end of the epidemic period (from 1990 to 1992 inclusively) there was a large amount of disturbance in all three stand types, perhaps caused by a final and unsustainable demographic explosion of the Sbw. However, all three disturbance agents produced increased tree mortality, not just by the Sbw: those three years represent 50% of all gap area created by the Sbw, 48% of all gap area created by wind, and 34% of all gap area created by senescence.

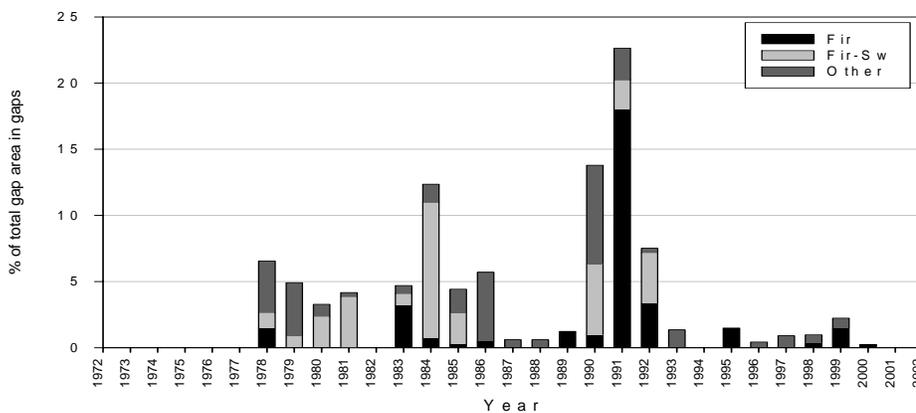


Figure 3.1. The annual amount of disturbance (% of total area in gaps) according to stand type.

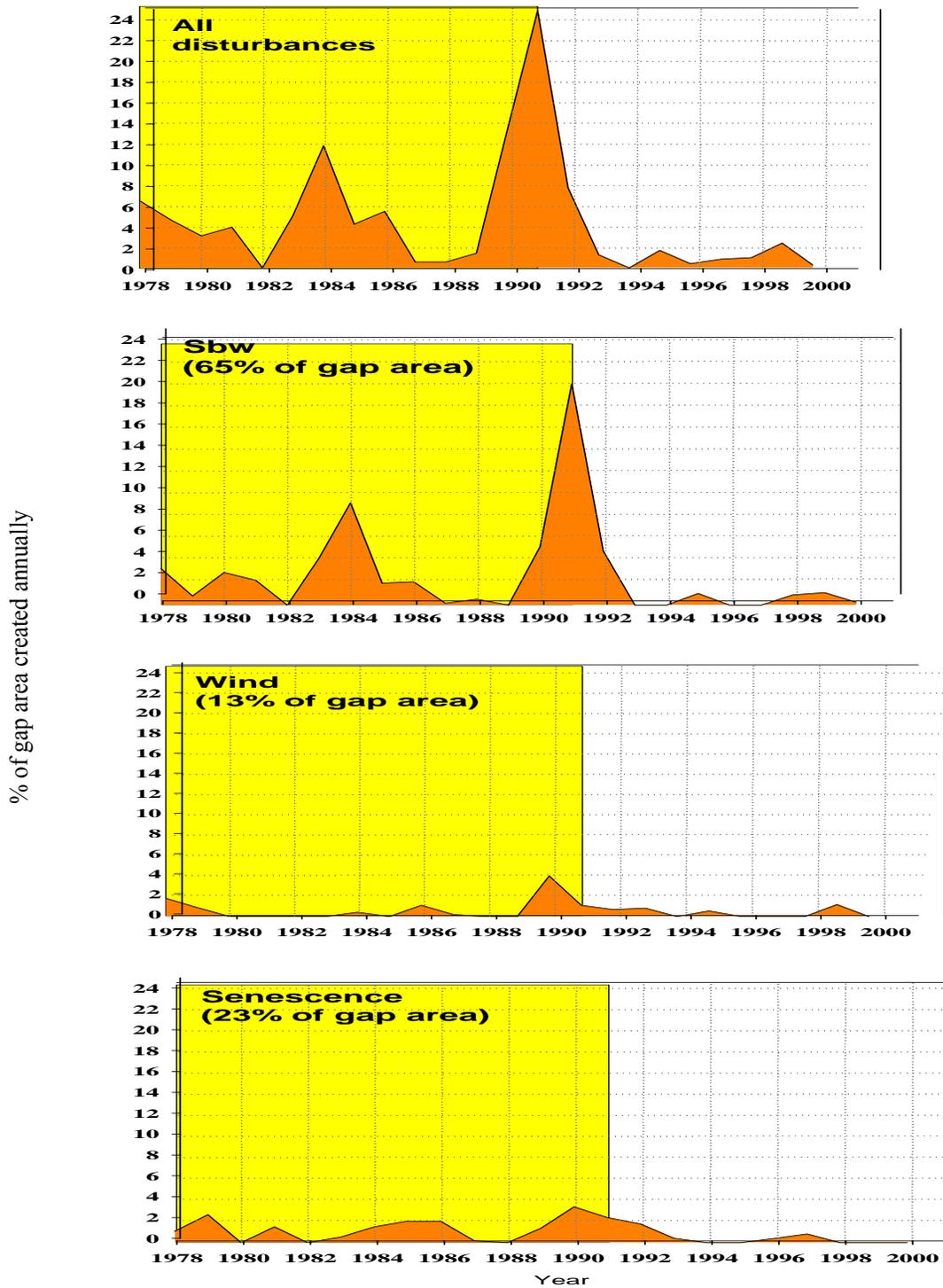


Figure 3.2. The temporal variability of disturbance intensity, for all disturbances together and for each agent separately (the Sbw epidemic period is shaded).

The variable amount of disturbance is not only apparent between Sbw epidemic and endemic periods, but also on an annual and periodic basis within the epidemic period. To estimate the intensity of disturbances it seems appropriate to distinguish sub-periods of low disturbance severity (0.4 % of the forest area opened annually), of medium severity (2.1 %/year), and of high severity (6.6 %/year), corresponding to return intervals of 263, 48 and 15 years respectively (Table 3.1). Since the average gap fraction (% of area or transect without forest cover) at the sites used to determine gap ages was different from the average gap fraction for all sites, the disturbance rate was calculated using the average disturbance severity (42 % gap fraction). However our sites showed a wide range of gap fractions (18% to 64%), which if taken into account could mean that the range of return intervals is potentially even greater (table 3.1). We don't have enough data to calculate the return interval for each disturbance agent separately.

Table 3.1

The disturbance rate and rotation periods calculated according to three levels of disturbance intensity (low, middle and high), and according to three levels of gap fraction (18%, 43% and 64%)

<i>Level of disturbance severity</i>	disturbance rate (% area/yr)			rotation period (yrs)		
	<i>18%</i>	<i>42%</i>	<i>64%</i>	<i>18%</i>	<i>42%</i>	<i>64%</i>
low: 1987-1989 and after 1992	0.2	0.4	0.6	629	263	177
middle: 1978-1986	0.9	2.1	3.1	115	48	32
high: 1990-1992	2.8	6.6	9.8	36	15	10
all the period: 1978-2001	0.7	1.8	2.7	143	56	37

Years of exceptionally intense disturbance occurred in all stand types, but values were more extreme in Fir stands, where 54 % of the area in gaps was created in a single year (1991), compared to a maximum of 10 % in any other year in the same stands. The amplitude was less in Fir-Sw stands and least in Low-Fir stands, where the maximum annual amount was 31 % and 23 % respectively. In years of exceptionally low disturbance intensity, mostly tree mortality occurs in Low-Fir stands (figure 3.2). Low-Fir stands show the least amplitude of annual rates of disturbance, the most continuous spread of disturbance (18/24 years compared to 13/24 and 10/24 years for Fir and Fir-Sw stands respectively), and the most equal contribution of all three agents on an annual basis. Maximum and minimum peaks in the disturbance rate are mostly the consequence of Sbw activity. During the 12 years of lowest disturbance intensity (or 52 % of the period), 7 % of the total Sbw-created gap area, 15 % of the total senescence-created gap area, and 23% of the total Wind-created gap area are produced. On the other hand, during the three years (or 13% of the period) of highest disturbance intensity, 57 % of the total Sbw-created gap area, 46 % of the total senescence-created gap area, and 32 % of the total Wind-

created gap area are produced. Considering the five most intensely disturbed years (table 3.2), which together represent 64 % of the total gap area but only 36 % of all gaps, it is apparent that years of exceptional disturbance occur in all three stand types, but that only Sbw is the principal cause of disturbance in all years. Extreme levels of Sbw activity mostly occur in Fir and less in Fir-Sw stands, while extreme levels of wind activity occur in Low-Fir stands. Gaps are not larger in stands with higher gap fractions (see chapter 2), but gaps do tend to be larger in years when the annual amount of disturbance is greater (95m² compared to the overall mean gap size of 68m²). Runkle (1982), in a different type of forest and disturbance regime, noted as well that when much disturbance occurs in a short lapse of time the size of gaps tends to be larger.

Table 3.2

The location and the disturbance origin of gaps in the five most disturbed years

year	% of total disturbance	% of total nb. of gaps	mean gap size (m ²)	% in Fir	% in Fir-Sw	% in Low-Fir	% by Sbw	% by Wind.	% by Sen.
1991	25	9	117	20	2	2	21	1	2
1990	13	9	34	1	5	7	6	4	3
1984	12	9	139	1	10	1	10	0	2
1992	8	6	78	4	4	0	5	1	2
1978	6	3	108	2	1	4	3	2	1
Total	64	36	95*	6*	4*	3*	9*	2*	2*

(*mean values)

The effects of none of the agents are persistently synchronous across stand types. Some aspects of the pattern of Sbw activity occur during the same years, for example the beginning and ending of the epidemic, and the temporary mid-period rate decrease, but not the maximum rate peak years. Major Sbw disturbances occurred in Fir stands in 1984, while in Fir-Sw stands it was in 1991. It is difficult to see a pattern of wind disturbances, either within or between stand types. Senescence disturbances also seem to occur randomly, except in Fir stands where there is a sudden concentration during two years (1989 and 1991). It is difficult to judge the level of interdependence among the agents, which in our case would most likely involve Sbw disturbances making trees more vulnerable to wind disturbances. It could be that in Fir stands the large amount of gap area created by the Sbw in 1991 facilitated or increased the relatively large amount of wind disturbances in 1994 and 1995. On the other hand, the

exceptional wind disturbances in Fir-Sw stands in 1990 (the only year affected by wind in such stands) can hardly be explained by the 1984 Sbw disturbances in the same stands. However, the concentration of high levels of disturbance by all three agents in the last years of the epidemic (1990-1992) is difficult to explain otherwise.

Within the limits imposed in our survey (canopy openings < 0.1ha), gap sizes are not significantly different according to their disturbance origin (fig. 3.3), just like they are not different among stand types (fig. 2.1). Most categories have too few samples to make a meaningful analysis (table 3.3). Even when comparing the size of Sbw-gaps, for which we have relatively many samples and which show very different mean values between stand types, a one-way Anova (with normalization of distributions through a $\log_{10}(x-2.5)$ transformation) shows that there is no significant difference ($P= 0.4279$) between stand types. Although not based on a statistical certainty, some idea of the importance of disturbance type and stand type can be attempted through the comparison of the mean gap sizes (table 3.3). The mean size of Sbw gaps varies a lot among stand types, compared to the other two disturbance agents. The Sbw gaps are very large in Fir-Sw stands and very small in Low-Fir stands. It is mostly because the Sbw gaps are on average so large in Fir-Sw stands, that overall the largest gaps are found in those stands. Wind gaps are on average the largest, but only few wind gaps samples are available. As expected, senescence gaps are generally the smallest, and the largest senescence gaps are found in Low-Fir stands and the smallest in Fir stands. Gaps with multiple origins are for some reason usually smaller.

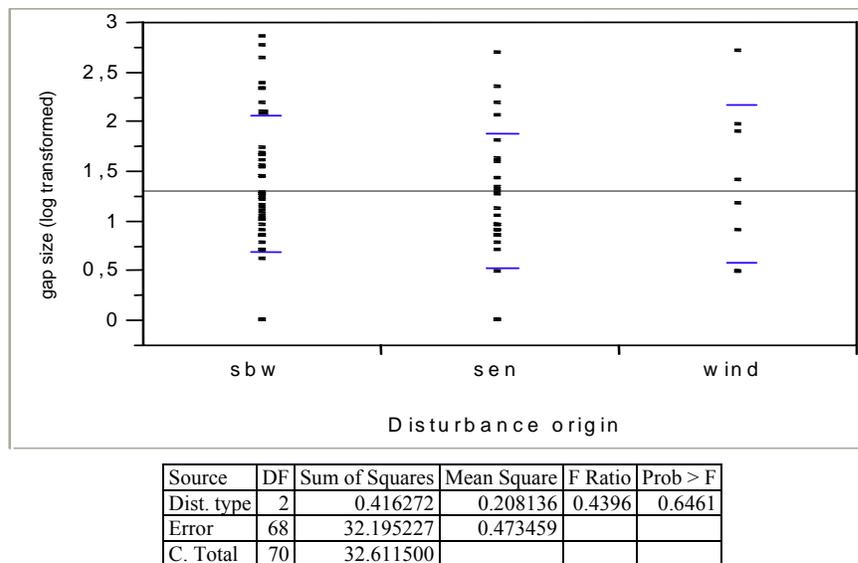


Figure 3.3. Gap size distributions according to disturbance origin (only gaps with a single disturbance origin), with grand mean and standard deviations. Below is the result from a one-way Anova.

Table 3.3

The mean size of gaps according to disturbance origin and stand type
(with the number of samples)(no corrections for the LIS bias have been applied)

	Sbw	Wind	Sen	Sbw+Wind	Sbw+-Sen	Wind+Sen	3 agents	all
Fir	71 (23)	95 (1)	21 (4)	45 (6)	43 (2)	-	-	60 (36)
Fir-Sw	148 (10)	-	54 (6)	62 (1)	99 (5)	19 (1)	15 (1)	100 (24)
Low-Fir	26 (6)	95 (7)	66 (14)	31 (4)	64 (5)	-	25 (3)	57 (39)
all	84 (39)	95 (8)	55 (24)	42 (11)	75 (12)	19 (1)	22 (4)	68 (99)

Fir saplings are most abundant in wind gaps and least abundant in senescence gaps, while white birch regeneration are most abundant in senescence and least abundant in wind gaps (table 3.4). The unequal number of samples, especially regarding wind gaps, makes these conclusions uncertain. The interpretation is also complicated because results from single-origin gaps seem to contradict those from multiple-origin gaps, in particular regarding of white birch abundance.

Table 3.4

The composition of gap fillers according to disturbance origin
(with the number of samples used)

	% fir	% Sw	% Sb	% birch	% tol. dec.	Nb. gaps
Sbw	79	3	3	10	5	31
wind	88	0	0	0	12	2
sen	66	5	0	13	16	14
Sbw+wind	70	4	3	19	4	9
Sbw+sen	72	9	1	3	15	11
wind+sen	75	0	0	0	25	1
all 3	69	0	0	31	0	3

N.B. Sw=white spruce; Sb=black spruce; birch=white birch; tol. dec.=tolerant deciduous.

Gap size apparently has no effect on the proportion of fir saplings (fig. 3.4), unlike for the proportion of white birch (fig. 1.2).

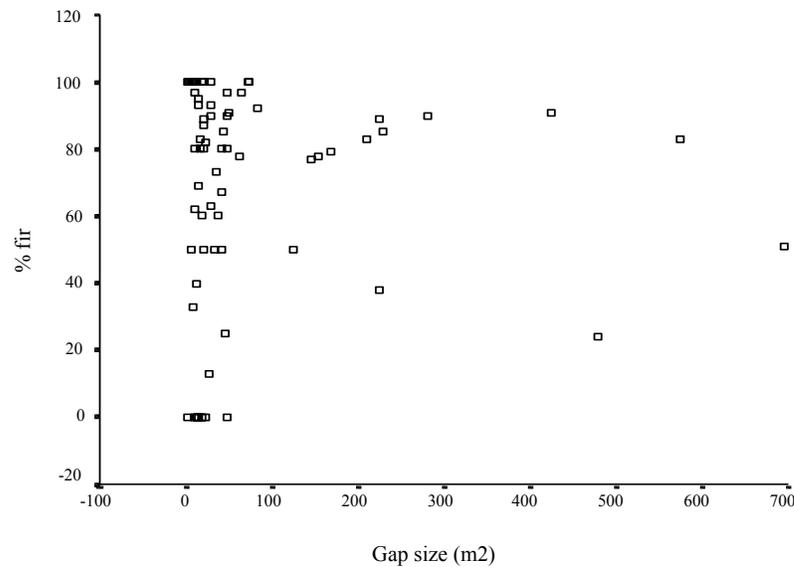


Figure 3.4. The proportion of fir (%) among gap filler saplings as a function of gap size.

Generally most gap makers are fir (72%) and most regenerating saplings are fir (77%) (table 3.5). In Fir-Sw and Low-Fir stand types, there was a disproportionate amount of fir killed, implying that disturbances occurred in parts of the stand where fir were particularly abundant. This was most evident in Low-Fir stands, where 66 % of gap makers were fir while only 37 % of the canopy trees are fir. This might refer to what MacLean (1980) describes as a "clumped or contagious distribution" of tree species. It was the opposite in Fir stands, where disturbances occurred in places with relatively less fir, but differences were not very large (87 % fir among gap makers compared to 91 % in the canopy). A circular mode of succession characterizes tree replacement within gaps in Low-Fir stands (68% fir replacing 66 % fir), in Fir-Sw stands there is augmentation of fir (89 % fir replacing 74 % fir), while in Fir stands fir loses ground at the expense of white birch (84 % fir replacing 87 % fir). The compositional change in Fir and Fir-Sw stands could however be less severe or even only temporary, because among seedlings spruce is more abundant in Fir-Sw stands and fir is more abundant in Fir stands (table 3.5). Nevertheless, the sapling and seedling communities in gaps, irrespective of the type of stand, have a composition which we classify as a Fir stand (table 3.6), meaning fir is generally becoming progressively dominant. In all stand types it is most often the reduction of spruce, both black and white, that explains this change. The presence of white birch is generally maintained. In Fir stands there is even an augmentation of white birch among saplings, but not among seedlings. In Low-Fir stands a higher combined proportion of the three species (fir, spruces, and w.birch) exists among

saplings than among seedlings (81 % compared to 73 %), suggesting that, despite the strong and persistent augmentation of fir, rarer species (71 %) will not be reduced as much as first appears. Competition by opportunist species was strongest and the diversity of species greatest in Low-Fir stands, including mountain maple (Ere)(*Acer spicatum*), striped maple (Erp)(*Acer pensylvanicum*), beaked hazelnut (Cor)(*Corylus cornuta*), Saskatoon berry (Ame)(*Amelanchier canadensis*) and mountain ash (Soa)(*Sorbus americana*). In Fir stands Soa invaded some gaps, and there was some Ere. Fir-Sw stands were the least affected, with very few Soa and Ame.

Table 3.5

The tree composition (%) among canopy trees, gap makers, and gap fillers
(all values are based on stem density).

	canopy trees			gap makers	gap saplings			gap seedlings		
	fir	spruces	birch	fir	fir	spruces	birch	fir	spruces	birch
Fir	91	2	3	87	84	1	14	95	1	3
Fir-Sw	64	29	7	74	89	2	9	85	11	3
Low-Fir	37	19	15	66	68	8	6	65	8	1
all	57	17	10	72	77	4	9	77	7	2

N.B. "spruces" include white and black, and "birch" includes only white birch

N.B. the proportions of fir as gap makers are approximations

Table 3.6

The stand type at the canopy, sapling and seedling levels

canopy	sapling	seedling	<u>Criteria:</u>
Fir	Fir	Fir	Fir: $\geq 70\%$ fir
Fir-Sw	Fir	Fir	Fir-Sw: $\geq 60\%$ (fir+w.spruce)
Low-Fir	Fir	Fir	Low-Fir: $< 60\%$ (fir+w.spruce)
All (= Fir-Sw)	Fir	Fir	

N.B. all values are based on the stem density,
of stems ≥ 12 cm dbh in the case of canopy trees

3.5 Discussion

Sbw activity determines the general pattern of disturbances in all stand types, and usually accounts for most of the annual disturbance rate variability. Our dates of increased canopy disturbances correspond closely to the period of the epidemic, even though the dating of gap events may be off by 1 to 3 years due to growth response delays for conifer (Parish *et al.* 1999; Kneeshaw *et al.* 1998; Greene *et al.* 1999; Kneeshaw *et al.* 2002) and deciduous (Nowacki and Abrams 1997) gap fillers. As expected there are fewer disturbances by senescence and wind, and generally no particular pattern results from them. Estimating an average rate of disturbance can be hazardous (Kneeshaw and Bergeron 1998), especially in our case where there is much variability within the region (gap fraction) and within stands (impact of Sbw epidemic). Conceiving of a Sbw-free disturbance rate is unrealistic because the period analyzed in this study is too short compared to the duration of the epidemic, and because the effect of the Sbw probably extends to periods between epidemics (the previous epidemic ended in 1958). The calculated rotation periods (on average 50 years) are however generally within the range observed elsewhere [Runkle (1982) suggests 50-200 years], but tend to be shorter than the average periods found in most (Lertzman and Krebs 1991; Foster and Reiners 1986; Spies and Franklin 1989; Kneeshaw and Bergeron 1998; White *et al.* 1985; Liu and Hytteborn 1991) but not all (Drobychev 2001) boreal or conifer forests.

Although it appears as if Sbw disturbances do not generally lead to increased amounts of wind disturbances, the simultaneous increased level of wind, Sbw, and senescence disturbances towards the end of the epidemic (1990-1992) would be difficult to explain otherwise. The unusual concentration of senescence mortality in Fir stands in 1989 and 1991 could likewise have been the consequence of other disturbances, or could represent the activity of some unidentified biotic or abiotic disturbance agent. To evaluate properly the interdependent causation of disturbances a detailed etiological study would be required (Worrall and Harrington 1988), as well as some information on the local historical wind circulation patterns (Ruel and Benoit 1999; Lévesque 1999). The absence of a relationship between gap size and gap age could mean that gap enlargement or fusion processes are relatively rare.

Because of the context of the Sbw epidemic and because only small gaps are considered, we expected Fir stands to have the highest gap fraction, to rotate more quickly, and to have a circular mode of succession, where numerous pre-established fir seedlings replace predominantly fir gap makers. Instead, even though Sbw activity was indeed much more important there, Fir stands were the least severely disturbed, and had smaller Sbw-gaps than in Fir-Sw stands. It could be that the Fir-Sw stands are located closer to Sbw population epicentres and therefore more intensely invaded by the Sbw, and

for that reason alone they have a higher gap fraction and larger Sbw gaps. However one wonders why then is only the fir targeted and not the white spruce? Since the canopy disturbances in Fir-Sw and Low-Fir stands have been showed to occur mostly in fir patches, the spatial agglomeration of fir in the stand could also explain why disturbances in Fir-Sw stands occur in larger pockets. An evaluation of Sbw activity at the landscape scale would be useful to resolve this question (Bergeron *et al.* 1995), taking into account in particular the topographic situation which is known to influence Sbw population displacement (Craighead 1925; Blais 1960). The fact that the sampled stands represent parts of the forest not yet managed could also be significant, especially since the government might have encouraged the salvage-logging of the more severely disturbed areas, which we hypothesized to be fir dominated stands.

Some authors have suggested exercising caution when using the mean size of gaps to compare (e.g.: the effect of disturbance origin) or calculate (e.g.: the rotation period) regime parameters, even when a significant difference among groups of values has been determined (Lawton and Putz 1988; Hunter and Parker 1993; Barden 1989; Spies and Franklin 1989; Ogden *et al.* 1991). This concern arises because of the generally very skewed distribution of gap sizes, as well the partiality of the sampling design sometimes used, including such aspects as the choice of minimum and maximum gap sizes, of maximum gap ages, and the exclusion of what are conceived to be exogenous disturbances. These limitations may also affect the gap fraction value (Liu and Hytteborn 1991), but the effect is not compounded by a skewed distribution.

In Low-Fir stands the relatively high concentration of fir in areas that were disturbed (in comparison to elsewhere in the stand) is maintained, meaning there is circular succession within the area in gaps. In Fir-Sw stands canopy disturbances occurred in areas moderately more composed of fir than generally in the canopy, and within gap areas there is convergence towards more fir (i.e.: a stronger contrast vis-à-vis the residual stand). In Fir stands disturbances occurred in areas a little less composed of fir compared to the canopy, and within the gaps there will be even less fir (i.e.: the contrast will be stronger). Overall, canopy disturbances took place in distinctly fir patches in the stand, and as a result of disturbances the composition of stands will become even more dominated by fir. Consideration of the seedling composition suggests that the predicted changes within gaps may in time be reversed in Fir stands, attenuated in Fir-Sw stands and won't change much in Low-Fir stands. From these findings it appears as if converging or circular modes of succession are not dependent on there being a high fir component in the stand. Furthermore, we find that fir regeneration is most successful in wind gaps, which tend to be the largest, suggesting the regional convergence towards fir is neither driven

specifically by Sbw (or senescence) disturbances, nor by smaller gap sizes. This is contrary to the effect of smaller gaps on fir regeneration reported in fir and mixed forests in eastern Québec (Kneeshaw and Bergeron 1998), and contrary to what one generally expects of wind gaps (Krasny and Whitemore 1992). However, the soil disturbance produced by wind disturbances was probably not an issue in our case, since most trees killed by winds had snapped trunks rather than uprooted, leaving the soil seldom overturned and pre-established seedlings generally intact. Perhaps the sudden and large amount of light introduced by wind disturbances does not benefit shade-intolerant species as much as it benefits the tallest pre-established gap fillers, which are usually fir. The great capacity of firs to react to dramatic increases of light, which has been demonstrated in Gaspésie for saplings as tall as 5.30m (Zarnovican 1983), could permit them to maintain their height advantage.

Our results could imply that thickets mainly composed of fir (in Fir-Sw and Low-Fir stands) are repeatedly attacked by the Sbw. Other parts of the stand, composed of species more resistant to the Sbw and other types of disturbances, would be rotating more slowly and evolving only gradually towards fir dominance. Such a multiple-speed rotation system is conceivable and not so surprising given that the intensity of Sbw activity can vary within a same stand despite an equal spread of susceptible species (Vincent 1962; MacLean 1980). This model does not take into account residual trees inside gaps that are not susceptible to the Sbw and have a head start in reaching the canopy (Chen and Popadiouk 2002), but such trees rarely existed in our small gaps. It is unlikely that the composition of the residual stand is diverse as a result of other species eventually supplanting fir without a disturbance in the canopy, since disturbance events are relatively frequent and because fir are among the most shade-tolerant and widespread species present. For fir thickets to replace fir thickets the cycle of disturbances must be short and the advance fir regeneration abundant, both conditions existing in our sites. Although the increased presence of w. birch in Fir stands is only temporary, it may indicate that the general tendency for fir to dominate stand compositions has a limit. Tree species other than fir maintain themselves at a generally low rate, with perhaps an equilibrium at a slightly lower rate than exists presently among canopy trees in Fir stands. Gap studies investigating the same areas for a period extending over two Sbw epidemics would be useful to more fully understand tree replacement processes.

CONCLUSION GÉNÉRALE

Le pourcentage d'ouverture des forêts régies par des perturbations de petite échelle est très variable (18 % à 64 %), et est en moyenne élevé (42 %). Les peuplements purs de sapins (Fir) sont en moyenne moins ouverts (35 %) que les peuplements composés de sapins et d'épinettes blanches (Fir-Sw)(45 %) et les peuplements mixtes ou bien composés d'une combinaison de sapins et d'épinettes noires (Low-Fir)(45%). La dimension des trouées varie de 3m² à 696m². La fréquence des dimensions de trouées suit dans tous les sites une distribution négative exponentielle, avec de nombreuses petites et peu de grandes trouées. La dimension moyenne est de 68m², mais lorsque des corrections sont apportées pour contrer le biais méthodologique elle est seulement de 28m², avec la moitié des trouées mesurant <11m² et la moitié de la superficie ouverte totale en trouées de dimensions <65m². En tenant compte de la hauteur moyenne de la canopée (15m) et de l'angle de déclinaison du soleil à cette latitude (23.45°), les "dimensions effectives" des trouées (ratio du diamètre de trouée sur la hauteur de la canopée) varient entre 0.1 et 2.1, avec une moyenne de 0.5 et une médiane de 0.3. Cela veut dire que seulement les trouées plus grandes que 35m² (ou 20% des trouées) reçoivent de la lumière au sol, mais puisque les arbres pré-établis ont souvent 1m de haut une plus grande proportion de trouées en réalité bénéficieraient d'un apport direct de lumière.

La création de trouées dans la canopée a un impact sur la date d'établissement, la densité, la composition et le taux de croissance des arbres en régénération, mais le processus de succession ne serait probablement pas radicalement changé en l'absence de perturbations. La présence de grandes trouées favorise la diversité spécifique de la forêt, notamment en favorisant la présence d'héliophiles comme le bouleau à papier, mais pas nécessairement au point d'aboutir à un changement significatif ou définitif de la composition des recruts. Il serait faux de concevoir, par exemple, une succession circulaire (sapins remplaçant sapins) fonctionnant dans les peuplements caractérisés par des petites trouées, et d'un autre côté une succession divergente ou convergente vers des espèces héliophiles dans des peuplements caractérisés par des grandes trouées. La gamme des dimensions des trouées est semblable dans tous les sites. Il n'y a pas lieu de croire que dans un peuplement les trouées sont regroupées spatialement selon leurs dimensions. La régénération du sapin n'est pas particulièrement favorisée dans les plus petites trouées. Contrairement à ce que l'on s'attendait, le sapin n'a pas plus

abondant dans les trouées créées par la Tbe ou la sénescence, qui pourtant en théorie produisent davantage d'ombrage toutes dimension de trouées confondues.

La variabilité de l'intensité des perturbations dans le temps est largement déterminée par l'impact de la Tbe. Le fait que le vent et la sénescence contribuent aussi au patron des perturbations pourrait suggérer qu'il y a une interdépendance entre les agents de perturbations, mais cela n'a pu être démontrée. En moyenne 2.1% de la forêt est ouverte par année, mais c'est très variable au cours de la période évaluée, ainsi que parmi les sites et selon le type de peuplement. L'activité de la Tbe produit une forte amplitude des taux annuels de perturbations, et surtout dans la sapinière pure (Fir). La plus faible amplitude est produite par la sénescence et dans les peuplements mixtes et composés d'épinettes noires (Low-Fir). Sans surprise la Tbe a été particulièrement influente dans les sapinières pures, mais il est surprenant que les peuplements composés d'essences moyennement attirantes pour l'insecte (sapins avec épinettes blanches) n'étaient pas plus attaqués que les peuplements composés de peu d'essences attirantes pour l'insecte (épinettes noires et feuillues). Dans ce dernier type de peuplement, ce sont particulièrement des endroits à forte présence de sapins qui furent perturbés, et en conséquence la régénération est aussi dominée par le sapin plus qu'autre part dans le peuplement. Dans tous les peuplements c'est principalement le sapin est mort (72 % en moyenne), et dans sa globalité la forêt à la suite des perturbations va être davantage composée de sapins puisque cette espèce représente 77 % des gaulis et des semis, mais seulement 57 % de la composition actuelle du peuplement. En évaluant les types de peuplement séparément, par contre, la convergence vers le sapin existe uniquement dans les sapinières avec épinettes blanches (Fir-Sw). Dans les sapinières pures le bouleau blanc est en voie d'augmenter sa quote-part dans les aires présentement en trouées, mais ce sera seulement temporaire. Dans tous les peuplements la régénération est très forte, surtout en sapins, et peu de trouées sont envahies par des arbustes ou arbres pionnières autres que le bouleau blanc.

Nos résultats suggèrent que le fonctionnement du régime est complexe, et qu'il est nécessaire de tenir compte des différents types de perturbations, même si l'activité de la Tbe lorsque épidémique est l'élément prépondérant et déterminant. Les facteurs associés avec la variabilité du régime ne sont pas pour la plupart ceux auxquels nous nous attendions : les peuplements plus perturbés ne contiennent pas plus de sapins et ne sont pas plus attaqués par la Tbe. L'altitude n'a pas d'effet significatif, en contraste avec les résultats obtenus dans plusieurs autres études, et contre toute attente les vents font moins de dégâts dans les sites plus en altitude. Malgré que la Tbe soit la principale cause de mortalité, les sites qui sont plus perturbés ont tendance à avoir plus souffert des vents, à être composés davantage

d'épinettes noires, et à être situés sur des versants ouest. Les peuplements qui sont exceptionnellement ouverts (>50 %) ont aussi tendance à se trouver sur des pentes fortes.

Comprendre le fonctionnement d'une forêt caractérisée par des petites trouées est difficile compte tenu de la grande variabilité des caractéristiques de trouée et de leurs impacts (Lawton and Putz 1988). Évaluer plus exactement les caractéristiques et la variabilité du régime de perturbations nécessiterait des données plus précises, comme le nombre d'arbres morts par exemple. Il serait intéressant aussi d'avoir une meilleure analyse de l'étiologie des perturbations, et surtout y inclure des informations à l'échelle du paysage, comme la localité des épices de populations de la Tbe, la composition des peuplements avoisinants, la situation topographique, et le patron des courants éoliens. Un projet de plus longue haleine pourrait approfondir nos conclusions, spécifiquement en mieux situant les sites, en interprétant des photos aériennes pour confirmer nos résultats, et en considérant une plus longue fenêtre de temps.

APPENDICE A

LOCATION OF STUDY SITES

Table F. The ecological classification of sites areas according to the MRNQ (1999) (see fig. A).

<i>Zone</i>	Sous-domaine bioclimatique
<i>North</i>	Sapinière à bouleau blanc de l'Est
<i>Central</i>	Sapinière à bouleau blanc de l'Est
<i>Central (A3)</i>	Sapinière à bouleau blanc de l'Est
<i>South</i>	Sapinière à bouleau jaune de l'Est

<i>Zone</i>	Sous-région écologique
<i>North</i>	5i-T Monts de Murdochville (Haut massif gaspésien)
<i>Central</i>	5i-T Monts de Murdochville (Haut massif gaspésien)
<i>Central (A3)</i>	5h-T Massif gaspésien
<i>South</i>	4g-T Côte de la Bair des Chaleurs

<i>Zone</i>	District écologique (et Unité de paysage)
<i>North</i>	111X005 Murdochville
<i>Central</i>	111C012 Murdochville
<i>Central (A3)</i>	109C013 Rivière Nouvelle
<i>South</i>	72C016 Saint-Edgar

Table G. Location of transects

site	zone	latitude	longitude	site	zone	latitude	longitude
1	south	48° 14' 48"	66° 09' 01"	18	north	48° 49' 10"	65° 38' 51"
2	south	48° 15' 17"	66° 01' 30"	19	north	48° 46' 53"	65° 35' 49"
3	central*	48° 20' 09"	66° 24' 51"	20	north	48° 46' 59"	65° 38' 49"
4	south	48° 15' 08"	66° 11' 00"	21	north	48° 48' 57"	65° 37' 55"
5	south	48° 15' 08"	66° 11' 00"	22	north	48° 49' 21"	65° 37' 44"
6	south	48° 14' 57"	66° 06' 15"	23	north	48° 49' 30"	65° 39' 03"
7	central	48° 30' 20"	66° 21' 41"	24	north	48° 48' 39"	65° 39' 27"
8	central	48° 29' 48"	66° 17' 11"	25	north	48° 48' 35"	65° 40' 03"
9	central	48° 29' 04"	66° 16' 40"	26	north	48° 44' 16"	65° 39' 45"
10	central	48° 28' 57"	66° 16' 27"	27	north	48° 46' 24"	65° 41' 37"
11	central	48° 28' 01"	66° 14' 47"	28	north	48° 48' 00"	65° 41' 54"
12	central	48° 27' 51"	66° 15' 23"	29	north	48° 48' 14"	65° 40' 46"
13	central	48° 30' 25"	66° 15' 40"	30	south	48° 15' 53"	66° 01' 48"
14	central	48° 30' 32"	66° 15' 31"	31	south	48° 15' 52"	66° 03' 35"
17	north	48° 47' 48"	65° 36' 42"				

APPENDICE B

IDENTIFYING DIAMETER GROWTH RELEASE AMONG GAP FILLERS

Like Orwig and Abrams (1995) and others (Nowacki and Abrams 1997, Rensch *et al.* 2002 and 2003), we consider the increment between the mean growth rates during the 10 years following a year from that of the 10 years preceding it, which gives the Percent Growth Change (%GC) around a particular year:

$$\%GC = \frac{100(M_2 - M_1)}{M_1}$$

Where: M_1 = the sequence of the 10 preceding years

M_2 = the sequence of the 10 following years

[For example: For the %GC of the year 1950, M_1 =1941-1950, and M_2 =1951-1960]

A one-year delay is integrated in the equation to account for the delayed growth response. Like Lorimer and Frelich (1989), the authors (e.g.: Orwig and Abrams 1995) suggest using time sequences of at least 3 to 5 years so that climatic artefacts (e.g.: annual humidity rates) do not obscure the dendrochronological signal. Ideally the length of the period used on either side of the year under evaluation (M_1 and M_2) should correspond to the average duration of released growth episodes, but 10 years probably represents quite well the intermediate intensity of small gap regimes (Orwig and Abrams 1995).

We recognize the existence of two distinct growth periods when the %GC reaches at least 100%. The following example, of a 58 year old fir gap filler, illustrates our approach (fig. D). The radial growth from 1946 to approximately 1980 is inferior to that between 1980 and 2002 (the bars represent mean ring growths over a three year sequence). The calculation of the %GC lets one quantitatively affirm the existence of two distinct periods, with a break point around 1979 (when $\%GC \geq 100\%$)(fig. E).

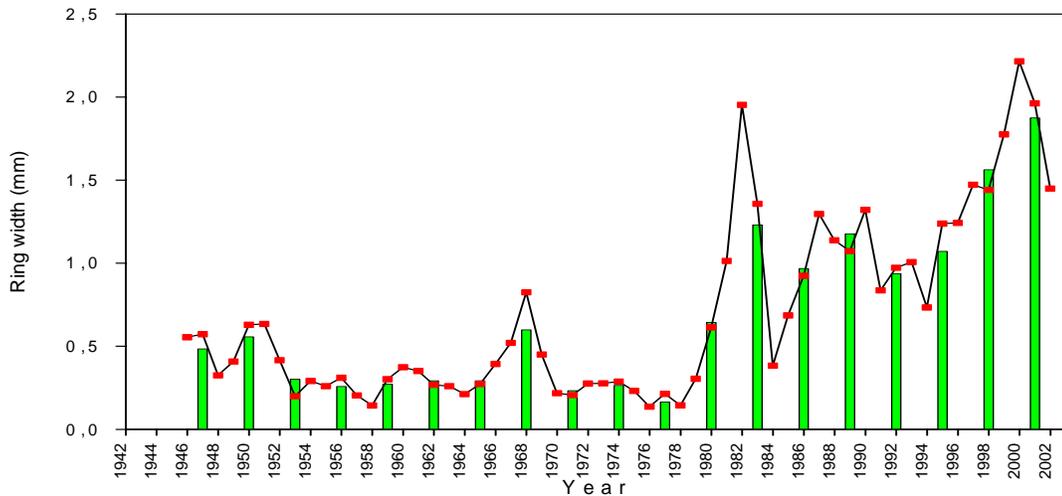


Figure D. Annual (red dots) and triennial (green bars) radial growth of a 58-year old fir gap filler.

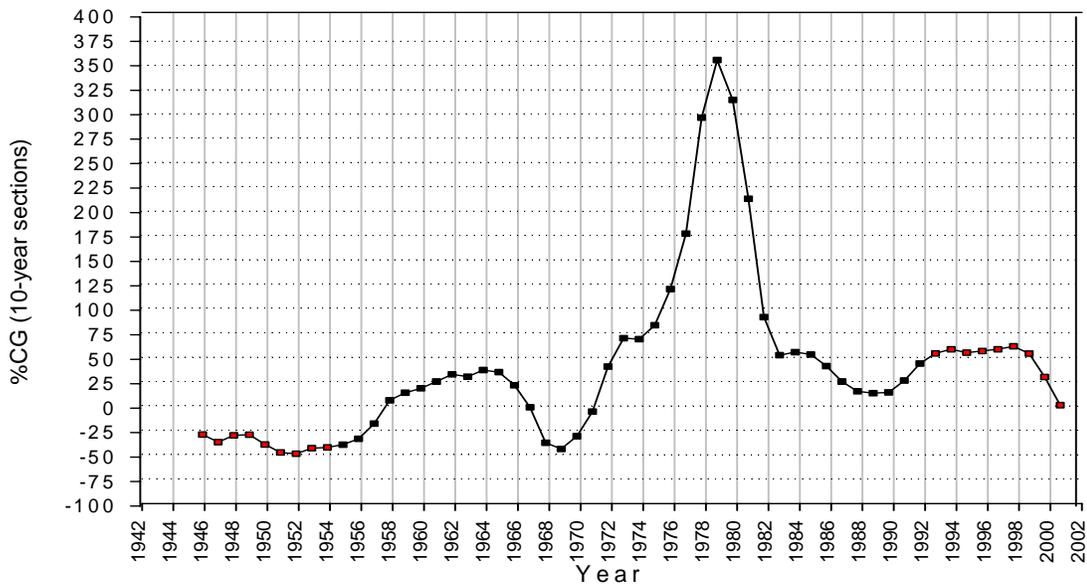


Figure E. The %GC values calculated for every year of ring growth (the first and last 9 values, in red, are those where complete 10-year sequences were not available).

Having identified a significant growth release, it remains to determine exactly the year when an exceptional rate of growth commenced. It is the first year showing a growth superior to the maximum

annual growth in the period preceding the 100%GC, which is before 1979. We exclude, however, the two maxima (1968 and 1951) occurring in this low growth rate period, because generally they represent exceptional events. If we had simply taken the average growth rate in the low growth rate period, likewise exceptional events such as herbivory could give a false idea of normal growth. The designated year is the latest date for a canopy disturbance event, and could be still off from the real date for a number of reasons, for instance depending on the season when the event occurred. In our example the mean rate during the slow-growth period is 0.34 mm/year, the maximum is 0.82 mm/year, the rate of reference is 0.64 mm/year, and the year of growth release is 1980. We often noticed a light growth release 3 years before the major growth release episode, possibly associated with an increase in white birch establishment. This could be due to serious defoliation by the Sbw, which then led to the tree death only one or a few years afterwards. Osawa (1994) also noted such a relatively weak and temporary effect a couple of years prior to the main response created by Sbw activity. Determining the date of disturbance events should not be based solely on the response of shade intolerant species, given their capacity to establish and survive for surprisingly long periods under intact canopies. In general only pre-established trees should be used. White birch gap fillers rarely showed a %GC of more than 100%, to the contrary of fir and to a certain extent spruces, but sometimes it did respond dramatically and could be used to confirm an impression.

The optimal situation is when all samples from a gap show the same dates of disturbance, and with clearly identifiable responses. Sometimes the plants are too young to allow comparison of 10-year sequences, and the calculation of the %GC based on fewer years then requires caution. It is ironic that stands which have a more porous canopy, where the effect of gaps may be less dramatic, are those which are easier to date because the pre-established trees are more developed. Care should also be taken when the growth release is very gradual or of short duration, and when the period preceding the 100%GC point includes another growth release episode. A %GC of more than 100% (even 500%) is not in itself a guarantee that a gap was created in the canopy. It is necessary to verify that the effect was sustained, and that it did not for instance result from a previous decreased growth rate. As well, what seems as a growth release could in fact be a normal growth rate if in general the rate is excessively low for some reason. There is a measure of ambiguity and uncertainty in these results, so exercising common sense is also necessary.

APPENDICE C

ESTIMATING THE DURATION OF GAPS

We estimated the least amount of time necessary for a gap filler to reach the canopy, which corresponds to the minimum lifespan of gaps. The age of four trees (2 fir, 1 black spruce, and 1 white birch) was measured at various stem heights: ground level, 50cm, 1m, and every meter afterwards, as well as at the top. For each stem section the number of years elapsing (e.i.: number of annual concentric growth rings) over the height variant shows the growth rate at that stage (fig. F). Samples were taken from middle-sized gaps, have at least 7m height, and show a generally vigorous diametric growth.

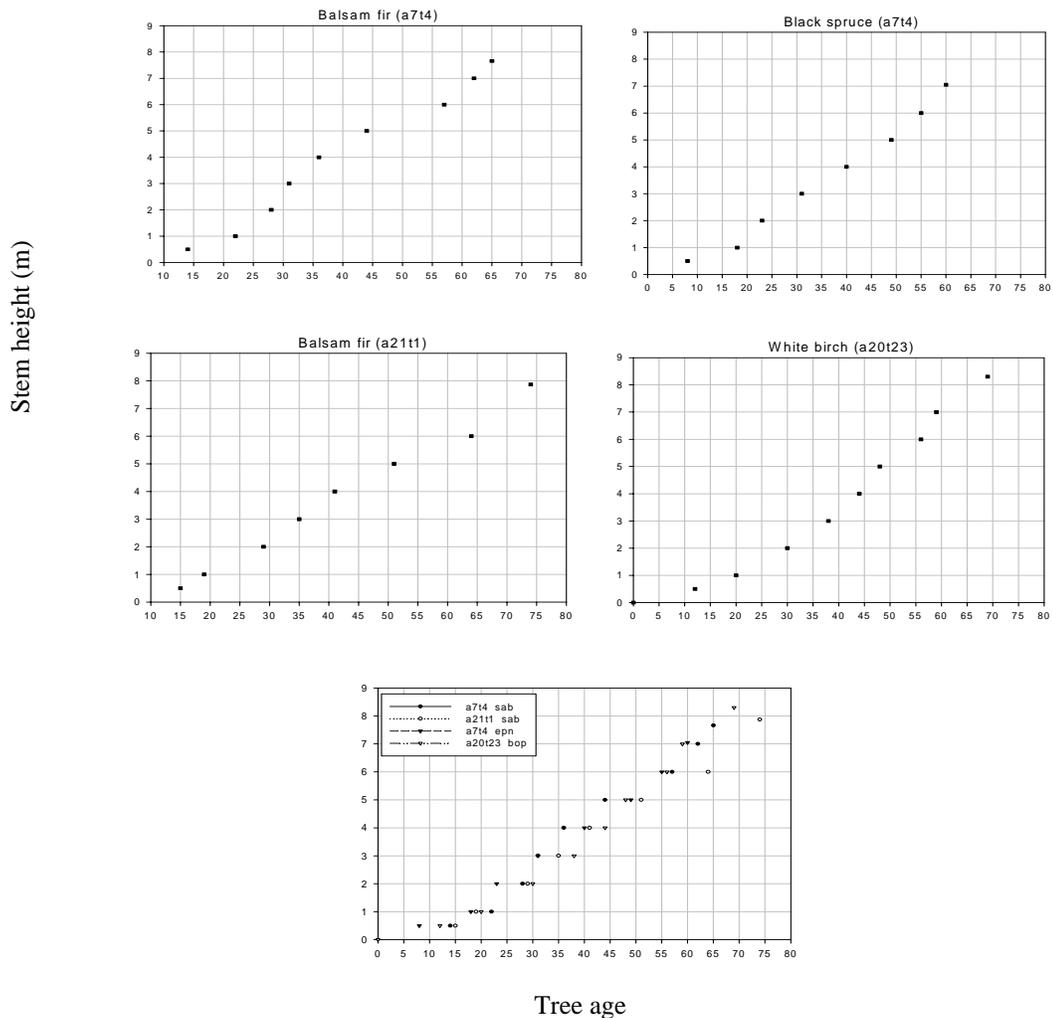


Figure F. Height growth as a function of tree age for 4 gap fillers individually and together.

The lower height of canopy is variable, but on average is about 10m. All 4 gap fillers would be approximately 80 years old when they reach that height. Not surprisingly, their growth rates are variable at different stages in their life, probably in part because of changes occurring in the canopy cover (fig.G).

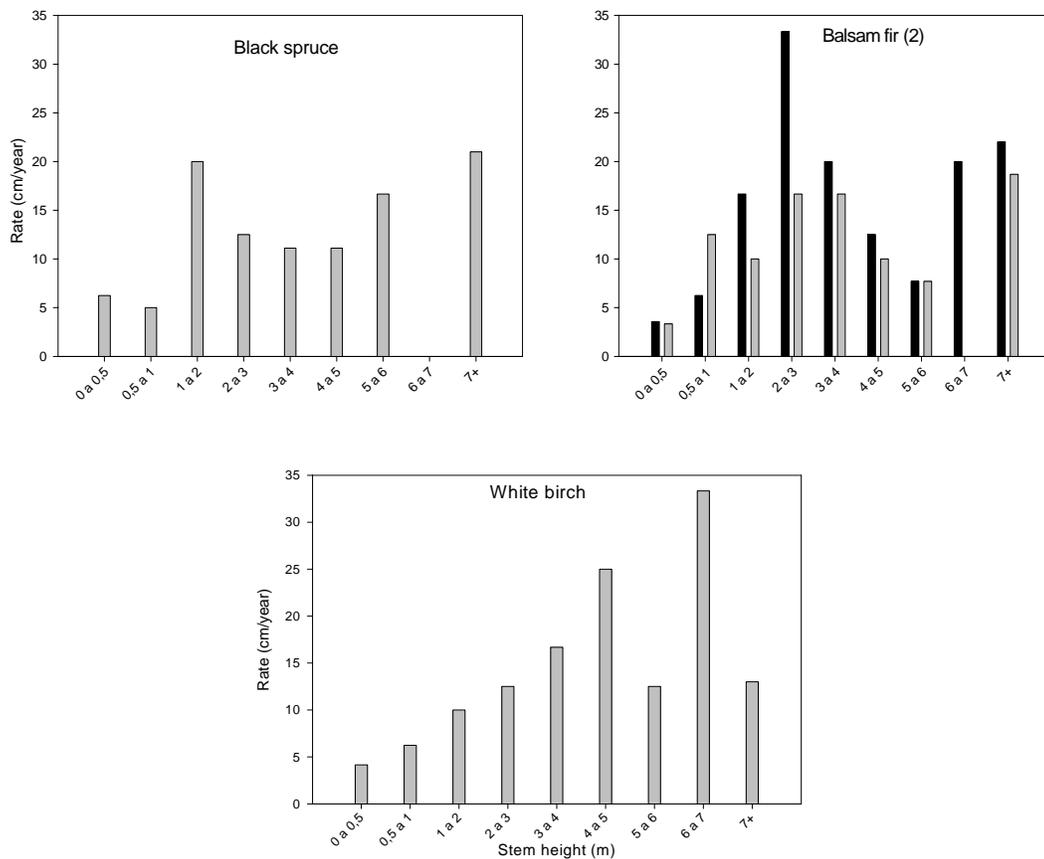


Figure G. Height growth rate (cm/year) at different stages, in three species of gap fillers.

Black spruce have a slower maximum growth rate. Fir trees, just like the white birch, reach a rate of 33cm/year. At this speed the gap will close in at least 30 years. Since most gap fillers are pre-established the duration of gaps could be somewhat shorter, although the greater intraspecific and interspecific competition at the seedling stage also could imply a slower mean growth rate than used here.

APPENDICE D

STAND CHARACTERISTICS

Table H. The species composition (%), based on the basal area of stems with dbh ≥ 10 cm.

stand	site	b. fir	w. spruce	b. spruce	w. birch	y. birch	s. maple	r. maple	P. cherry	m. ash	thuya
Fir	1	70	0	0	30	0	0	0	0	0	0
Fir	3	75	10	0	10	0	0	0	5	0	0
Fir	7	91	0	4	4	0	0	0	0	0	0
Fir	10	82	15	0	3	0	0	0	0	0	0
Fir	14	81	3	6	10	0	0	0	0	0	0
Fir	22	77	11	0	11	0	0	0	0	0	0
Fir	23	80	20	0	0	0	0	0	0	0	0
Fir	27	71	7	21	0	0	0	0	0	0	0
Fir-Sw	4	70	11	0	7	11	0	0	0	0	0
Fir-Sw	6	59	7	28	7	0	0	0	0	0	0
Fir-Sw	8	68	0	29	3	0	0	0	0	0	0
Fir-Sw	9	67	31	3	0	0	0	0	0	0	0
Fir-Sw	13	52	17	24	7	0	0	0	0	0	0
Fir-Sw	17	58	15	19	8	0	0	0	0	0	0
Fir-Sw	21	65	30	2	2	0	0	0	0	0	0
Fir-Sw	24	68	27	5	0	0	0	0	0	0	0
Fir-Sw	25	59	28	13	0	0	0	0	0	0	0
Fir-Sw	28	61	0	39	0	0	0	0	0	0	0
Low-Fir	2	25	6	0	13	25	0	31	0	0	0
Low-Fir	5	43	0	33	19	0	0	0	0	5	0
Low-Fir	11	52	0	48	0	0	0	0	0	0	0
Low-Fir	12	54	4	42	0	0	0	0	0	0	0
Low-Fir	19	25	3	69	3	0	0	0	0	0	0
Low-Fir	20	25	22	53	0	0	0	0	0	0	0
Low-Fir	26	19	0	81	0	0	0	0	0	0	0
Low-Fir	30	11	0	49	24	16	0	0	0	0	0
Low-Fir	31	28	10	3	0	34	10	14	0	0	0
Fir	mean	78	8	4	9	0	0	0	1	0	0
Fir-Sw	mean	63	17	16	3	1	0	0	0	0	0
Low-Fir	mean	31	5	42	7	8	1	5	0	1	0
All	mean	57	10	21	6	3	0	2	0	0	0

Table I. The tree basal area of the stands (trees with dbh ≥ 10 cm)

stand	site	b. fir	w. spruce	b. spruce	w. birch	y. birch	s. maple	r. maple	P. cherry	m. ash	thuya	tot
Fir	1	28	0	0	12	0	0	0	0	0	0	40
Fir	3	15	2	0	2	0	0	0	1	0	0	20
Fir	7	21	0	1	1	0	0	0	0	0	0	23
Fir	10	27	5	0	1	0	0	0	0	0	0	33
Fir	14	25	1	2	3	0	0	0	0	0	0	31
Fir	22	27	4	0	4	0	0	0	0	0	0	35
Fir	23	33	8	0	0	0	0	0	0	0	0	41
Fir	27	20	2	6	0	0	0	0	0	0	0	28
Fir-Sw	4	19	3	0	2	3	0	0	0	0	0	27
Fir-Sw	6	17	2	8	2	0	0	0	0	0	0	29
Fir-Sw	8	21	0	9	1	0	0	0	0	0	0	31
Fir-Sw	9	26	12	1	0	0	0	0	0	0	0	39
Fir-Sw	13	15	5	7	2	0	0	0	0	0	0	29
Fir-Sw	17	15	4	5	2	0	0	0	0	0	0	26
Fir-Sw	21	28	13	1	1	0	0	0	0	0	0	43
Fir-Sw	24	15	6	1	0	0	0	0	0	0	0	22
Fir-Sw	25	23	11	5	0	0	0	0	0	0	0	39
Fir-Sw	28	20	0	13	0	0	0	0	0	0	0	33
Low-Fir	2	4	1	0	2	4	0	5	0	0	0	16
Low-Fir	5	9	0	7	4	0	0	0	0	1	0	21
Low-Fir	11	11	0	10	0	0	0	0	0	0	0	21
Low-Fir	12	13	1	10	0	0	0	0	0	0	0	24
Low-Fir	19	9	1	25	1	0	0	0	0	0	0	36
Low-Fir	20	9	8	19	0	0	0	0	0	0	0	36
Low-Fir	26	6	0	25	0	0	0	0	0	0	0	31
Low-Fir	30	4	0	18	9	6	0	0	0	0	0	37
Low-Fir	31	8	3	1	0	10	3	4	0	0	0	29
Fir	mean	25	3	1	3	0	0	0	0	0	0	31
Fir-Sw	mean	20	6	5	1	0	0	0	0	0	0	32
Low-Fir	mean	8	2	13	2	2	0	1	0	0	0	28
All	mean	17	3	6	2	1	0	0	0	0	0	30

Table J. The tree stem density of the stands (trees with dbh ≥ 10 cm)

stand	site	b. fir	w. spruce	b. spruce	w. birch	y. birch	s. maple	r. maple	P. cherry	m. ash	thuya	tot
Fir	1	421	0	0	425	0	0	0	0	0	0	846
Fir	3	676	23	0	207	0	0	0	76	0	0	982
Fir	7	1558	0	14	17	0	0	0	0	0	0	1589
Fir	10	984	162	0	113	0	0	0	0	0	0	1259
Fir	14	1442	10	27	304	0	0	0	0	0	0	1783
Fir	22	809	67	0	102	0	0	0	0	0	0	978
Fir	23	1867	247	0	0	0	0	0	0	0	0	2114
Fir	27	1498	72	329	0	0	0	0	0	0	0	1899
Fir-Sw	4	1057	26	0	145	58	0	0	0	0	0	1286
Fir-Sw	6	530	43	243	91	0	0	0	0	0	0	907
Fir-Sw	8	953	0	276	59	0	0	0	0	0	0	1288
Fir-Sw	9	1510	699	20	0	0	0	0	0	0	0	2229
Fir-Sw	13	546	150	385	69	0	0	0	0	0	0	1150
Fir-Sw	17	589	107	420	54	0	0	0	0	0	0	1170
Fir-Sw	21	759	337	32	38	0	0	0	0	0	0	1166
Fir-Sw	24	372	110	16	0	0	0	0	0	0	0	498
Fir-Sw	25	1276	375	130	0	0	0	0	0	0	0	1781
Fir-Sw	28	1019	0	653	0	0	0	0	0	0	0	1672
Low-Fir	2	149	6	0	83	106	0	212	0	0	0	556
Low-Fir	5	488	0	240	209	0	0	0	0	44	0	981
Low-Fir	11	656	0	314	0	0	0	0	0	0	0	970
Low-Fir	12	845	23	436	0	0	0	0	0	0	0	1304
Low-Fir	19	416	32	986	64	0	0	0	0	0	0	1498
Low-Fir	20	529	356	798	0	0	0	0	0	0	0	1683
Low-Fir	26	327	0	1042	0	0	0	0	0	0	0	1369
Low-Fir	30	149	0	682	745	142	0	0	0	0	0	1718
Low-Fir	31	349	63	22	11	220	45	208	0	0	14	932
Fir	mean	1157	73	46	146	0	0	0	10	0	0	1431
Fir-Sw	mean	861	185	218	46	6	0	0	0	0	0	1315
Low-Fir	mean	434	53	502	124	52	5	47	0	5	2	1223
All	mean	806	108	262	101	19	2	16	3	2	1	1319

APPENDICE E

THE ORIENTATION AND SHAPE OF GAPS

The shape and orientation of gaps affect the influence of gap size on plant regeneration. Many studies have shown that gap filler density, composition and growth rate are often different in areas within the gap according to the cardinal direction. This is especially the case in northern latitudes where the arc of the sun's itinerary is further from the zenith (Canham and al, 1990). The ecotone area, which in many cases plays a particular ecological role, will be proportionally greater in gaps with irregular shapes, since there is a longer perimeter for a given area. The effect of gap size, conceived as the distance from the gap's edge to center, is distorted when the gap shape differs from that of the circle, and additionally so when the orientation is considered. The orientation of gaps, however, usually receives little attention in gap regime evaluations. Liu and Hytteborn (1991) in boreal conifer forests of Sweden have found no particular gap orientation, and neither have we.

Probably for reasons of sampling difficulty, gaps are often taken to be circular or elliptical in shape, and their areas determined by simply measuring the length of the longest axis (L) and the length of the longest axis (W) perpendicular to it. An eccentricity rating is then used on the basis of the L:W ratio, a circle having a ratio of 1:1 (Holeska *et al.* 2001; Runkle 1990; Perkins *et al.* 1992; Hunter and Parker 1993; Battles and Fahey 1996). In our case, we felt that deciding on what constitutes length and width axes was too arbitrary an exercise, especially when the gap shape was very irregular. We therefore measured a number of width axis (W) in each gap in order to have a more accurate estimation of gap area and perimeter. Only a few studies have evaluated the eccentricity of shapes by considering the Perimeter : Area ratio (Lertzman *et al.* 1991; Gagnon *et al.* 2003), making comparisons unprofitable. To calculate the perimeter of gaps with areas corresponding to L and W values used as benchmarks in the literature (1:1, 2:1, 3:1, 4:1), we used the formula developed by S. Ramanujan (1887-1920): $P \approx \pi[3(a+b) - ((3a+b)(a+3b))^{0.5}]$, where $a=L/2$ and $b=W/2$. Most of our gaps are roughly elliptical in shape, not surpassing a ratio of 2:1 and practically all are below a 4:1 ratio, much like what has been observed in northern temperate deciduous forests (Runkle 1990). Larger gaps seem to have slightly more eccentric shapes, particularly those greater than 200 m² (fig. H). Lertzman *et al.* (1991) also noted this.

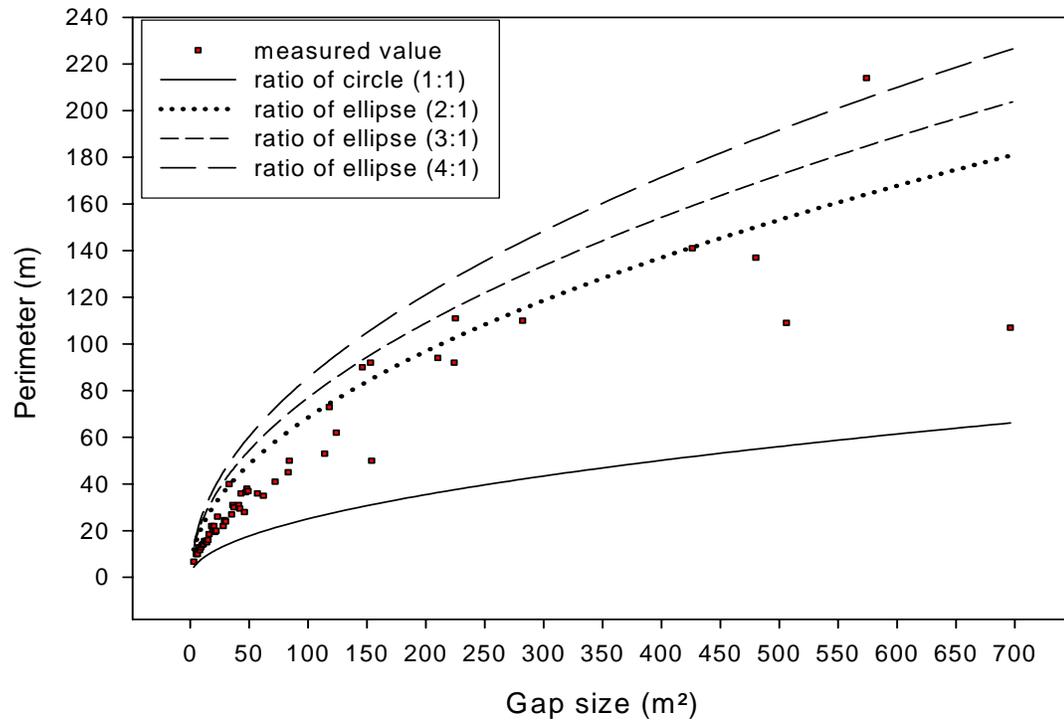


Figure H. The perimeter of gaps as a function of their surface area.

APPENDICE F

AN ATTEMPT AT USING TRANSECT SEGMENTS AS INDICATORS OF GAP DIAMETERS

An attempt was made to use segments of the transect lines without canopy (which were used to calculate the gap fraction) as approximations of the gap diameters, in order to realize a more extensive evaluation of the gap size distribution. Measuring the size of gaps is time consuming and always to some degree inaccurate, and so an approximation of size using transect segments would be useful. No gaps are perfectly circular, and none will ever be traversed exactly through the origin (center of the circle). If a large enough number of gaps are sampled, it could be that as many of them are traversed lengthwise as sideways, but it does seem inevitable that all chords (a line segment within a circle that touches 2 points on the circle) will be shorter than the diameter and of course on average as well. Because of our results, we decided not to evaluate the size distribution this way.

When compared to the true areas calculated from 101 gaps, the areas of 68% of gaps were either over- or under-estimated by at least 50%, with a mean of 26% and a median of 46% area underestimation. Excluding 4 strongly overestimated values, the range of values is 374%, from -100% to 274% (fig. I). An example of the distorted values found in one transect section is shown (fig. J).

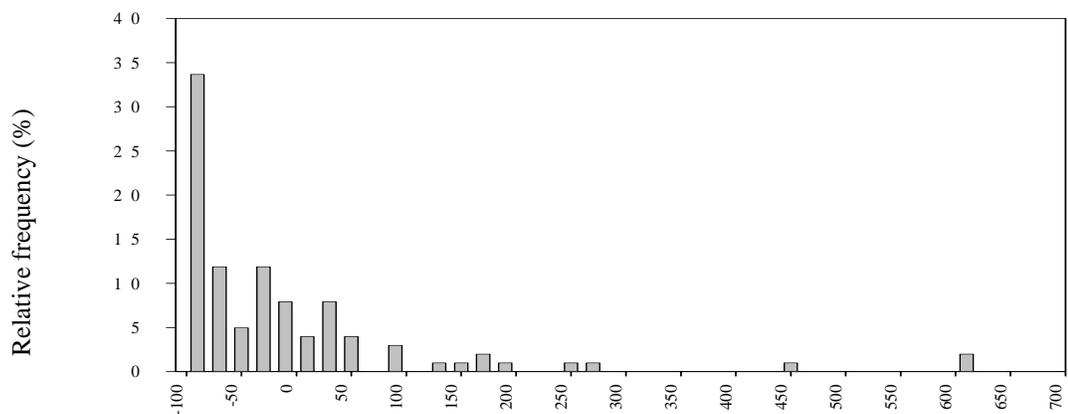


Figure I. The frequency of under- and over-estimations of gap area (one value of 1270% is not shown).

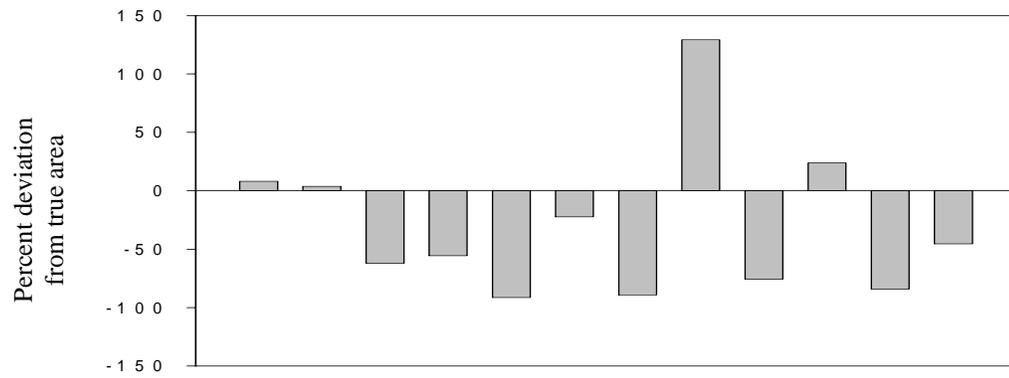


Figure J. Example of the overestimated and underestimated areas of 12 gaps along a stretch of transect 150m. long (the distance between gaps is ignored).

APPENDICE G

AERIAL SPRAYING AGAINST THE SPRUCE BUDWORM

Aerial applications of insecticides against the Sbw probably had an impact on the disturbance regimes in Gaspé. In our evaluation of the regime's variability we did not consider this factor because of the lack of knowledge on the use and the impact of the applications (Mackinnon and MacLean 2002), but its potential influence is too important to ignore. In 1954 the Québec government (today's Ministry of Natural resources, Fauna and Parks) began a province-wide program of chemical and biological aerial spraying to limit the damage caused by the Sbw during epidemics. In our sites four chemically-based and three biologically-based solutions were applied, among them so-called B.t. (*Bacillus thuringiensis* (MRNQ 2001). Most studies describing or evaluating natural disturbances in forests attacked by the Sbw do not take into account of spraying programs because their impact is considered insignificant (Dupont *et al.* 1991), because there was no spraying at all in the area (Morin 1994; Bergeron *et al.* 1995) or for some unspecified reason (Kneeshaw and Bergeron 1998; Pham *et al.* 2004; Bergeron and Leduc 1998; Filion *et al.* 1998). Morin (1998), in an article comparing Sbw epidemics in different regions of Québec, doesn't mention the use of insecticides. And yet aerial applications can totally prevent defoliation during the year (Baskerville 1975; Blais and Martineau 1960; D.A. MacLean, personal communication), and can prolong the actual epidemic and increase the susceptibility of an area during the next epidemic (Blais 1984 and 1974). The Gaspé region has been the subject of much more spraying than other regions (fig. K), the territory serving to evaluate the efficiency of the exercise (Veilleux and Sheedy 1978; Blais 1974), and therefore more attention to its impact is perhaps necessary here.

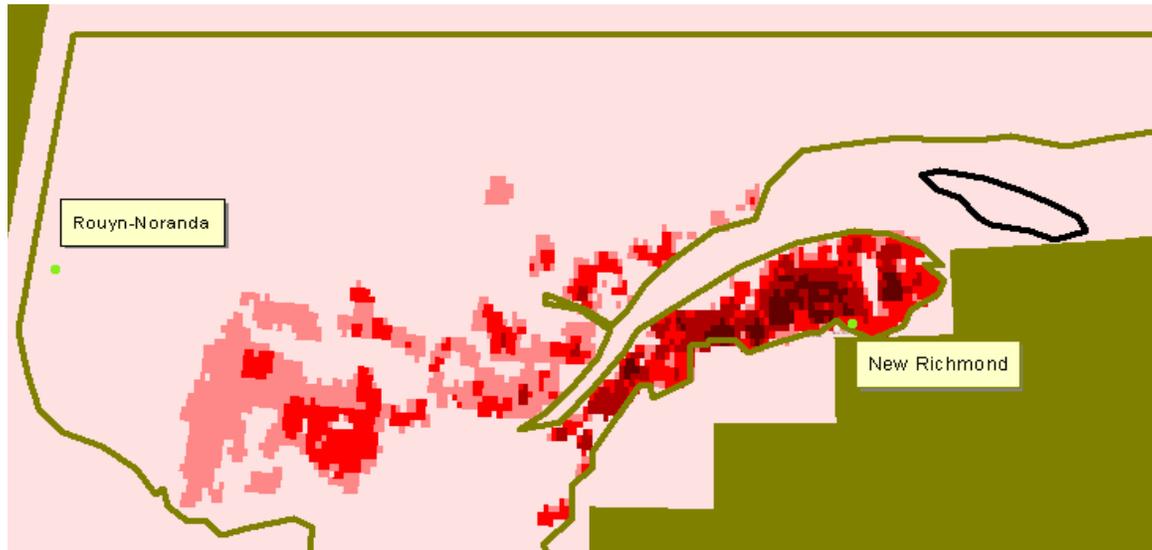


Figure K. The varying intensity of insecticide applications against the Sbw in Québec between 1954 and 1991, according to data from the MRNFPQ (recorded in pixels of 5 min.²). (See legend below).

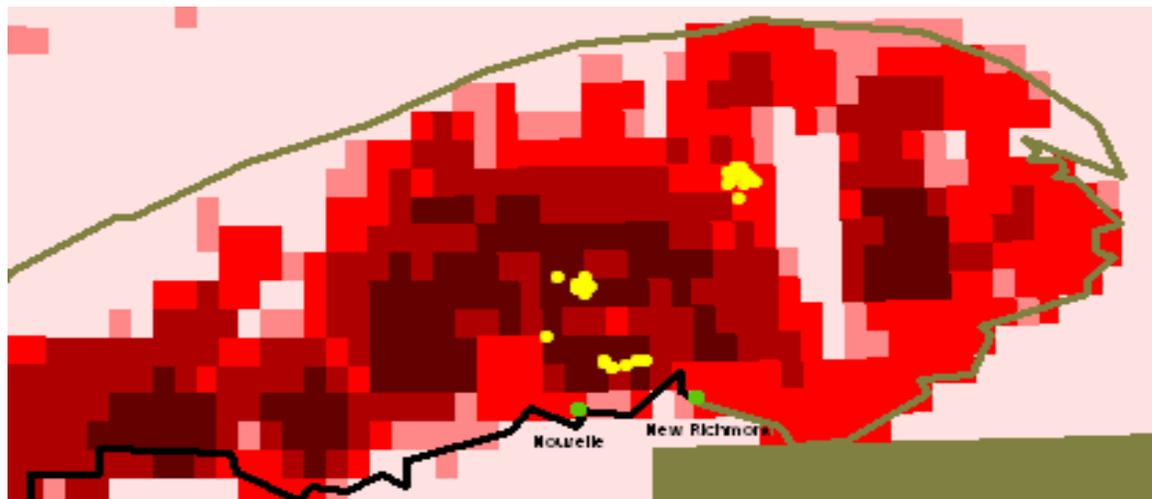
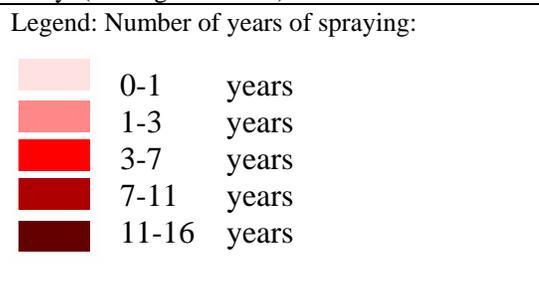


Figure L. The varying intensity of insecticide applications against the Sbw in Gaspé between 1954 and 1991, according to data from the MRNFPQ (recorded in pixels of 5 min.²), with sites from our study. (See legend below).



Within Gaspé also the insecticides were unequally applied spatially (fig.L). Sites in our northern zone were less intensely treated (from 6 to 7 years) than sites in the south (from 11 to 16 years), where were located most Other-type stands. Considering these sites more individually, (see table K), one sees that stands composed of black spruce were much more affected than stands composed of tolerant deciduous species (e.g.: yellow birch). Thus it appears as if sites containing more fir were not necessarily more sprayed. Perhaps this indicates that the actual stand composition does not reflect the composition prior to disturbances (see Study area and methods section), or perhaps priority in the spraying program was accorded to some stand types over others, for example pure fir stands being less sprayed because they are considered irrecoverable (Ketela 1975). It is surprising that it is stands having more black spruce (but not those having the most black spruce: b.spruce + fir) which are both more sprayed and have higher gap fractions, since spraying should lessen the amount of Sbw damage and therefore result in a lower gap fraction. In any case, as far as we can tell from the data, spraying intensity cannot explain why it is not fir-dominated stands which were more severely disturbed.

Table K

The varying intensity of insecticide applications (% number of years in the period), according to stand composition, during both Sbw epidemics (1948-1991), and during the latest Sbw epidemic (1973-1991).

stand type	1948-1991		1973-1991	
	A	B	A	B
mixte	60	39	59	47
b.spruce + fir	56	41	69	55
fir + b.spruce	62	45	75	60
fir + w.spruce	56	41	67	56
fir	57	41	71	55

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