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RÉSUMÉ DE LA THÈSE

Les épidémies de livrée des forêts (*Malacosoma disstria* Hbn.) sont une importante perturbation en forêt boréale feuillue et mixte dominées par le peuplier faux-tremble (*Populus tremuloides* Michx). Bien que l'importance et la récurrence des infestations aient conduit à une meilleure compréhension des cycles épidémiques et des dynamiques de défoliation, il y a peu de connaissances des impacts de cette perturbation sur la mortalité des arbres et la réponse des peuplements. Le principal objectif de cette thèse était de documenter les effets d'une épidémie de livrée des forêts sur la mortalité du peuplier faux-tremble et la dynamique de succession forestière de la sapinière à bouleau blanc de l'ouest du Québec.

La récente épidémie qui a affectée l'ouest du Québec entre 1999 et 2002 a permis de caractériser la vulnérabilité des peupliers observée à l'échelle d'une portion de paysage de 300 km^2. La probabilité de mortalité augmentait avec le nombre d'années de défoliation (passant de 5 à 35% entre 0 et 3 années de défoliation modérées et sévères) et elle était plus importante dans les peuplements feuillus et mixtes dominés par les peupliers dont l'âge cartographique était de 50 ans.

L'échantillonnage de 20 peuplements feuillus et 12 peuplements mixtes à dominance feuillue sélectionnés le long d'un gradient d'intensité de défoliation a montré une augmentation du taux d'ouverture du couvert forestier, de la taille moyenne des trouées et de la proportion des trouées de grandes tailles avec l'intensité de la défoliation. La formation de trouées a modifié les conditions de lumière en sous couvert, favorisant le drageonnement du peuplier faux-tremble dans les peuplements feuillus et le recrutement et la croissance du sapin baumier (*Abies balsamea* (L.) Mill.) dans les peuplements mixtes. Du point de vue de la succession forestière, les épidémies de forte intensité tendent à favoriser le renouvellement du couvert dans les peuplements feuillus alors qu'elles tendent à accélérer la conversion du couvert des peuplements mixtes vers des stades à dominance résineuse. Les patrons de mortalité suggèrent que la formation de trouées créent des structures inéquiennes à l'échelle du peuplement et que la variabilité dans l'intensité des épidémies de livrée des forêts créent une large gamme de peuplements de structure équienne à inéquienne à l'échelle du paysage.

Finalement, une expérimentation de défoliation artificielle réalisée dans de jeunes peuplements de peuplier faux-tremble a permis de tester l'effet d'une défoliation simulée sur la mortalité des arbres. Les patrons observés après défoliation artificielle ont confirmé certains patrons observés en peuplements naturels après épidémie, tels que l'augmentation du taux de mortalité et du diamètre des arbres morts avec le nombre d'années de défoliation, ou encore l'agrégation spatiale des arbres morts à l'origine de la formation des trouées. Cette expérimentation suggère qu'une défoliation sévère répétée plusieurs années pendant une épidémie pourrait expliquer une importante part de la mortalité des arbres.

Cette thèse apporte des connaissances fondamentales sur les effets des épidémies de livrée des forêts en forêt boréale mixte de l'est du Canada. Les informations qu'elle présente devraient permettre de mieux prédire les impacts des épidémies de livrée des forêts et devraient contribuer à améliorer les modalités d'aménagement écosystémique qui visent à s'inspirer de ce type de perturbation.

Mots-clés : épidémies de livrée des forêts, peuplier faux-tremble, défoliation, mortalité, trouées, régénération, dynamique de succession forestière.

INTRODUCTION GÉNÉRALE

En forêt boréale d'Amérique du nord, l'étude du rôle des épidémies d'insectes dans la dynamique naturelle de succession a longtemps été marginalisée, ayant souvent cédée le pas à l'étude du régime des feux dans ce contexte. Pourtant, les épidémies d'insectes ont été dans les dernières décennies le principal agent de perturbation dans l'est comme dans l'ouest du continent (Volney et Fleming 2000). Les insectes aux dynamiques de population éruptives souvent mal comprises, se manifestent de façon moins spectaculaire que les feux de forêts. Toutefois, à l'instar de ces derniers, ils peuvent affecter d'importantes superficies et causer de profondes modifications de la structure, de la composition et du fonctionnement des écosystèmes forestiers. Compte tenu de la pression anthropique exercée sur la dynamique de succession forestière par la lutte contre les feux et l'aménagement forestier (Bergeron *et al.* 1998; Kuuluvainen 2002), de la difficulté à prédire les effets des changements climatiques sur la dynamique des perturbations naturelles (Fleming et Candau 2004), et de la capacité adaptative des insectes face à leur environnement changeant (Parmesan 2006), il apparait légitime de se demander qu'elle pourrait être la dynamique naturelle des peuplements et paysages forestiers boréaux sous un régime de perturbation dominé par les épidémies d'insectes. De plus, avec l'intérêt grandissant pour le nouveau paradigme d'aménagement forestier écosystémique (Bergeron et Harvey 1997; Seymour et Hunter 1999; Gauthier *et al.* 2008) qui vise à développer des stratégies d'aménagement sylvicole en s'inspirant de la dynamique naturelle des peuplements forestiers, il est aisé de comprendre que la pertinence des connaissances des effets des épidémies d'insectes sur la dynamique forestière devient de plus en plus incontournable.

En forêt boréale mixte de l'est du continent nord-américain, les peuplements dominés par des essences feuillues initient généralement la succession naturelle après feu (Bergeron 2000). En absence de perturbation secondaire telles que les épidémies d'insectes ou les chablis, ces peuplements monospécifiques composés d'essences pionnières intolérantes à l'ombre tendent à évoluer vers des stades de mixité où la proportion d'essences conservatrices résineuses et tolérantes à l'ombre, augmente habituellement avec le temps depuis le dernier feu (Bergeron 2000). Au cours de cette phase de transition, la mortalité naturelle des arbres dominant la canopée entraîne la formation de trouées qui modifient les conditions abiotiques à l'échelle locale et favorisent le recrutement et la croissance des espèces présentes en sous couvert forestier (Kneeshaw et Bergeron 1998; Chen et Popadiouk 2002). Ultimement, les essences pionnières feuillues peuvent disparaître au profit des essences résineuses dont la dominance se perpétue généralement jusqu'au passage d'une perturbation majeure, souvent le feu en forêt boréale. Au cours de cette succession forestière qui peut se produire sur plusieurs centaines d'années, les traits biologiques des espèces et les interactions biotiques entre ces dernières jouent un rôle primordial dans le remplacement des espèces dominantes (Bergeron 2000; Chen et Popadiouk 2002). Du point de vue des épidémies d'insectes, elles ponctuent cette dynamique de succession forestière d'évènements qui peuvent altérer les patrons de mortalité naturelle et modifier la trajectoire des peuplements (Bergeron *et al.* 1995; Bouchard *et al.* 2006; 2007) en initiant un important processus écologique : la succession secondaire.

Les épidémies de livrée de forêts, un vorace défoliateur d'essences feuillues, constituent une importante perturbation de la forêt boréale méridionale nord-américaine (Witter 1979). Au Canada, les épidémies de livrée des forêts ont affecté près de 81 millions d'hectares entre 1980 et 1996, faisant de cette perturbation la plus importante en termes de superficie affectée par les épidémies d'insectes au cours de cette période (Simpson et Coy 1999). Avec une récurrence de 9 à 13 ans (Cooke et Lorenzetti 2006), les épidémies de livrée des forêts durent généralement de 1 à 6 années (Duncan et Hodson 1958; Hildahl et Campbell 1975; Ives et Wong 1988) et peuvent se produire au-delà du 50$^{\text{ème}}$ degré de latitude nord (Huang *et al.* 2008). En forêt boréale méridionale, les épidémies de livrée des forêts affectent les peuplements feuillus et mixtes de début de succession dominés par l'une des espèces les plus largement distribuées en Amérique du nord, le peuplier faux-tremble (*Populus tremuloïdes* Michx.). La livrée des forêts possède aussi de nombreux hôtes secondaires ou hôtes alternatifs parmi lesquels le bouleau blanc (*Betula papyrifera* Marsh.) et le peuplier baumier (*Populus balsamifera* L.) (Hodson 1941; Hildahl et Campbell 1975; Witter 1979; Ives et Wong 1988) sont les plus communs en forêt boréale méridionale.

Les causes de ces phénomènes éruptifs que constituent les épidémies de livrée des forêts restent à ce jour encore méconnues. Toutefois, il semblerait qu'une succession d'évènements climatiques favorables à la survie hivernale des amas de pontes et à l'émergence larvaire, ainsi qu'un synchronisme phénologique entre le développement de l'insecte et celui du feuillage de ses hôtes puissent affecter de telles explosions démographiques des populations de livrée des forêts (Hodson 1941; Hildahl et Campbell 1975; Daniel et Myers 1995). Les dynamiques de défoliation par la livrée des forêts ont fait l'objet d'une plus grande attention, et ont été rapportées sensibles à l'effet de l'hétérogénéité forestière, principalement la fragmentation du paysage et l'effet de bordure (Roland 1993; Cooke et Roland 2000, 2003; Roland 2005). Ainsi, l'hétérogénéité forestière augmenterait la durée des épidémies en réduisant les capacités de dispersion des diptères parasitoïdes (Roland et Taylor 1997) tels que la mouche *Arachnidomyia aldrichi* (Hodson 1941; Sippell 1962; Hodson 1977; Witter 1979) et la transmission de virus tel que la polyhédrose nucléaire (Stairs 1966; Roland et Kaupp 1995; Rothman et Roland 1998) qui sont souvent associés au déclin de densité de population de livrée des forêts.

Les effets des épidémies de livrée des forêts dépendent généralement de la durée et de la sévérité des défoliations. Les défoliations sévères, qui correspondent à une perte totale ou quasi-totale du feuillage, entraînent une réduction du nombre de branches (Ives et Wong 1988) et une diminution de la croissance radiale (Duncan et Hodson 1958; Churchill *et al.* 1964; Hildahl et Campbell 1975; Hogg et Schwarz

1999) généralement associée à la formation de cernes de croissance pâles caractéristiques (Hogg et Schwarz 1999; Hogg *et al.* 2002b; Sutton et Tardif 2005; Huang *et al.* 2008). À l'inverse des effets sur la croissance, il demeure une polémique quant aux effets de la défoliation par la livrée des forêts sur la mortalité des arbres affectés. La défoliation, considérée comme facteur incitant ou déclenchant (Manion 1981; Frey *et al.* 2004), n'entraînerait qu'un affaiblissement des arbres, la mortalité survenant de façon post-traumatique par l'effet combiné de facteurs prédisposant (gel, dégel, sècheresse, âge) et/ou contribuant (agents secondaires : insectes, pathogènes ou chablis) (Hogg et Schwarz 1999; Candau *et al.* 2002; Hogg *et al.* 2002a; Brandt *et al.* 2003). Au contraire, certains travaux ont présenté la mortalité des arbres comme directement imputable à l'effet de la défoliation par la livrée des forêts (Hildahl et Reeks 1960; Churchill *et al.* 1964). Des taux de mortalité plus élevés sont généralement rapportés chez les arbres supprimés (Duncan et Hodson 1958; Hildahl et Reeks 1960), toutefois Churchill et al (1964) ont montré que la proportion d'arbres dominants morts augmentait avec l'intensité (sévérité et durée) de la défoliation. Plus récemment, Man *et al.* (2008) et Man et Rice (2010) ont rapporté un effet de la vigueur des arbres en montrant que la mortalité suite à la défoliation par la livrée des forêts était plus importante chez les arbres qui présentaient les plus faibles taux de croissance avant épidémie.

Du point de vue de la dynamique de succession forestière, les épidémies permettent le maintien de la composition du couvert forestier dans les peuplements dominés par les essences feuillues intolérantes à l'ombre (Man et Rice 2010), alors qu'elles favorisent la conversion du couvert dans les peuplements mixtes (Reinikainen *et al.* 2012). Bien que les mécanismes de remplacement des espèces aient été identifiés dans un contexte post-épidémique (Bergeron 2000; Bergeron *et al.* 2002; Chen et Popadiouk 2002), peu de connaissances des effets l'intensité de la perturbation par la livrée des forêts sur la dynamique spatio-temporelle de la mortalité des espèces hôtes ont été acquises à ce jour. Un des objectifs de cette thèse est de combler ces lacunes, du moins en partie, en mettant une emphase particulière sur l'effet de la durée et de la sévérité des épidémies de livrée des forêts sur les patrons de mortalité et de régénération qui caractérisent la dynamique naturelle par trouées en peuplements feuillus et mixtes dominés par le peuplier faux-tremble.

Le peuplier faux-tremble est une espèce peu longévive dont le dépérissement et la mortalité synchrone étudiés au Québec (Pothier *et al.* 2004) et en Ontario (Candau *et al.* 2002) ont été, entre autres, reliés aux effets des épidémies de livrée des forêts. Depuis le début de la colonisation et de l'ère industrielle au Québec, les essences pionnières dites de lumière, telle que le peuplier faux-tremble, ont vu leur taux d'occupation du territoire augmenter de façon significative. Cette augmentation peut être expliqué par l'interaction entre la coupe et les feux d'abatis échappés lors du défrichement et à l'utilisation systématique des coupes totales de ces dernières décennies (Carleton et MacLellan 1994; Dery 1995; Archambault *et al.* 1998; Weir et Johnson 1998; Lefort *et al.* 2003; Laquerre *et al.* 2009). Ce phénomène, qualifié d'enfeuillement (Grondin *et al.* 2003), a généré un important réservoir de peuplements dominés par le peuplier faux-tremble, et a donc potentiellement contribué à l'augmentation de la proportion des surfaces susceptibles aux infestations par la livrée des forêts à l'échelle du paysage.

Le peuplier faux-tremble est une espèce pionnière bien adaptée au feu qui régénère principalement par drageonnement (Brown et DeByle 1987). Ce mécanisme de reproduction végétative conduit à la formation d'unités génétiques composées de plusieurs arbres inter-reliés par une même racine mère, et que l'on qualifie de clones (Farmer 1962). En plus de son mode d'établissement qui entraîne la connexion racinaire d'individus génétiquement identiques, le peuplier faux-tremble est sujet à des greffes racinaires (DesRochers 2000) qui entraînent la connexion entre individus génétiquement différents et forment de véritables unités physiologiques ou clones physiologiques (Jelínková *et al.* 2009). Les effets de l'interconnexion racinaire entre les arbres ont été peu étudiés en contexte épidémique (voir Baret et DesRochers 2011 qui testent l'effet d'une défoliation artificielle sur des couples d'arbres situés sur une même racine mère) et apportent un degré de complexité à la compréhension des mécanismes de mortalité du peuplier faux-tremble. Compte tenu que les questions d'échange et de partage des ressources entre arbres interconnectés sont encore mal comprises (Eis 1972; Stone 1974; Tarroux *et al.* 2010), il est difficile d'appréhender les mécanismes de mortalité pour de telles structures génétiques et physiologiques. D'ailleurs, il est légitime de se demander si le synchronisme et l'agrégation de la mortalité du peuplier faux-tremble observés en forêts matures (Candau *et al.* 2002; Pothier *et al.* 2004) et lors de la formation des trouées (Kneeshaw et Bergeron 1998), ne pourraient pas en partie s'expliquer par l'effet de connexions racinaires lié au drageonnement (Kneeshaw et Bergeron 1998) et aux greffes racinaires (DesRochers 2000).

D'un point de vue physiologique, la perte de dominance apicale chez le peuplier faux-tremble (suite à une coupe, un annelage ou un évènement de chablis) entraîne une altération des mécanismes hormonaux à l'échelle de l'arbre qui se traduit par un déséquilibre entre la quantité d'auxine produite au niveau foliaire qui inhibe le drageonnement (Schier *et al.* 1985) et la quantité de cytokinine produite au niveau racinaire qui le favorise (Hungerford 1988). Ce mécanisme est bien connu (Farmer 1962) mais n'a jamais été étudié dans un contexte d'épidémie de livrée des forêts (voir Baret et DesRochers 2011, expérimentation de défoliation artificielle). La défoliation par la livrée des forêts survient après le développement du feuillage et ne devrait pas modifier le rapport des concentrations tissulaires auxine/cytokinine à l'échelle de l'arbre. Par conséquent, la défoliation par la livrée des forêts ne devrait pas induire une réponse de drageonnement. Toutefois, si une défoliation devait entraîner la mort de la partie aérienne de l'arbre et que la partie souterraine restait en vie, alors la perte de dominance apicale devrait favoriser (l'année subséquente) une production de drageons qui pourrait être d'autant plus importante que les taux de mortalité seraient grands.

L’objectif principal de cette thèse est de documenter les effets d’une épidémie de livrées des forêts sur les patrons de mortalité du peuplier faux-tremble et de décrire leurs répercussions sur la dynamique successionnelle en forêt boréale méridionale de l’ouest du Québec. Cet objectif se divise en sous-objectifs plus spécifiques :

- Déterminer l’effet de l’intensité de la défoliation par la livrée des forêts et des caractéristiques écoforestières des peuplements sur les patrons de mortalité des espèces hôtes;
- Décrire les conséquences d’une épidémie de livrée des forêts sur la dynamique par trouées des peuplements feuillus et mixtes dominés par le peuplier faux-tremble;
- Tester expérimentalement l’effet d’une défoliation artificielle sur les patrons spatio-temporels de mortalité du peuplier faux-tremble.

Cette thèse qui comprend 4 chapitres a été réalisée sur la ceinture d’argile abitibienne, dans le nord-ouest du Québec (Vincent et Hardy 1977; Veillette 1994). Ce territoire a subit une épidémie de livrée des forêts entre 1998 et 2003 qui a fait l’objet d’un suivi aérien mené par le Ministère des Ressources naturelles et de la Faune du Québec pour chacune des années de défoliation couvrant la période 1999 à 2002. Les superficies défoliées cumulées au cours de ces 4 années avoisinaient 1,4 million d’hectares, faisant de ce sixième cycle épidémique répertorié en Abitibi depuis 1938, le second en termes de durée, d’étendue et de sévérité (Cooke et Lorenzetti 2006).

Le premier chapitre, intitulé « Effects of forest tent caterpillar defoliation and stand characteristics on deciduous tree mortality » présente une analyse des patrons de mortalité pour un fragment de paysage de 30 000 hectares perturbé par la livrée des forêts lors de la dernière épidémie. Les données de mortalité et de défoliation provenant d’inventaires aériens ont été combinées aux données écoforestières issues de photo-interprétation pré-datant l’épidémie et ont permis d’évaluer les effets des attributs forestiers et de l'intensité de la défoliation sur la probabilité de mortalité des espèces hôtes. Le principal objectif de ce chapitre était de discriminer les principaux facteurs associés aux patrons de mortalité observés à l'échelle du peuplement. Les connaissances acquises par cette étude devraient permettre de mieux appréhender les impacts des épidémies de livrée des forêts.

Les deuxième et troisième chapitres sont respectivement intitulés « Gap dynamics in aspen stands of the clay belt of northwestern Quebec following a Forest tent caterpillar outbreak » et « Effects of a forest tent caterpillar outbreak on the dynamics of mixedwoods boreal forests of eastern Canada ». Ces études ont été réalisées à partir des données récoltées dans 20 peuplements monospécifiques et 12 peuplements mixtes dominés par le peuplier faux-tremble. Ces peuplements ont été sélectionnés de sorte à limiter l'hétérogénéité entre les sites en considérant les critères suivants : l'âge cartographique, le type de sol, la classe de drainage, la situation topographique, le type et le taux d'occupation de la végétation en sous couvert forestier. Ces chapitres documentent l'effet de l'intensité de la défoliation par la livrée des forêts sur la dynamique par trouées (patrons de mortalité et de régénération) des peuplements feuillus et mixtes dominés par le peuplier faux-tremble. Elles fournissent des informations fondamentales sur la dynamique successionnelle des peuplements affectés par les épidémies de livrée des forêts en forêt boréale méridionale.

Le quatrième chapitre, intitulé « Growth and mortality of trembling aspen (*Populus tremuloides*) in response to artificial defoliation: a three-year experiment at the stand level » utilise un dispositif expérimental de défoliation artificielle installé dans 3 jeunes peuplements purs de peuplier faux-tremble âgés de 8 ans. Ce chapitre vise à caractériser les effets d'une défoliation artificielle répétée pendant trois années consécutives sur la réponse de croissance et les patrons spatio-temporels de mortalité du peuplier faux-tremble. Le principal objectif de cette étude est de tester et mesurer les effets d'une défoliation simulée *in situ* et en conditions contrôlées sur la croissance et la mortalité du peuplier faux-tremble. Le second objectif de ce chapitre est de tester l'effet de la défoliation artificielle sur la distribution spatiale de la mortalité, soit de vérifier si les patrons de mortalité du peuplier faux-tremble observés après défoliation artificielle confirment les patrons d'agrégation observés après épidémie en peuplements naturels.

CHAPITRE I

EFFECTS OF FOREST TENT CATERPILLAR DEFOLIATION AND STAND CHARACTERISTICS ON DECIDUOUS TREE MORTALITY

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1.1 ABSTRACT

Forest tent caterpillar (*Malacosoma disstria* Hbn.) is one of the most important epidemic insect in deciduous forests of North America for which trembling aspen (*Populus tremuloides* Mixch.) is its preferred host in the northern part of its distribution. In this study, effects of forest tent caterpillar defoliation and forest stand characteristics on host tree mortality were investigated in northwestern boreal forest of Quebec. In this region, the most recent forest tent caterpillar outbreak occurred between 1999 and 2002. Aerial defoliation (1999-2002), mortality (2005) and forest inventory (early 1990's) databases were used to test at the stand level, how defoliation intensity, forest cover composition, stand age, stand density, drainage and surface deposit affect host tree mortality? This study clearly demonstrated that probability of mortality increased with repeated forest tent caterpillar defoliation and revealed that probability of mortality was higher in deciduous than coniferous dominated stands. Contrary to the expected results that older and high density stands would be more vulnerable, we found that middle aged stands (50 years old) and low density stands presented the highest probability of mortality. Finally, effect of drainage and surficial deposit could not be tested probably because of the low variability of such variables at the study scale. This case study should be replicated in another forest tent caterpillar disturbed landscape to confirm effects of forest tent caterpillar defoliation and forest characteristics on host tree mortality observed at the stand level.

Keywords: insect outbreak, defoliation, mortality, aspen, forest composition, landscape

1.2 RÉSUMÉ

La livrée des forêts (*Malacosoma disstria* Hbn.) est un des plus importants insectes épidémiques en forêts feuillues nord américaine pour qui le peuplier faux-tremble (*Populus tremuloides* Mixch.) est l'hôte préférentiel dans la partie nord de sa distribution. Dans cette étude, les effets de la défoliation par la livrée des forêts et des caractéristiques des peuplements sur la mortalité des arbres hôtes ont été évalués dans la forêt boréale du nord-ouest du Québec. Dans cette région, la plus récente épidémie de livrée des forêts est survenue entre 1999 et 2002. Des bases de données d'inventaires aériens de défoliation (1999-2002), de mortalité (2005) et écoforestier (début des années 1990) ont été utilisées pour déterminer à l'échelle du peuplement, comment l'intensité de la défoliation, la composition du couvert forestier, l'âge et la densité du peuplement, le drainage et le dépôt de surface pouvaient affecter la mortalité des arbres hôtes? Cette étude a clairement montré que la probabilité de mortalité augmentait avec les défoliations répétées et qu'elle était plus importante dans les peuplements feuillus que dans les peuplements résineux. Contrairement aux résultats attendus qui prévoyaient une plus forte vulnérabilité des vieux peuplements et des peuplements les plus denses, nous avons montré que les peuplements d'âge moyen (50 ans) et de plus faible densité présentaient la plus forte probabilité de mortalité. Finalement, à cause de la faible variabilité du drainage et du dépôt de surface à l'échelle de notre aire d'étude, l'effet de ces variables sur la mortalité des arbres n'a pas pu être testé de façon concluante. Cette étude de cas devrait être répliquée dans un autre paysage perturbé par la livrée des forêts afin de confirmer les effets de la défoliation et des caractéristiques des peuplements forestiers observés dans cette étude à l'échelle du peuplement.

Mots-clés : épidémies d'insectes, défoliation, mortalité, peuplier, composition forestière, paysage.

1.3 INTRODUCTION

In the boreal zone, wildfires are considered as the primary agent of disturbance (Bergeron, 2000). However, many insect species characterized by eruptive population dynamics, such as the spruce budworm (*Choristoneura fumiferana* (Clemens)), the mountain pine beetle (*Dendroctonus ponderosae* (Hopk.)), the large aspen tortrix (*Choristoneura conflictana* (Walker)), the hemlock looper (*Lambdina fiscellaria* (Guenée)) and the forest tent caterpillar (*Malacosoma disstria* (Hübner)), are also considered as important disturbances in the boreal forest (Cooke et al., 2007). In recurrently disturbed areas, outbreaks can profoundly modify the structure and the composition at both stand and landscape levels (Bergeron et al., 1995; Bouchard et al., 2006; 2007).

In the deciduous and mixed deciduous-dominated boreal forest of North America, the forest tent caterpillar (FTC) is one of the major disturbances causing insect (Witter, 1979; Fitzgerald, 1995). The FTC is a voracious defoliator of deciduous trees species for which trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.) and balsam poplar (*Populus balsamifera* L.) are the preferred host tree species in the boreal zone (Witter, 1979; Peterson and Peterson, 1992). FTC outbreaks occur at 9 year intervals (Cooke and Lorenzetti, 2006) and as far north as 54° of latitude (Huang et al., 2008).

FTC defoliations vary from light to severe (complete defoliation) (Hildahl and Campbell, 1975). Short events of light or partial defoliations have small effects on tree growth and can be offset by a compensatory photosynthesis in the residual leaves (Reichenbacker et al., 1996; Hart et al., 2000). Severe and repeated FTC defoliation however strongly reduces photosynthesis capacity and depletes carbohydrate reserves (Duncan and Hodson, 1958; Hildahl and Reeks, 1960; Kosola et al., 2001; Hogg et al., 2002) and root nutrient uptake for years (Kosola et al., 2001). Severe FTC defoliation decreases tree growth (Hildahl and Reeks, 1960; Hogg et al., 2002) and forest productivity (Bergeron and Charron, 1994; Hogg and Schwarz, 1999; Candau et al., 2002) and increases the probability of tree mortality (Churchill et al., 1964; Hildahl and Campbell, 1975). However, tree mortality is more frequently associated with predisposing, inciting and contributing factors (Manion, 1981, see also Frey et al., 2004), such as climate (Hogg et al., 2008), age (Brandt et al., 2003), wood-boring insects (Hogg et al., 2002), or fungal pathogens (Brandt et al., 2003) than with FTC defoliation itself (Churchill et al., 1964; Candau et al., 2002; Brandt et al., 2003; Man et al., 2008; Man and Rice, 2010; Moulinier et al., 2011). Tree mortality in stands severely defoliated over multiple years can occur up to six to ten years after FTC outbreak collapse (Duncan and Hodson, 1958; Churchill et al., 1964).

Several factors that influence FTC population and defoliation dynamics at the landscape and the stand level have been well described. Effects of climate, forest cover diversity, abundance of host trees species, forest fragmentation and natural enemies population dynamics are known to positively or negatively affect FTC outbreaks (Roland, 1993; Cooke and Roland, 2000, 2003; Roland, 2005; Charbonneau et al., 2012). Yet, factors involved in host tree mortality in a context of FTC outbreaks are less understood. Understanding how FTC defoliation dynamics and forest characteristics affect tree mortality is essential to predict vulnerability at the stand level.

The purpose of this study was to evaluate the effects of FTC defoliation intensity and stand characteristics such as composition, age, density, surficial deposit and drainage on trembling aspen mortality. Surprisingly, these factors have seldom been examined in the past. First, our main assumption was that FTC defoliation repeated through time should increase host tree mortality. Therefore, we expected that the probability of mortality should be higher in defoliated than undefoliated stands and that the probability of mortality should increase with defoliation duration. Second, because FTC defoliation intensity and duration have been reported to increase with the abundance of host tree species (Charbonneau et al., 2012), we expected that defoliation-induced mortality should tend to be higher in pure deciduous than in mixed or coniferous-dominated stands. Third, it is usually accepted that trembling aspen productivity and vigour decline in 60 to 80 year-old stands in the boreal zone (Kneeshaw and Bergeron, 1998; Bergeron, 2000; Cumming et al., 2000; Brandt et al., 2003; Pothier et al., 2004). We thus speculated that old stands should be more vulnerable and we expected a higher mortality probability of host trees in old than in young defoliated stands. Fourth, interaction between FTC defoliation and natural thinning has been observed to decrease density of high-density poplar stands (Duncan and Hodson, 1958; Hildahl and Reeks, 1960; Man et al., 2008; Man and Rice, 2010). Thus, we expected that defoliation-induced host tree mortality should be higher in dense than sparse stands. Finally, recent studies have reported that high tree vigour prior to FTC defoliation was generally associated with low mortality rates (Man et al., 2008; Man and Rice, 2010). Therefore, it was reasonable to think that stand characteristics that influence tree vigour, such as drainage and surficial deposit, could be related to tree mortality. Therefore, we expected that stands with extreme drainage conditions, which accumulate excessive amount of water (Landhausser and Lieffers, 2003) or drain water away (Shields and Bockheim, 1981), and stands with nutritional limitation such as rock, sandy and organic soils (Stoeckler, 1960) should reduce tree vigour and thus should increase the probability of host tree mortality.

To achieve these objectives, the effects of defoliation intensity and forest attributes on the probability of trembling aspen mortality have been tested at the stand level within a forest landscape that experienced from 0 to 3 years of moderate to severe FTC defoliation.

1.4 MATERIAL AND METHODS

1.4.1 Study area

Located within the northwestern Quebec Clay Belt and within the Abitibi lowland, the study area (Fig. 1) covers 300 km^2 (48°39'N - 48°45'N; 78°21'W -

78°40'W). The study area is characterized by a flat landscape (Vincent and Hardy, 1977) and a continental climate with cold dry winters and short mild summers. Included in the balsam fir–white birch bioclimatic domain (Robitaille and Saucier, 1998; Saucier et al., 1998), coniferous stands are dominated by balsam fir (*Abies balsamea.*), white spruce (*Picea glauca*), black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana*) while deciduous stands are dominated by trembling aspen (*Populus tremuloïdes*), balsam poplar (*Populus balsamifera*) and white birch (*Betula papyrifera*). Like the ecological region, the study area included deciduous, mixed and coniferous stands but was dominated by deciduous stands.

The most recent FTC outbreak occurred in northwestern Quebec from 1999 to 2002 (Fig. 1). This outbreak was the sixth event recorded since 1938 within the Abitibi lowland and was the longest, most extended and most severe since the 1950's (Cooke and Lorenzetti, 2006). With a maximum extent in 2001 of close to 1 million hectares moderately to severely defoliated (Bordeleau, 2001), this outbreak affected over 1.4 million hectares and was mostly restricted (around 70% of the total area defoliated) to the Abitibi lowland (Ecological region 5a, Blouin and Berger, 2002, Fig. 1). Only 21% of the forest territory was lightly or not at all defoliated during this outbreak, whereas 27%, 21% and 31% were moderately or severely defoliated during 1, 2, and 3-4 years respectively (Fig. 2).

1.4.2 Data

Data for mortality, our response variable was derived from an aerial survey of mortality in the study area conducted by F. Lorenzetti in September 2005. During this aerial survey, mortality was visually estimated and classified in 5 classes (0: no mortality, A: 1-25%, B: 26-50%, C: 51-75%, D: 76-100%). Only poplar mortality was evaluated to include mortality. Hence, for example, if all of the poplars were dead in a mixedwood stand (i.e. 50% aspen), the stand would have been classified as a mortality class D (and not as a class B). Mortality information was digitized and georeferenced in ArcGis (ESRI Inc. 2009, version 9.3). Mortality patches represented a total of 1155 ha. A subsample of stands (n=25) were visited in 2007 to corroborate aerial mortality data by ground survey (unpublished data).

Digitized and georeferenced defoliation data used in this study came from annual aerial survey of defoliation conducted from 1999 to 2002 by the Quebec Ministry of Natural Resources and Wildlife. During each annual survey, the proportion of foliage lost to defoliation was visually estimated for each stand and was classified in 4 classes (undetectable 0%, light 1-25%, moderate 26-65% or severe 66-100%) originally defined by the Forest Insect and Disease Survey (FIDS) program of the Canadian Forest Service. Defoliation data was also corroborated by ground survey data (Bordeleau et al., 2004).

Forest stand characteristics from which were derived our explanatory variables came from digitization and georeferencing of photo interpretation data (Letourneau et al., 2003) and were provided by the MRNF forest inventory maps. All data of mortality, defoliation and forest stand characteristics were computed and overlaid in ArcGis to build our data matrix.

1.4.3 Variables and statistical analysis

To test the effects of defoliation intensity and forest stand attributes on the probability of host tree mortality at the stand level, a logistic regression analysis was performed using mortality as the response variable. To the end, the original mortality data in four classes was reclassified as a binary variable with two classes (presence or absence of mortality). We selected randomly 768 stands (248 with mortality and 520 without) of 0.5 to 48 hectares for a total area of 5 120 hectares. Explanatory variables were defoliation intensity (i.e., the number of year of moderate and severe defoliation, from 0 to 3 years), forest cover composition (deciduous, mixed deciduous, mixed coniferous, or coniferous), mean stand age (10, 30, 50, or 70+ years), crown closure (an indirect estimation of stand density; A: more than 60%, B:

less than 60%), surficial deposit (clay, sand, till, organic, or rock) and drainage (very rapidly to well drained, moderately to imperfectly drained, or poorly to very poorly drained). Explanatory variables were all categorical.

We used a model selection analysis to assess which factors significantly affected the probability of mortality. We formed sets of plausible models to identify which of the predictor variables and their interactions might explain patterns of mortality. The fit of the global model was assessed for each analysis and models were compared using the second order Akaike Information Criterion (AIC_c) and the information theoretic approach presented by Burnham and Anderson (2002). We considered models with delta AICc values ≤ 2 to have strong support and we also calculated model weights from the AICc values to indicate the level of support for each of the models considered (Burnham and Anderson, 2002). Because only one model provided the best fit to the data, model averaging was not performed and the best model was selected and interpreted. The predictive power was calculated for each model with the Nagelkerke pseudo-R^2. All statistical analyses were performed using R software version 2.10.1 (R Development Core Team, 2010).

1.5 RESULTS

Among the 6 candidate models considered for the model selection analysis, the one which provided the best fit to the data (AIC_c weight, $w_i = 0.99$) included defoliation intensity, forest cover composition, mean stand age and crown closure (Table 1). No other model had strong support ($\Delta AIC_c \leq 2$), hence no model averaging was attempted. The best model had a pseudo-R^2 of 0.178 (Table 1). The logistic regression analysis (Table 2) revealed that the probability of mortality of host trees in stands defoliated 2 and 3 years was significantly higher than the probability of mortality of undefoliated stands ($P < 0.01$, Fig. 3). The analysis also showed that the probability of mortality after 1 year of defoliation was marginally significant compared to undefoliated stands ($P = 0.06$). Effects of stand composition showed that probability of mortality was significantly lower in coniferous-stands ($P \leq 0.01$) and lower in mixed coniferous dominated stands ($P \leq 0.09$) than in deciduous stands (Fig. 3 and 4). Although the probability of mortality in mixed deciduous stands was lower than in pure deciduous stands ($\beta = -0.42$), we did not observe a significant difference in the probability of mortality of mixed and pure deciduous dominated stands ($P = 0.20$). Effects of mean stand age revealed that probability of mortality was significantly higher in 50-year-old stands than in stands >70 years old ($P \leq 0.01$, Table 2), whereas no difference was observed between young (10 and 30 years old) and old (70+ years old) stands (Fig. 4). The last result of this analysis showed that the probability of host tree mortality tended to be higher in open stands (density class B or less than 60% of crown closure) than in dense stands (P = 0.09, Table 2). Drainage and surficial deposit used as proxy of stand vigour were not present in the best model, indicating a minor effect of such variables on the probability of host tree mortality.

1.6 DISCUSSION

This study shows a close relationship between FTC defoliation intensity and the probability of poplar mortality. In accordance with our hypothesis, the probability of host tree mortality increased with the number of years of moderate or severe FTC defoliation (Fig. 3). These results corroborate Man and Rice's (2010) findings which reported that mortality of poplar in Ontario was strongly linked to consecutive years of FTC defoliation. The probability of mortality observed in stands defoliated one year (Fig. 3) was lower than in undefoliated stands, although only marginally so ($P = 0.06$, Table 2), and demonstrated that one year of FTC defoliation was sufficient to increase poplar mortality. This effect of one year FTC defoliation has been reported to result from the death of the most vulnerable trees, such as suppressed trees (Churchill et al., 1964), small diameter trees (Moulinier et al., 2011), and less vigorous trees (Man et al., 2008; Man and Rice, 2010), whereas the increase in mortality observed in stands defoliated two and three years would be more related to the death of dominant and codominant trees of large diameter (Churchill et al., 1964; Moulinier et al., 2011).

Our results also reveal that mortality probability of host tree species differs between forest cover type (Fig. 3 and 4). The probability of mortality of poplar in deciduous stands was significantly higher than coniferous stands ($P < 0.01$, Table 2) and sub-significantly higher than in mixed coniferous-dominated stands ($P = 0.09$, Table 2). This effect of forest cover composition was consistent with mortality patterns reported by Man and Rice (2010), which described that higher poplar basal area or composition resulted in greater loss of poplar basal area or density. However, it is still difficult to understand why, for the same defoliation intensities, the probability of host tree mortality varies with forest cover composition and why mortality occurs in some stands but not others (Peterson and Peterson, 1992; Candau et al., 2002).

Contrary to our expectation, stands close to the age of stand decline (more than 60 years old, Pothier et al., 2004) were not more vulnerable to FTC defoliation than younger stands. In fact, middle-aged stands of 50 years (40 to 60 years old) presented the highest mortality probability, whereas the vulnerability of older and younger stands did not differ significantly (Fig. 4, Table 2). This effect contradicts Man and Rice's (2010) results that showed no difference in vulnerability between stand ages. However, our results are consistent with FTC defoliation patterns described in the same region area by Charbonneau et al. (2012), which reported higher susceptibility in 50-year-old stands. The susceptibility and vulnerability of middle-aged stands suggested that more detailed information on foliage suitability is needed to better understand FTC defoliation dynamics and how the relationship between FTC defoliation and tree age affects the probability of mortality at the stand level.

Tree density estimated by crown closure shows that mortality probability of host trees tended to be marginally higher in opened than in closed canopy stands ($P = 0.09$, Table 2). First, this effect of stand density could results from a sampling effect. In fact, crown closure or tree density of coniferous and mixed coniferous-dominated stands is usually higher than in deciduous-dominated stands. Therefore, the low mortality probability of high-density coniferous-dominated stands has possibly contributed to decrease the effect of host tree density on host tree mortality. Second, the evaluation of crown closure is *a priori* a better estimate of stand basal area and site index than stand density. Therefore, stands with low crown closure were possibly in low productivity sites. The higher vulnerability of such stands indicates a site effect that could not be captured by the variables of drainage and surficial deposit.

1.7 CONCLUSION

This study on stand vulnerability mostly corresponds (besides some differences) to what makes stands susceptible (Charbonneau et al., 2012). Our findings show that FTC defoliation-induced poplar mortality was mainly related to defoliation duration, forest cover composition, and stand age. In agreement with our assumptions, the probability of host tree mortality increased with repeated defoliation and the abundance of host trees (forest cover composition). Contrary to the expectation that FTC defoliation-induced mortality would be higher in older stands, middle-aged stands (50 years) were in fact the most vulnerable. To confirm patterns of host tree mortality observed in this study and to better understand host tree vulnerability at the stand level in this region, such analysis should be replicated at the landscape level with more contrasted forest stand characteristics, especially surficial deposit and drainage. Further research on the relationship between tree vigour, tree age, foliage quality, insect performance and FTC defoliation intensity and severity is required to understand why mortality affects some trees (Man et al., 2008) and some stands (Candau et al., 2002) and not others.

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Figure 1.1 Map of the study area showing tree mortality in 2005 (from 1 to 100% of mortality) and the number of year of moderate and severe forest tent caterpillar defoliation during the last outbreak that occurred from 1999 to 2002 in northwestern Quebec.

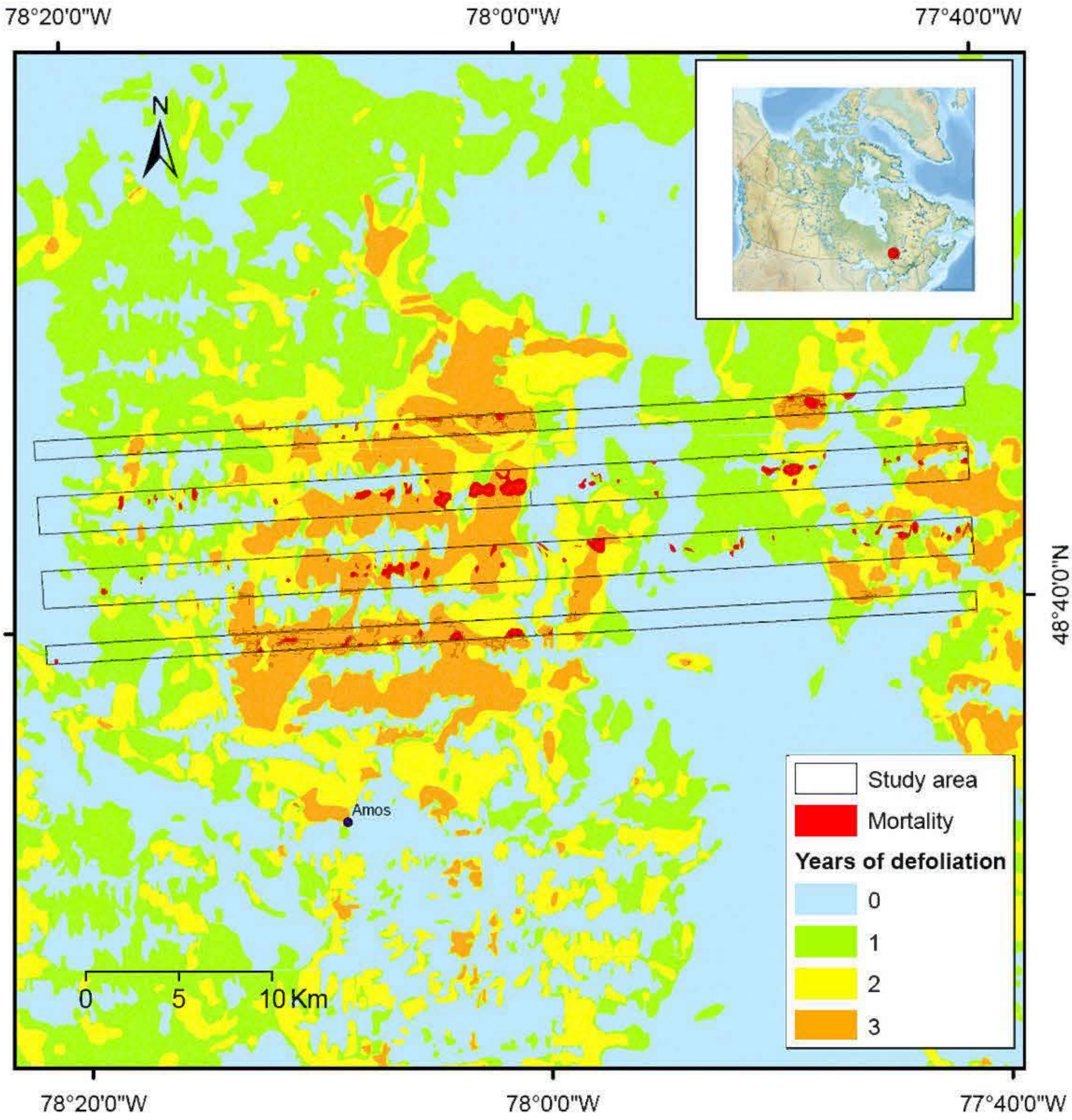

Figure 1.2 Predicted mortality probabilities (mean ± SE) in relation to defoliation duration for each forest cover types.

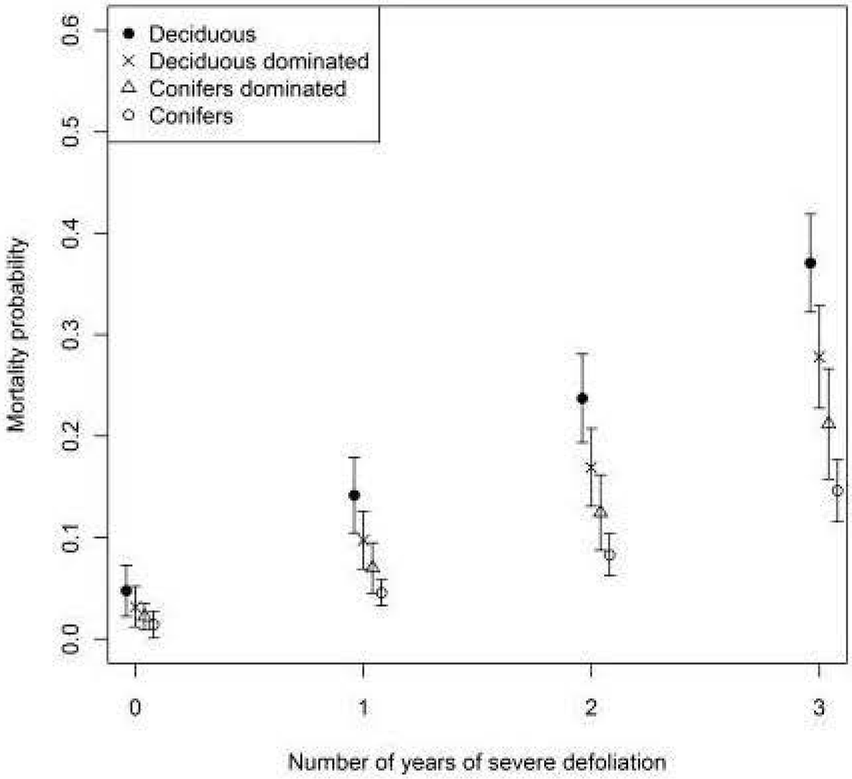

Figure 1.3 Predicted probability of mortality (mean ± SE) in relation to stand age class for each forest cover types.

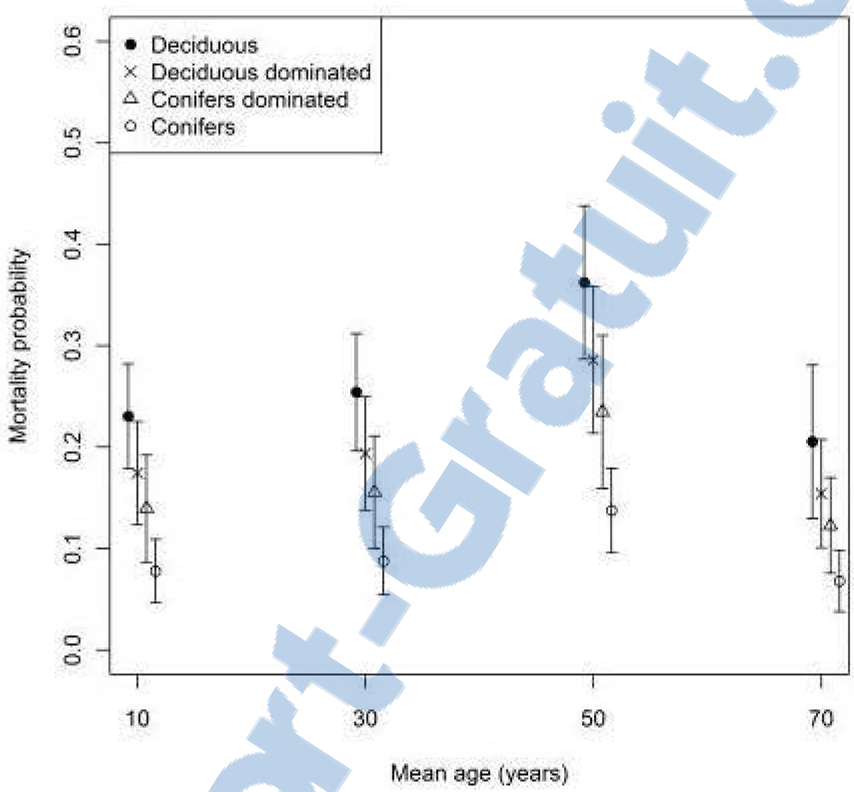

Table 1.1 Top ranking models for the analysis of the probability of mortality at the stand level.

Model	K^{*}	$AIC_c^{\dagger}$	$\Delta AIC_c^{\ddagger}$	$w_i^{\S}$	Nagel $R^{2\phi}$
Def+Cover type+Age+Density	13	1066.2	0.00	0.99	0.178
Def+Cover type+Age+Density+Drainage +Surface deposit+[Def×Cover type]	28	1077.9	11.78	0.00	0.198
Def+Cover type+[Def×Cover type]	16	1089.6	23.40	0.00	0.164
Def+Drainage+Surficial deposit	10	1100.9	34.70	0.00	0.142
Def	4	1113.5	47.32	0.00	0.114
Cover type	4	1132.1	65.89	0.00	0.098

[*] K = no. of parameters.

[†] AIC_c = Akaike's Information Criterion corrected for small sample sizes.

[‡] ΔAIC_c = AIC_c relative to the best model

[§] w_i = AIC_c model weight.

[ϕ] Nagel R^2 = Nagelkerke's pseudo R^2

Table 1.2 Parameter estimates and standard errors with z value and *P*-values from logistic regression analysis describing probability of mortality at the stand level. Tested levels are shown in parentheses for qualitative covariates. Reference levels are no defoliation (0), deciduous for Cover type (D), density A for crown closure (up to 60 %), and 70 years old for stand age. Tested levels are shown in brackets, and parameter estimates with probability in bold are terms with significant effect (P < 0.05).

Parameter	Estimate	SE	z value	*P*
Intercept	-4.08	0.56	-7.35	<0.01
Defoliation (1)	1.19	0.55	2.17	0.06
Defoliation (2)	1.83	0.53	3.43	**<0.01**
Defoliation (3)	2.47	0.52	4.71	**<0.01**
Cover type (MD)	-0.42	0.22	-1.91	0.20
Cover type (MC)	-0.78	0.29	-2.62	0.09
Cover type (C)	-1.23	0.21	-5.73	**<0.01**
Crown closure (B)	0.29	0.16	1.76	0.09
Age (10)	0.69	0.25	2.88	0.65
Age (30)	0.80	0.24	3.13	0.38
Age (50)	0.88	0.26	3.38	**<0.01**

CHAPITRE II

GAP DYNAMICS IN ASPEN STANDS OF THE CLAY BELT OF NORTHWESTERN QUEBEC FOLLOWING A FOREST TENT CATERPILLAR OUTBREAK

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2.1 ABSTRACT

Forest tent caterpillar (FTC; *Malacosoma disstria* Hübner) outbreaks represent an important natural disturbance in broadleaf-dominated stands; however, their effects on forest gap dynamics are not well understood. To describe such effects on canopy gaps and tree recruitment patterns, we investigated 20 trembling aspen (*Populus tremuloides* Michx.) dominated stands defoliated severely over 0 to 3 years during the last outbreak (1998–2003) in the northwestern Clay Belt of Quebec. Results show that canopy opening more than tripled (12.3%–43.7%) from 0 to 3 years of severe defoliation, and mean gap size was more than 12 times greater (7.2–87.5 m2) over the same gradient. Regeneration patterns suggest that aspen recruitment is not sufficient to completely restore closed canopies in stands defoliated 0, 1, and 2 years, whereas it should be sufficient in stands defoliated 3 years, where large gaps allow trembling aspen establishment. Our results clearly indicate that FTC outbreaks represent an important factor of gap formation in trembling aspen stands. At the stand level, gaps create uneven stand structures, and at the landscape level, FTC defoliation duration creates a large range of even to uneven stand structures.

Keywords: insect outbreak, trembling aspen, gap dynamics, forest succession,

2.2 RÉSUMÉ

Les épidémies de Livrée des forêts (LDF; *Malacosoma disstria* Hübner) constituent une importante perturbation naturelle dans les peuplements dominés par les feuillus. Cependant leurs effets sur la dynamique des trouées ne sont pas bien compris. Afin de décrire les effets de ces épidémies sur les trouées et les patrons de recrutement, nous avons étudié 20 peuplements dominés par le peuplier faux-tremble (*Populus tremuloides* Michx.) ayant subi entre 0 et 3 années de défoliation sévère lors de la dernière épidémie survenue dans la ceinture d'argile du nord-ouest du Québec de 1998 à 2003. Les résultats montrent que le taux d'ouverture du couvert a plus que triplé (12,3–43,7 %) en passant de 0 à 3 années de défoliation et que la surface moyenne des trouées a augmenté d'un facteur 12 (7,2–87,5 m2). Les patrons de régénération indiquent que le recrutement de peuplier faux-tremble ne devrait pas être pour complètement refermer le couvert des peuplements sévèrement défoliés pendant 0, 1 et 2 années, alors qu'il devrait l'être suffisant dans les peuplements défoliés 3 ans où les grandes trouées permettent l'établissement du peuplier faux-tremble. Nos résultats montrent clairement que les épidémies de LDF représentent un facteur important dans la formation de trouées dans les peuplements de peuplier faux-tremble. Les trouées créent des structures inéquiennes à l'échelle du peuplement et la durée de la défoliation par la LDF crée une large gamme de peuplements de structure équienne à inéquienne à l'échelle du paysage.

Mots-clés : épidémies d'insectes, peuplier faux-tremble, dynamique par trouées, succession forestière.

2.3 INTRODUCTION

The boreal forest is recognized as a disturbance-controlled ecosystem in which fire and insect outbreaks are defined as the main disturbances that determine stand species composition and structure (McCullough et al. 1998; Bergeron 2000). Although fire has been considered as the major disturbance in this system, insect outbreaks are currently the agent of natural disturbance causing the most important losses in boreal forests (Logan et al. 2003). In Canada, only 20 million hectares were burned between 1997 and 2007, whereas more than 120 million hectares were disturbed by insect outbreaks during the same period (Natural Resources Canada 2010). This is partly explained by the increase in fire return interval observed over the last century in several boreal regions (Bergeron and Archambault 1993) but also by human intervention via fire suppression, which has contributed to the increase in the impact of insect outbreaks on boreal forest dynamics. Moreover, the effects of global warming should tend to increase insect demographic parameters such as phenology, survival, growth, and reproduction (Ayres and Lombardero 2000; Parmesan 2006; Altermatt 2010), and therefore, insect outbreaks should continue to increase in importance.

The forest tent caterpillar (FTC; *Malacosoma disstria* Hübner) is a major disturbance-causing insect in hardwood and mixedwood forests across North America (Witter 1979). The FTC is a generalist insect and a voracious defoliator whose preferred host tree species in the boreal zone are trembling aspen (*Populus tremuloides* Michx.), white birch (*Betula papyrifera* Marsh.), and balsam poplar (*Populus balsamifera* L.) (Witter 1979; Peterson and Peterson 1992). In Quebec and Ontario, FTC outbreaks are recurrent events with a periodicity of 9 to 13 years (Cooke and Lorenzetti 2006) that can occur as far north as 54° of latitude (Huang et al. 2008). Outbreaks usually last only 1–2 years, but local infestations may persist for up to 5 years (Cooke et al. 2009). Moreover, within three cores areas situated in Quebec and Ontario where six outbreaks were reported since 1938, Cooke et al.

(2009) have demonstrated that individual outbreaks tended to last for 2.6 ± 0.5 years. Severe defoliations have been shown to cause a reduction in radial growth (Hildahl and Reeks 1960; Hogg et al. 2002) and a consequent decrease in forest productivity (Bergeron and Charron 1994; Hogg and Schwarz 1999; Candau et al. 2002). Authors generally agree that defoliation reduces tree growth; however, defoliation caused tree mortality appears to be a more complex, less understood, and controversial phenomenon. Indeed, tree mortality in defoliated stands is generally associated with other factors such as age (Brandt et al. 2003; Sutton and Tardif 2007), drought (Hogg et al. 2008), wood-boring insects (Hogg et al. 2002), or fungal pathogens (Brandt et al. 2003) rather than FTC defoliation (Churchill et al. 1964; Brandt et al. 2003; Man and Rice 2010). Tree mortality in stands severely defoliated over multiple years can extend for 6 to 10 years after the end of an FTC outbreak (Duncan and Hodson 1958; Churchill et al. 1964).

In the absence of large-scale disturbances in the boreal forest, stands dynamics is controlled by the creation of gaps (McCarthy 2001). Such gaps commonly originate from discrete disturbance events such as localized insect outbreaks or windstorms and by the senescence of trees. Gap dynamics theory aims at inferring forest stand dynamics by understanding patterns of tree recruitment in canopy gaps (see Shugart 1998). In boreal forest ecosystems of North America, gap dynamics is a research field that has recently gained more interest (Kneeshaw and Bergeron 1998; Cumming et al. 2000; McCarthy 2001; Hill et al. 2005). In the absence of an exogenous disturbance, small gap formation in early successional deciduous stages of the boreal forest is controlled mainly by the death of individual trees or small groups of trees. During this early stage, gap-phase replacement can maintain nearly pure deciduous stands but can also favour the recruitment of shade-tolerant species when coniferous trees are present in the subcanopy (Cumming et al. 2000; Hill et al. 2005). The presence of shrubby understory species such as hazel (*Corylus cornuta*), raspberry (*Rubus idaeus*), mountain maple (*Acer spicatum*), or alder (*Alnus* spp.) can limit hardwood regeneration, as well as delay conifer establishment. In late successional coniferous-dominated stages, spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks drive the gap dynamics and allow the establishment of tolerant conifers in small gaps and the persistence of intolerant hardwood in large openings (Kneeshaw and Bergeron 1998).

Although these studies provide a good portrayal of the diverse gap dynamic patterns and trajectories of the boreal forest successional stages with the time since fire, there is still a real lack of knowledge on the impacts of FTC outbreaks on gap dynamics in deciduous stands. A more complete understanding of such outbreak effects on stand dynamics would be valuable (see also Man and Rice 2010), particularly in the present context in which sustainable forest management systems include the emulation of natural disturbance as the best management practice (Gauthier et al. 2008).

Resilience is an emergent property of a natural system that may be estimated from the magnitude of disturbance that this system can absorb without undergoing significant transformational change of its functions, structure, identity, and feedbacks (Holling 1973; Walker and Meyers 2004). In the forest ecosystem, it refers to the capacity to recover from severe disturbance such as fire, insect outbreaks, or logging to an original state. In this study, resilience after FTC defoliation in deciduous-dominated stands is estimated by the potential replacement of lost canopy trees so as to eventually regain a closed canopy structure. In other words, here we ask: Will aspen regeneration in gaps be sufficient to replace dead canopy trees after FTC outbreak?

Contrary to previous studies using typical stand-level analyses to describe FTC outbreak effects on stand dynamics (Churchill et al. 1964; Hogg et al. 2002; Man and Rice 2010), our theoretical approach was based on gap dynamics and patterns of regeneration at gap level to infer post-outbreak forest succession at the stand level. The main objective of this study was to provide a better understanding of the effect of severe FTC defoliations on gap formation in early deciduous stages of boreal succession. The second objective was to characterize the post disturbance tree recruitment response and evaluate stand resilience. Our major hypothesis was that the duration of the FTC disturbance should modify gap and tree recruitment patterns of trembling aspen stands. Our main predictions were as follows: (i) increased mortality of trembling aspen with increasing defoliation duration will increase the proportion of canopy gaps; (ii) gap area and proportion of large gaps (aggregated mortality) should increase with defoliation duration; and (iii) compared with small gaps, large gaps should provide better environments for recruitment and consequently have higher regeneration density. This study took place in the mixedwood boreal forest of northwestern Quebec 5 years after the last FTC outbreak (1998–2003) in stands dominated by trembling aspen that experienced severe defoliation over 0 to 3 years during the outbreak.

2.4 MATERIAL AND METHODS

2.4.1 Study area

The study area is located in Abitibi–Témiscamingue region, Quebec, Canada (48°N–48°50′N; 77°40′W–79°15′W). This area is situated within the Clay Belt, a vast physiographic region created by lacustrine deposits from the proglacial Lakes Barlow and Ojibway where clay soil dominates but organic soils and glaciofluvial deposits are also common (Veillette 1994). With less than 300 m of variation in elevation, the landscape is generally flat but punctuated by rocky outcrops and eroded morainic deposits forming hills (Bergeron et al. 1982). The climate is continental, with cold, dry winters and short, mild summers (average annual temperature, 1.2 °C; average annual precipitation, 918.4 mm; Environment Canada 2009). The region is mainly in the balsam fir – white birch bioclimatic domain (Saucier et al. 1998), which forms the southern limit of the coniferous boreal forest. Common tree species include balsam fir (*Abies balsamea* (L.) Mill.), trembling aspen (*Populus tremuloides* Michx), black spruce (*Picea mariana* (Mill.) BSP), white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), and jack pine (*Pinus banksiana* Lamb.).

In this region, the most recent FTC outbreak occurred from 1998 to 2003. This was the sixth such event recorded since 1938. This last outbreak was exceptional for its extent, severity, and duration, unseen since the early 1950s. During the 1999–2002 period, annual aerial surveys were conducted by the Quebec Ministry of Natural Resources and Wildlife to quantify the severity and extent of the defoliation. In every survey, the proportion of foliage lost to defoliation in each stand was estimated and classified as low (1%–25%), moderate (26%–65%), or severe (66%–100%). Survey data were then digitized to generate georeferenced maps. The cumulative area disturbed during this last outbreak was approximately 1.4 million hectares, with a larger extent in 2001 of more than 0.9 million hectares. In the study area, 30% of the forest territory entirely escaped FTC defoliation, 38% was defoliated for 1 year, 24% for 2 years, 7% for 3 years, and less than 1% for 4 years.

2.4.2 Stands selection

Defoliation data from the aerial surveys were overlaid on digitized forest cover maps (1 : 20 000 scale) from the Quebec Ministry of Natural Resources and Wildlife using ArcView 3.3 (ESRI, Redlands, California). Twenty deciduous stands (Appendix A, Table A1) dominated by trembling aspen were selected: no defoliation or control (n = 3) and after 1 year (n = 9), 2 years (n = 5), and 3 years (n = 3) of severe defoliation. To control for stand origin, all selected stands were classified as either originating from fire (dated between 1932 and 1959; n = 9) or from clearcuts (dated between 1940 and 1963; n = 11). Stand origin was determined by using forest cover maps that included harvest years, overlayed with fire history maps from the Quebec Ministry of Natural Resources and Wildlife. Drainage was moderate to imperfect, with low to nonexistent slopes in all stands. Analyses of cores sampled at breast height from 10 dominant canopy trees in each stand were used to confirm defoliation regimes and to determine maximum stand age.

2.4.3 Stand measurements

Data acquisition in the field was carried out in July and August 2008. In each stand, one transect varying from 500 to 1100 m was established to evaluate the percentage of canopy opening. The start point of each transect was randomly assigned after applying a 50 m buffer to any open area such as a road, lake, wetland, or clearcut. At each metre along the transect, the overhead canopy cover directly above the stop point was visually inspected. The canopy was classified as closed if a virtual vertical line perpendicular to the transect intersected a live tree crown or as open if the line extended to the open sky because of the presence of one or more dead trees (following Kneeshaw and Bergeron 1998). Canopy opening at the stand level was subsequently calculated as the relative frequency of open canopy to total transect length (Runkle 1992). Natural large interstices between trees were also noted but not integrated in the calculation of canopy opening as they do not result from tree mortality. A total of 14.4 km of stand transects were surveyed: 6.2 and 8.2 km in fire- and clearcut-initiated stands, respectively, and 2.1, 6.5, 3.6, and 2.2 km in control stands and stands severely defoliated for 1, 2, and 3 years, respectively.

To understand pre-disturbance stand characteristics, three to five 400 m2 plots were also sampled in each stand under closed canopy at fixed intervals along the transect. Tree species composition basal area and stem density were measured in each plot (Appendix A, Table A1). In each plot, diameter at breast height (DBH) of all living trees > 9.9 cm was recorded, as well as species and status (suppressed, codominant, dominant). Mean height of stand was also approximated by randomly measuring 10 trees within each plot using a clinometers.

2.4.4 Gap characterization

A canopy gap is created by the death of an individual or a group of trees and is defined as the projection on the ground of the canopy opening. The expanded gap is the area circumscribed by the stems of the trees surrounding the gap and is usually larger than the gap itself (Runkle 1982). In each stand, gap characterization was performed on gaps encountered along the first one-third of the total transect length (232 gaps sampled out of 728). For circular-shaped gaps, measures of the longest and shortest perpendicular axes of canopy and expanded gaps were recorded. Multiple extra axis measurements were performed in the case of irregular shaped gaps. Dead trees within the gaps, referred to as gap makers, were counted, identified, measured (DBH), and classified as either standing dead, snapped, uprooted, or crown damaged.

To measure the potential impact of gap size on the direct light reaching the forest floor, the gap diameter to canopy height ratio or sky view factor (Lieffers et al. 1999) was calculated for each gap. Because the maximum sun elevation decreases with increased latitude (Canham 1988), shadow length also varies with latitude and is 1.1224 times the canopy height on the summer solstice at the latitude of this study. This means that a gap must have a larger diameter than the height of the trees at its perimeter for direct sunlight to reach the forest floor.

2.4.5 Gap regeneration

Regeneration was inventoried in the 232 characterized gaps. An exhaustive count of regeneration by species was achieved in the smaller gaps (area < 100m2), whereas three 2 m wide transects perpendicular to the north–south axis (north, center, south) were used for larger gaps. Regeneration was categorized in three height classes: suckers (<1 m), saplings (1–2 m), and poles (2–5 m). The poles class was also referred to as gap fillers because they are likely to reach the canopy and to partially or completely close the gap. Because trembling aspen represented more than 80% of the total sampled regeneration (other species were balsam fir, black spruce, and white birch), results are only presented for this species. Aspen regeneration density was calculated for each gap in total and by height class. Finally, tree replacement probability was estimated per height classes as the ratio of the number of stems to the number of gap makers for each gap to estimate stand resilience capacity.

2.4.6 Statistical analysis

2.4.6.1 Stand origin

Analysis of covariance (ANCOVA) was conducted to determine the effect of stand origin on gap characteristics using the number of years of severe defoliation as covariate. There was no significant effect of stand origin alone or in interaction with defoliation. This permitted simplification of statistical analysis from covariance models to linear regressions. Only the results of the latter are presented.

2.4.6.2 Canopy opening and gaps

Canopy opening, mean canopy gap size, mean expanded gap size, proportion of gaps with a single gap maker, number of gap makers per gap, and proportion of gap maker types were analyzed to determine stand-level changes in gap characteristics in relation to defoliation duration. Log transformations were performed on mean gap area and expanded gap area, and residuals were examined to ensure that statistical assumptions of normality and homoscedasticity were met. When extreme values were identified, analyses were tested without them to ensure that they did not represent a source of bias; however, no datum had to be removed.

Gaps were grouped in classes of 25 m^2 increments of surface area, with upper class limits ranging from 25 to 950 m^2. Comparisons of gap size class distributions between defoliation regimes were done using Kolmogorov–Smirnov tests. As we applied multiple comparisons, Bonferroni corrections were performed to adjust the significance level a (0.05) to α/n (0.008), with n (= 6) being the number of comparisons. The same analyses of distribution were performed with the sky view factor and DBH of gap makers. DBH were grouped into classes of 5 cm increments for gap makers and into classes of 0.1 increments for the sky view factor (the last class, 1.2, including all values > 1.1224).

2.4.6.3 Regeneration

Linear mixed-effect models (Pinheiro et al. 2008) were used to analyze log-transformed regeneration density of trembling aspen as a function of defoliation duration, origin, gap area, and height class. We used model selection analyses to assess which factors significantly affected total gap regeneration density and regeneration density in each height class. We considered defoliation, origin, gap area, and the defoliation × gap area interaction in all models, and we added defoliation × origin for the first model and height class, gap area × height class, and defoliation × height class for the second model. Stand was considered as a random effect in both analyses and gap was added as random effect in the second. For each analysis, we formed sets of plausible models to identify which of the predictor variables and their interactions might explain patterns of regeneration density. The fit of the global model was assessed for each analysis, and models were compared using the second-order Akaike information criterion (AICc) and the information theoretic approach presented by Burnham and Anderson (2002). We considered models with ΔAICc values ≤ 2 to have strong support, and we also calculated model weights from the AICc values to indicate the level of support for each of the models considered (Burnham and Anderson 2002). Model averaging was performed to discriminate if a variable had a significant effect on regeneration density using all models in which the corresponding variable was present (Burnham and Anderson 2002). This enabled the computation of unconditional 95% confidence intervals for the variables of interest. Variables with confidence intervals excluding 0 were deemed good predictors of log-transformed regeneration density. Estimates obtained with this method have better precision and less bias than when based on a single model (Anderson et al. 2000).

The tree replacement probability was categorized in two classes (<0.5 or >0.5) and analyzed with mixed logistic regression to test the effects of defoliation, origin, gap area, and height class and of the interactions gap area × height class and defoliation × height class using stand and gap as random effects. Log transformation of regeneration density and gap area were done for all analyses. All statistical analyses were performed using R software (version 2.10.1; R Development Core Team 2010).

2.5 RESULTS

2.5.1 Gap characteristics

The mean percentage of canopy opening showed a significant positive relationship with defoliation duration ($P < 0.01$; Fig. 1a) with an increase from 12.3% to 43.7% across the defoliation gradient (Table 1). Mean gap area and expanded gap area responded to defoliation by increasing 11.9 times and 3.7 times, respectively, and regression analysis showed a positive and significant effect of duration of defoliation on these two variables (Table 1; Figs. 1b and 1c).

The mean proportion of gaps with a single gap maker was highest in control stands (28.3%) and decreased significantly with defoliation duration ($P < 0.014$; Fig. 1d) to zero in stands defoliated for 3 years. The mean number of gap makers per gap increased significantly with defoliation duration (Fig. 1e), doubling from 0 to 3 years of severe defoliation (3.9 to 8.2 trees/gap). Gap makers were classified as snapped (69.4%), standing dead (22.9%), uprooted (4%), or crown damaged (3.7%). Snapped trees significantly increased from control (47.9%) to stands with 3 years of defoliation (84.9%), whereas the proportion of standing dead and crown-damaged trees decreased with defoliation (Fig. 1f). Uprooted trees were not significantly related to defoliation duration ($P = 0.344$; Table 1).

Analysis of gap patterns indicated that gap size distributions differed with duration of defoliation ($P < 0.008$) except for stands defoliated for 2 or 3 years ($P = 0.806$). Small gaps dominated the undefoliated stands, but the proportion of small gaps decreased with defoliation duration (Fig. 2a). On the other hand, the proportion of large gaps increased with defoliation duration, revealing that FTC disturbance changed gap size distribution patterns.

Distributions of the sky view factor also differed with defoliation duration (*P* < 0.008), except for stands defoliated for 2 or 3 years (P = 0.725). The frequency of gaps in the 1.2 ratio class increased with defoliation from 0% to 16% with increasing defoliation duration (Fig. 2b), demonstrating an increase in the proportion of gaps receiving direct sunlight at the forest floor with defoliation duration.

Analysis of the distribution of gap maker DBH classes showed no difference between control and stands defoliated 1 year (*P* = 0.243) and between stands defoliated 2 and 3 years (*P* = 0.168), whereas all other comparisons were significantly different (P < 0.008). This result indicates a shift in the size distribution of gap makers (Fig. 2c), with dead tree diameters increasing with defoliation duration.

2.5.2 Regeneration

Among the nine candidate models considered for total regeneration density, the one that provided the best fit to the data (AICc weight (wi) = 0.37) was based on defoliation duration and gap area (Table 2). There were three other models with strong support (ΔAICc $\leq$ 2), including all variables tested, alone or combined, and one interaction. These four first models accounted for 97% of the cumulative AICc weight (i.e., sum of the wi). Model averaging showed that total density of regeneration increased significantly with gap area (0.49 ± 0.09), whereas none of the other variables was significant (Table 3).

The analysis of regeneration density by height class showed that only one of the 13 models considered had strong support, with a w_i of 0.92 (Table 2). Model averaging revealed significant effects of gap area × height class and defoliation × height class interactions on the density of aspen suckers (Table 3). The density of saplings (1–2 m) increased with gap area (0.42 ± 0.09; Fig. 3a) and defoliation duration (0.30 ± 0.12; Fig. 3b). The density of suckers (<1m) and poles (2–4 m) did not show any trend with gap size and defoliation duration, and the overlapping of their confidence intervals demonstrated that the density of suckers did not significantly differ from that of poles (Figs. 3a, 3b). Total density and height class density analyses indicated that stand origin did not have a significant effect on aspen regeneration following FTC disturbance.

2.5.3 Replacement probability

The mixed logistic regression analysis (Table 4) reports a significant and positive effect of defoliation duration ($P = 0.05$) and gap area ($P = 0.04$) on the replacement probability of gap makers. Results also showed that the replacement probability of saplings and suckers differed from that of poles ($P < 0.01$; Table 4) and more than half of the tree replacement potential was represented by saplings (Figs. 4a, 4b). Finally, there was a contrasting pattern of replacement probability that was a function of defoliation duration. In stands that were not defoliated or in small gaps, less than 50% of gap makers would potentially be replaced, whereas this potential rises to more than 80% in most defoliated stands or in large gaps (Figs. 4a, 4b).

2.6 DISCUSSION

2.6.1 Canopy, gaps, and tree mortality

Our study shows that FTC disturbance represents an important factor structuring trembling aspen stands. The proportion of canopy openings observed in control stands compared well with those reported for young aspen stands (44–78 years) in Quebec (11.3%; Kneeshaw and Bergeron 1998), Ontario (14%; Hill et al. 2005), and Alberta (4%–19%; Cumming et al. 2000), although the proportion of canopy openings in stands severely defoliated for 2 or 3 successive years were more comparable with rates reported for 120-year-old (35%; Hill et al. 2005) and 124-year-old (32%; Kneeshaw and Bergeron 1998) aspen stands. Thus, our results indicate that FTC deciduous stands, conferring canopy structural attributes of older stands to younger stands. These results also show that FTC outbreaks may explain an important part of the phenomenon of aspen dieback reported for the province of Quebec (Pothier et al. 2004).

The increase in gap size and in the number of gap makers per gap, as well as the decrease of the proportion of gaps with a single gap maker correlated with defoliation duration, are consistent results regarding the effects of FTC defoliations on gap dynamics. The small gaps observed in control stands, which originate from the mortality of isolated trees or of a small group of trees, are in accordance with the post-fire gap dynamic reported in boreal young aspen stands (Kneeshaw and Bergeron 1998; Cumming et al. 2000; Hill et al. 2005). Inversely, the increase in the proportion of large gaps with defoliation duration confirms that exogenous factors such as insect outbreaks represent one of the main factors creating large canopy openings (Kuuluvainen 1994). Although our experimental design did not account for the spatial distribution of tree mortality, our observations confirm the aggregative patterns of aspen mortality described in post-fire boreal mixedwood succession (Kneeshaw and Bergeron 1998). The decreasing proportion of gaps with a single gap maker with the increase in defoliation duration revealed that aggregative mortality of canopy trees was significantly amplified after repeated defoliations. Such aggregative mortality patterns have been proposed to be linked to the clonal establishment of aspen (Kneeshaw and Bergeron 1998), and several recent studies in aspen genetics and root grafting (Namroud et al. 2005, 2006; Jelínková et al. 2009) suggest that root connections represent an important factor in aggregated tree mortality and gap creation.

As reported in northeastern Ontario poplar stands (Man and Rice 2010), our results confirm that the increase in aspen mortality is closely related to defoliation duration (Fig. 1e). The response of gap maker diameter to defoliation duration (Fig. 2c) also confirms the results of Churchill et al. (1964), who associated an increase in mortality with dominant, codominant, and intermediate canopy trees rather than with suppressed ones. Our observations also corroborate Churchill et al.'s (1964) findings of no apparent and identifiable cause of mortality (e.g., fungal pathogens, wind, or insect borers) for the majority of dead trees for which mortality was regarded as resulting from FTC defoliation. The large number of snapped trees constitutes one of the most outstanding footprints of repeated severe FTC defoliations (Fig. 1f). Snapped trees generally result from wind breakage, but the low proportion of up-rooted trees (less than 4% of total gap makers) revealed that windstorm events were not associated with tree mortality, and contrary to our expectations, the increase in canopy opening did not affect the proportion of up-rooted trees. In aspen-dominated stands, fungal pathogens such as cankers and polypores are common cause of mortality and represent a contributing factor long after FTC outbreaks capable of increasing aspen mortality at a later time (Churchill et al. 1964; Hogg et al. 2002). Given the low evidence for such pathogens on gap makers (our personal observations), we think that fungal pathogens did not represent an important cause of mortality in our study and attribute the main part of tree death to FTC defoliation.

2.6.2 Regeneration and resilience

The picture that emerges from the study of aspen regeneration, 5 years after the collapse of the outbreak, is that saplings (1–2 m height class) dominate in all defoliated stands and in gaps larger than 10 m2 (Figs. 3a, 3b). Given height growth rates reported for aspen in the study area (close to 0.4 m/year during the first 10 years following establishment; Grondin et al. 2000), saplings in our study were likely recruited precisely at the time of the outbreak collapse. Poles (>2 m) established sometime during the outbreak itself, or even before. Their low density is typical of undisturbed stands (Bergeron and Charron 1994). Suckers (<1 m) thus appear to be the tail end of a single bout of recruitment induced by the FTC outbreak. As expected, aspen recruitment improved with gap size (Fig. 3a). Larger gaps with a sky view factor allowing for uninterrupted transmission of direct beam light at ground level increased in frequency with outbreak duration (Fig. 2b). Greater light incidence and ground temperature, which stimulates aspen root suckering (Peterson and Peterson 1992; Prévost and Pothier 2003; Frey et al. 2004), likely played a key role in the establishment of the observed sapling cohort. Thus, our results clearly show that FTC defoliation affects significantly aspen root suckering by creating large canopy openings and providing a better understory environment.

Driven by the density of aspen regeneration, the replacement probability indicates that canopy stand resilience increased significantly with gap size (Fig. 4a) and defoliation duration (Fig. 4b). It clearly appears that saplings will replace the main part of gap makers and will assume mainly canopy stand resilience. In large gaps, almost the entire gap makers will be replaced (quasi total resilience), whereas less than half of dead trees would potentially be replaced in small gaps (partial resilience). Also, the limited survival of stems in shaded environments should tend to decrease the predicted replacement probabilities, particularly in small gaps (Prévost and Pothier 2003). Because of the low regeneration density in control stands, replacement probability is also low. This indicates that in small gaps, regeneration would not compensate tree loss, and in the absence of large-scale disturbance and consequently gap formation, the canopy would tend to open over time (Hill et al. 2005). After 1 and 2 years of defoliation, more regeneration was present than in control stands, but the replacement probabilities appeared insufficient to provide complete resilience. Besides, if all suckers reached the canopy layer (and assuming the trees that survived defoliation persist), such disturbed stands would recover to a more open canopy than existed prior to disturbance. Inversely, the density of aspen regeneration in stands defoliated for 3 years showed that large gaps improved aspen recruitment enough to promote the replacement of all gap makers and a reestablishment of the stand canopy over time. The density of aspen regeneration in such stands is comparable with that reported after FTC defoliation in the understory of trembling aspen stands in northeastern Ontario (Man and Rice 2010).

Finally, although our study focused on aspen regeneration, we observed that independent of defoliation duration and gap size, shade-tolerant regeneration would in some cases contribute to canopy stand resilience (in the sense of maintaining a closed canopy) and canopy conversion (Man and Rice 2010). Our observations are consistent with the actual gap dynamics knowledge of the balsam fir-white birch forest succession of eastern Canadian boreal forest where, in absence of coniferous regeneration, trembling aspen regenerate in gaps and create multicohort aspen stands (Cumming et al. 2000). Thus, our results and observations confirm that factors creating gaps such as FTC disturbance favour the establishment of new cohorts of trembling aspen during trembling aspen-balsam fir transition (Bergeron 2000; Namroud et al. 2005). In absence of coniferous regeneration, it leads to pure trembling aspen stands with uneven structure (Cumming et al. 2000).

2.7 CONCLUSION

This study is the first to describe gap and regeneration patterns in pure and nearly pure aspen stands following an FTC outbreak. Our results clearly show that FTC disturbance constitutes an important agent of gap formation in trembling aspen stands. The effect of defoliation duration results in profound changes in gap patterns and gap makers. The increase of canopy opening size in response to defoliation duration contributes to increases in aspen recruitment and stand resilience. Patterns of regeneration suggest that stands maintain a pure aspen composition even after multiple defoliations, but also that duration of FTC defoliation tends to generate a large range of uneven stand structures. In other words, gaps create uneven stand structure at the stand level and FTC defoliation duration creates both even-aged stands (short duration) and uneven-aged stands with multicohorts of trembling aspen (long duration). The expected persistence of pure aspen stands may delay the expected succession to dominance by tolerant coniferous species. Man and Rice (2010) estimated that 40 to 50 years were necessary for the regenerating aspen to mature in declined stands following FTC outbreaks. In other cases, such as old trembling aspen stands or mixed stands where shrub species and shade-tolerant regeneration are more represented in the understory, the post-outbreak gap dynamics and forest succession pathways may be different.

Finally, given that aspen stands in Abitibi exhibit a large range of age at which the onset of stand decline is observed (Pothier et al. 2004) and given that the

FTC historical records for the region show patchiness in defoliation recurrence (Cooke and Lorenzetti 2006), the results presented here suggest that aspen stands as observed today follow, to different degrees, the footprints of past FTC outbreaks.

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Figure 2.1 Relationship between defoliation duration and (a) canopy opening (%), (b) mean gap area (log-transformed), (c) mean expanded gap area (log-transformed), (d) gap with a single gap maker (%), (e) mean number of gap makers per gap, and (f) proportion of gap makers per status.

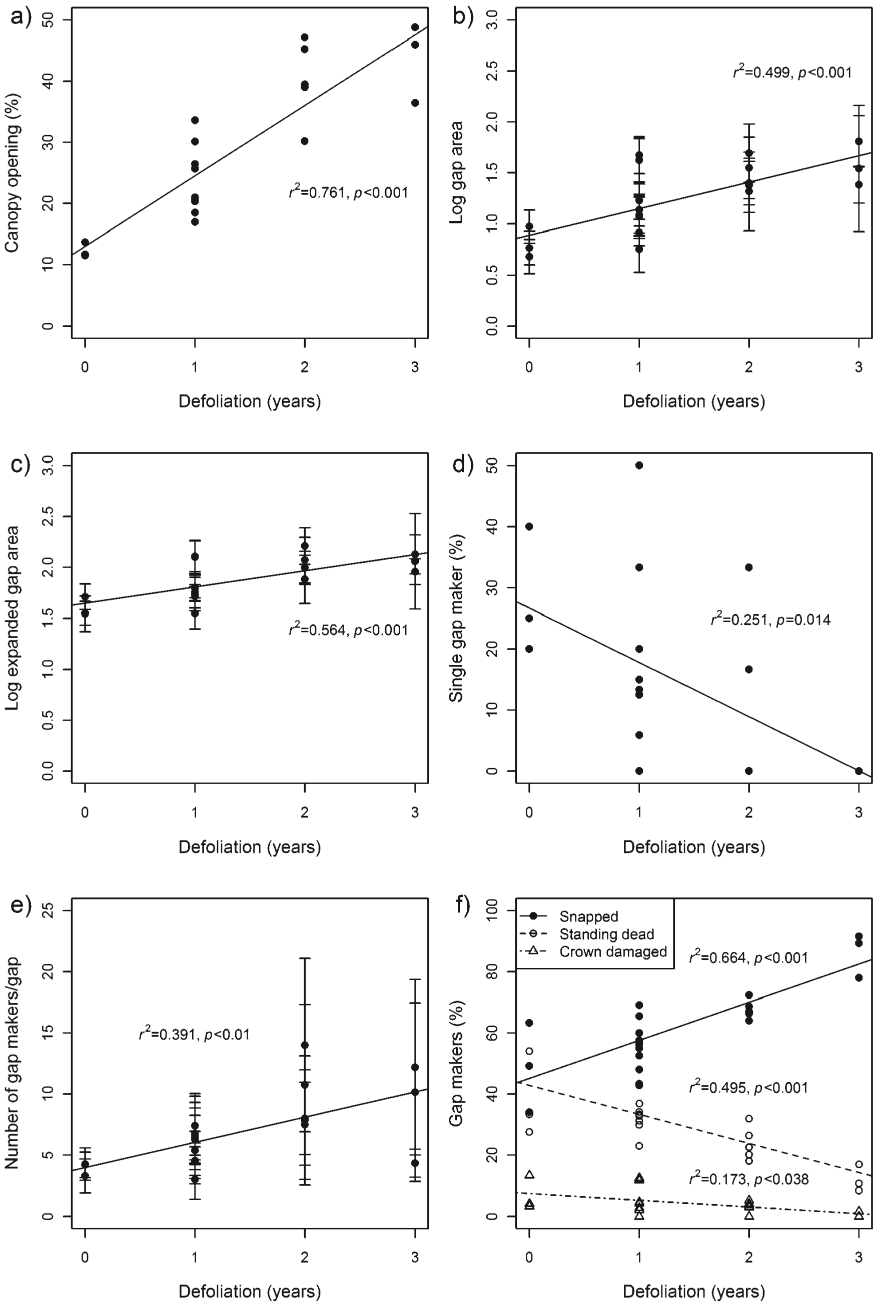

Figure 2.2 Distribution of the relative frequency of (a) gap size, (b) sky view factor, and (c) gap makers diameter (DBH) for stands defoliated 0, 1, 2, and 3 years (n = 3, 9, 5, 3) during the last outbreak of forest tent caterpillar in the Abitibi region (1998–2003). Note that gap size was log-transformed and grouped into classes of 0.25 increments of log-transformed surface gap to draw Fig. 2.a.

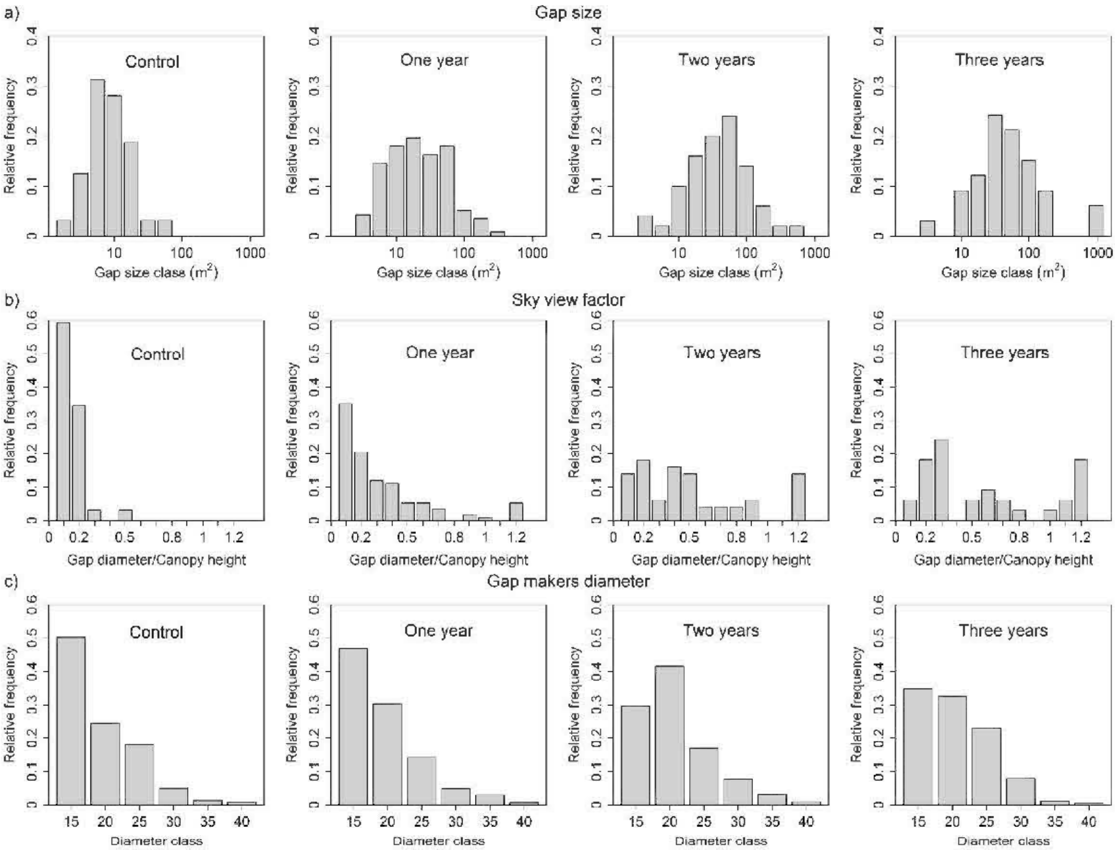

Figure 2.3 Effect of (a) gap area and (b) defoliation duration on the density of the different height classes of trembling aspen regeneration (with 95% confidence intervals).

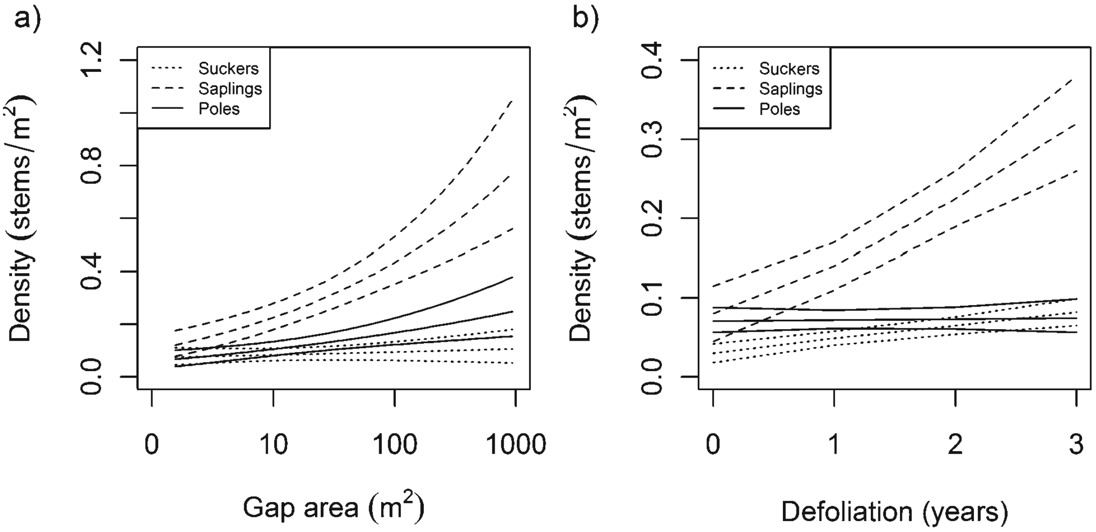

Figure 2.4 Effect of (a) gap area and (b) defoliation duration on the replacement probability of dead trembling aspen by sucker roots of different height classes.

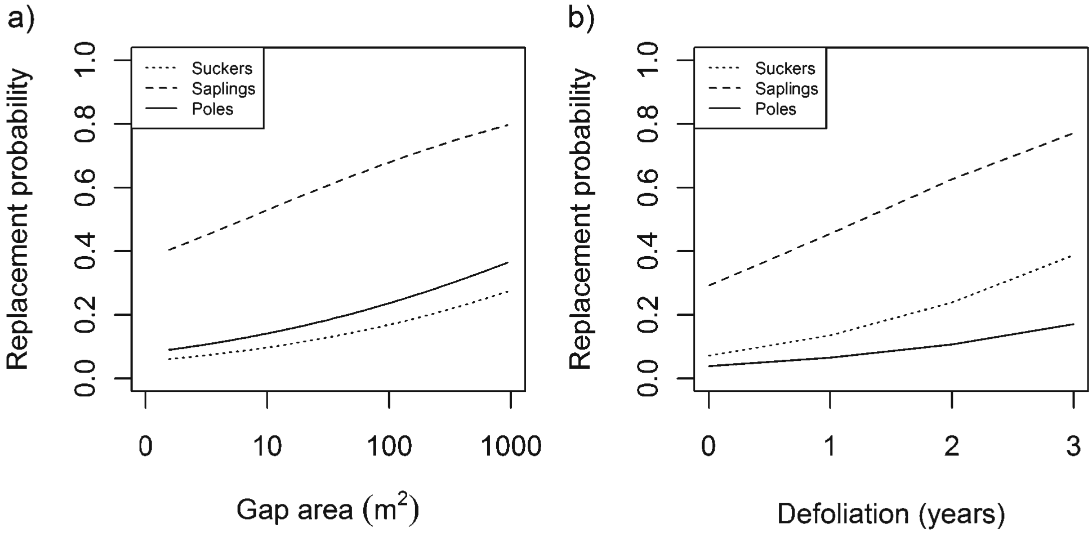

Table 2.1 Summary of linear regression analyses testing the effect of defoliation duration (number of years of severe defoliation) on gap and gap maker characteristics at the stand level (n = 20).

	b_0	b_1	R^2	$F_{(1.18)}$	P
Gaps					
Co	12.97	11.53	0.761	**61.51**	**<0.01**
Gap	0.88	0.26	0.499	**19.90**	**<0.01**
EGap	1.66	0.21	0.564	**25.64**	**<0.01**
Sgm	26.67	-8.87	0.251	**1.36**	**0.01**
Gap makers					
Gm	3.97	2.07	0.391	**13.19**	**<0.01**
Snp	45.14	12.44	0.664	**38.49**	**<0.01**
Upr	4.50	-0.73	0.049	0.94	0.34
Crd	7.49	-2.19	0.173	**4.97**	**0.04**
Std	42.85	-9.52	0.495	**19.61**	**<0.01**

Note: Co = canopy opening (%), Gap = gap area (log transformed), EGap = expanded gap area (log transformed), Sgm = single gap maker (%), Gm = mean number of gap makers per gap, Snp = snapped (%), Upr = uprooted (%), Crd: crown damaged (%), Std: standing dead (%). Significant effects are shown in bold ($P < 0.05$).

Table 2.2 Top-ranking models for analyses of total density and height class density of aspen regeneration. Only the five first models are shown for brevity.

Model	K^{*}	$AIC_c^{\dagger}$	$\Delta AIC_c^{\ddagger}$	$w_i^{\S}$
Total density model				
Def+Gap	5	810.2	0.00	0.37
Gap	4	810.6	0.41	0.30
Def+Gap+[Def×Gap]	6	811.9	1.67	0.16
Def+Origin+Gap	6	812.2	1.99	0.14
Def+Origin+Gap+[Def×Gap]+[Def×Origin]	8	815.8	5.65	0.02
Height class density model				
Def+Origin+Gap+Hc+[Gap×Hc]+[Def×Hc]	12	1013.8	0.00	0.92
Gap+Hc+[Gap×Hc]	8	1026.3	4.94	0.08
Def+Origin+Gap+Hc+[Def×Gap]+[Gap×Hc]	11	1039.5	25.74	0.00
Def+Gap+Hc	7	1055.5	39.94	0.00
Def+Origin+Gap+Hc	8	1073.4	57.83	0.00

Note: Def, defoliation duration; Gap, gap area; Hc, height regeneration class; ×, interaction; K, number of parameters; AICc, Akaike's information criterion corrected for small sample sizes; ΔAICc, AICc relative to the most parsimonious model; wi, AICc model weight.

Table 2.3 Model-averaged parameter estimates, number of models used for model averaging (K), standard errors (SE), and 95% confidence intervals for the two analyses of aspen regeneration density: total density and height class density. Tested levels are shown in parentheses for qualitative covariates; reference level is poles (class 3).

				Confidence interval	
	K	Estimate	SE	Lower	Upper
Total density model					
Def	5	0.31	0.17	-0.07	0.68
Origin (Fire)	3	0.07	0.39	-0.70	0.84
Gap	5	**0.49**	**0.09**	**0.31**	**0.67**
Def×Origin (Fire)	1	0.09	0.38	-0.65	0.84
Def×Gap	2	0.06	0.10	-0.13	0.45
Height class density model					
Def	5	0.14	0.13	-0.12	0.39
Origin (Fire)	4	0.16	0.20	-0.23	0.56
Gap	5	**0.30**	**0.05**	**0.19**	**0.40**
Hc (2)	4	**1.43**	**0.10**	**1.23**	**1.64**
Hc (1)	4	**0.29**	**0.10**	**0.09**	**0.49**
Def×Gap	2	0.03	0.06	-0.08	0.14
Gap×Hc (2)	2	**0.42**	**0.09**	**0.24**	**0.61**
Gap×Hc (1)	2	**0.22**	**0.09**	**0.04**	**0.41**
Def×Hc (2)	2	**0.30**	**0.12**	**0.06**	**0.53**

Note: Parameter estimates in bold correspond to terms with statistically significant effect. Def, defoliation duration; Gap, gap area; Hc, height regeneration class; Hc (1), suckers; Hc (2), saplings; Hc (3), poles (reference level); ×, interaction.

Table 2.4 Parameter estimates and standard errors (SE) with z values and P values from mixed logistic regression analysis describing replacement probability of trembling aspen considering defoliation × height and gap area × height interactions. Tested levels are shown in parentheses for qualitative covariates; reference level is poles (3).

Parameter	Estimate	SE	z value	P
Intercept	-4.42	0.78	-5.60	<0.01
Def	0.73	0.36	1.94	**0.05**
Origin (Fire)	0.47	0.51	0.93	0.35
Gap	0.84	0.41	2.03	**0.04**
Hc (2)	2.27	0.57	3.84	**<0.01**
Hc (1)	2.18	0.58	3.76	**<0.01**
Def×Hc (2)	0.11	0.34	0.34	0.73
Def×Hc (1)	-1.53	0.40	-3.70	0.30
Gap×Hc (2)	0.02	0.01	1.09	0.27
Gap×Hc (1)	0.01	0.01	1.63	0.11

Note: Parameter estimates in bold correspond to terms with significant effect ($P < 0.05$). Def, defoliation duration; Gap, gap area; Hc, height regeneration class; Hc (1), suckers; Hc (2), saplings; Hc (3), poles (reference level); ×, interaction.

Table 2.5 Appendix A. Stand characteristics.

Site	Defoliation duration	Origin	Age (years)	Basal area	density (stem/ha)	Composition (%)						
						as	bf	bs	wb	bp	jp	tk
1	0	cc	45	27.8	1037	99	0	1	0	0	0	0
2	0	cc	55	35.8	858	85	0	4	1	5	4	1
3	0	fire	50	36.8	1450	100	0	0	0	0	0	0
4	1	cc	68	27.7	787	86	0	14	0	0	0	0
5	1	cc	62	29.5	766	86	9	5	0	0	0	0
6	1	cc	61	25.2	833	100	0	0	0	0	0	0
7	1	cc	53	25.3	800	95	0	2	0	3	0	0
8	1	fire	68	22.1	650	73	13	0	4	0	0	10
9	1	fire	50	17.6	575	100	0	0	0	0	0	0
10	1	fire	61	32.6	783	90	1	3	6	0	0	0
11	1	fire	76	42.7	1050	92	0	5	3	0	0	0
12	1	fire	57	24.3	900	74	0	0	26	0	0	0
13	2	cc	62	30.0	725	93	4	3	0	0	0	0
14	2	cc	52	25.7	637	73	20	5	2	0	0	0
15	2	cc	53	25.6	900	88	10	0	2	0	0	0
16	2	cc	48	21.3	500	81	3	15	0	1	0	0
17	2	fire	49	29.4	875	82	10	4	1	0	3	0
18	3	cc	61	27.7	716	94	3	3	0	0	0	0
19	3	fire	54	23.4	541	100	0	0	0	0	0	0
20	3	fire	54	34.3	1062	100	0	0	0	0	0	0

Note: cc, clearcut; as, trembling aspen; bf, balsam fir; bs, black spruce; wb, white birch; bp, balsam poplar; jp, jack pine; tk, tamarack.

CHAPITRE III

EFFECTS OF A FOREST TENT CATERPILLAR OUTBREAK ON THE DYNAMICS OF MIXEDWOODS BOREAL FORESTS OF EASTERN CANADA

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3.1 ABSTRACT

In boreal mixedwood stands dominated by trembling aspen, forest tent caterpillar (*Malacosoma disstria* Hübner, FTC) outbreaks are recurrent events for which effects on stand dynamics are poorly documented. To describe and characterize effects of such disturbance, we assessed canopy opening, gap size, and understory tree recruitment in 12 stands dominated by trembling aspen (*Populus tremuloides* Michx.) that had experienced different levels of FTC defoliation (in terms of severity and duration) during the last outbreak in northwestern Quebec (1999-2002). Undertaken in 2009, this study showed a significant increase in canopy opening and gap size with defoliation intensity. Patterns of gap size and gap makers revealed that the proportion of large gaps and aspen mortality increased with defoliation intensity. Balsam fir (*Abies balsamea* (L.)) regeneration benefited from changes in the canopy structure caused by the FTC, while aspen recruitment did not. Forest succession in mixedwood stands that had been defoliated for 1 year were not profoundly affected, while multiple years of defoliation suggested more rapid canopy transition from aspen to fir, given recruitment and growth of balsam fir that was observed in the understory and in small gaps. By creating a variety of gaps, FTC outbreaks modify stand structure in ways that differ from succession to coniferous dominance controlled by single-stem exclusion.

Keywords: Boreal mixedwood succession, insect disturbance, gap dynamics, tree recruitment, trembling aspen, forest tent caterpillar.

3.2 RÉSUMÉ

En forêt boréale mixte dominée par le peuplier faux-tremble, les épidémies de livrée des forêts (*Malacosoma disstria* Hübner, *LDF*) sont des évènements récurrents dont les effets sur la dynamique des peuplements ont été peu documentés. Afin de décrire et caractériser les effets d'une telle perturbation, nous avons évalué l'ouverture du couvert, la taille des trouées et la régénération dans 12 peuplements dominés par le peuplier faux-tremble (*Populus tremuloides* Michx.) ayant subi différents niveaux de défoliation (en termes de sévérité et de durée) durant la dernière épidémie survenue dans le nord-ouest du Québec (1999-2002). Conduite en 2009, cette étude a montré une augmentation significative de l'ouverture du couvert et de la taille des trouées avec l'intensité de la défoliation. Les patrons de taille des trouées ont révélé que la proportion de grandes trouées et de peuplier morts augmentaient avec l'intensité de la défoliation. La régénération en sapin baumier (*Abies balsamea* (L.)) a bénéficié des changements à la structure des peuplements entraînés par la LDF alors que ce n'était pas le cas pour le peuplier. La trajectoire successionnelle des peuplements mixtes défoliés une année ne semblait pas être affectée alors que le recrutement et la croissance du sapin baumier en sous-couvert et dans les petites trouées suggèrent une conversion plus rapide d'un couvert mixte feuillu vers mixte résineux dans les peuplements défoliés plusieurs années. En créant une variété de trouées, les épidémies de LDF modifient la structure des peuplements d'une façon qui diffère de la succession vers une dominance en conifères contrôlée par l'exclusion de tiges individuelles.

Mots clés: succession forestière, peuplements mixtes, épidémie d'insectes, trouées, peuplier faux-tremble, régénération, livrée des forêts.

3.3 INTRODUCTION

Mixedwood stands are widespread throughout North American boreal forests, where they constitute one the most productive and diversified forest ecosystems (Chen & Popadiouk, 2002). In such boreal forests, compositional change in dominant tree species is related to time-since-fire and depends upon species life-history traits (Bergeron, 2000). After fire, pioneer and shade-intolerant tree species such as trembling aspen (*Populus tremuloides* Michaux) and white or paper birch (*Betula papyrifera* Marshall) generally initiate forest stand succession and generate an even-aged stand structure. With the increase in time-since-fire, intra- and inter-specific competition increase intolerant hardwood stem exclusion and favour shade-tolerant softwood establishment and growth (Bergeron, 2000; Taylor & Chen, 2011; Bergeron *et al.*, 2013). Also, the death of dominant canopy trees, either from ageing or from non-stand-replacing disturbances such as wind or insect outbreaks, enable the recruitment of shade-tolerant coniferous trees from the understory to the main canopy (Greene *et al.*, 1999; Chen & Popadiouk, 2002). Therefore, mixed stands that are dominated by intolerant hardwoods generally switch to softwood-dominated stands and, in the absence of fire, they ultimately develop into uneven-aged coniferous stands.

During the fire-free interval, insect outbreaks play an important role in mixedwood stand dynamics. In mixedwood forests that are dominated by conifers, outbreaks of the spruce budworm (*Choristoneura fumiferana* (Clem.)) have well-known effects and have been well-documented (Morin *et al.*, 1993; Morin, 1994; Bergeron *et al.*, 1995; Bouchard *et al.*, 2006, 2007). In contrast, the effects of insect outbreaks, such as forest tent caterpillar (*Malacosoma disstria* Hübner), on mixedwood forests that are dominated by deciduous tree species are just beginning to be understood (Senecal *et al.*, 2004; Man *et al.*, 2008; Man & Rice, 2010; Reinikainen *et al.*, 2012).

Forest tent caterpillar (FTC) outbreaks are important insect-driven disturbances in the southern boreal forests of North America (Witter, 1979; Fitzgerald, 1995). FTC is a voracious defoliator of trembling aspen, white birch, and balsam poplar (*Populus balsamifera* L.) (Witter, 1979; Peterson & Peterson, 1992). Outbreaks of FTC generally last 1 to 6 years (Cooke *et al.*, 2009), with recurrence every 9 to 13 years (Cooke & Lorenzetti, 2006), and occur as far north as 54°N in Quebec (Huang *et al.*, 2008). Severe FTC defoliations reduce tree growth (Hildahl & Reeks, 1960; Hogg *et al.*, 2002) and decrease forest productivity (Bergeron & Charron, 1994; Hogg & Schwarz, 1999; Candau *et al.*, 2002). Tree mortality, particularly that of trembling aspen, is more frequently associated with predisposing, inciting and contributing factors (see Frey *et al.*, 2004), such as climate (Hogg *et al.*, 2008), age (Brandt *et al.*, 2003; Sutton & Tardif, 2007), wildlife damage (Peterson & Peterson, 1992), wood-boring insects (Hogg *et al.*, 2002) or fungal pathogens (Brandt *et al.*, 2003), than with FTC defoliation itself (Churchill *et al.*, 1964; Candau *et al.*, 2002; Brandt *et al.*, 2003; Man *et al.*, 2010; Moulinier *et al.*, 2011).

In mixed boreal stands, canopy transition from mixed deciduous to conifer-dominated stands generally involves autogenic processes such as tree senescence and competition, but it is also affected by other exogenous factors, such as disease, insects or climatic events. In the absence of fire, insect outbreaks may occur frequently and create canopy gaps (Kneeshaw & Bergeron, 1998; McCarthy, 2001). Further, gaps modify understory conditions, principally the availability of resources such as light and water (Canham, 1988; McCarthy, 2001). Consequently, gaps may favour different tree species depending on gap size and the life-history traits of the species present (longevity, growth rate, shade-tolerance) (Bergeron, 2000). Small gaps (< 200 m^2, following McCarthy, 2001) have less of an effect on light levels and tend to favour shade-tolerant softwoods, while large gaps (> 200 m^2) generally alter light levels and improve the recruitment of intolerant hardwoods. Moreover, dominant deciduous and coniferous tree species can have different effects on the recruitment and growth of understory species. On one hand, for example, the litter of deciduous species generally improves soil nutrient conditions (Thiffault & Jobidon, 2006), but it can represent a significant barrier to conifer seed germination (Zasada *et al.*, 1992; Simard *et al.*, 2003). On the other hand, litter of coniferous species usually reduces soil nutrients (Légaré *et al.*, 2005) and increases organic soil layer thickness (Laganière *et al.*, 2009), which can reduce soil temperature and warming that is required for seed germination and suckering of aspen (see Frey *et al.*, 2003).

Recent studies have documented forest succession and gap dynamics following FTC outbreaks in pure poplar stands of Quebec and Ontario (Man & Rice, 2010; Moulinier *et al.*, 2011), but the effects of such disturbances in mixedwood boreal stands have yet to be described. The last FTC outbreak (1999-2002) that occurred in the mixedwood boreal forests of northwestern Quebec exhibited great variation in defoliation intensity (in terms of severity and duration) and constituted a real opportunity for studying how such disturbances can affect the dynamics of mixed stands that are dominated by trembling aspen. The main objective of this study was to describe the effects of different FTC outbreak intensity regimes on overstory and understory stand structure, and on the composition of mixedwood forests. Specifically, we hypothesized that (1) the proportion of canopy openings would increase with the increase in FTC outbreak intensity, (2) gap characteristics, such as gap size and number of gap makers per gap (dead trees which form gaps), would increase as defoliation intensity increased, (3) gap size following FTC defoliation would affect understory tree recruitment, with small gaps favouring shade-tolerant conifers and large gaps favouring intolerant deciduous species, and (4) growth of pre-established conifers should be higher in defoliated than in undefoliated stands. Our study was undertaken 6 years after the last year of FTC defoliation by sampling 12 mixedwood stands dominated by *P. tremuloides* that had experienced different levels of FTC defoliation intensity.

3.4 MATERIAL AND METHODS

3.4.1 Study area

The study area (48°40'N - 48°59'N; 77°10'W - 78°20'W) is located in Abitibi-Temiscamingue, a northwestern region of Québec, Canada. This area is situated within the Québec portion of the Quebec-Ontario Clay Belt (Vincent & Hardy, 1977) and is included in the balsam fir–white birch bioclimatic domain (Robitaille & Saucier, 1998; Saucier *et al.*, 1998). The climate is continental with cold, dry winters and short, mild summers. Common tree species include trembling aspen, balsam fir, white birch, white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), and jack pine (*Pinus banksiana* Lambert).

In this region, the most recent FTC outbreak occurred from 1998 to 2003, and was the sixth event recorded since 1938 (Cooke & Lorenzetti, 2006). In 1998 and in 2003, defoliation was much localized and was monitored at the ground level by the Quebec Ministry of Natural Resources (MRNQ). During the period 1999-2002, the extent of the defoliation was great enough to warrant annual aerial surveys by ministry. We will thus refer to 1999-2002 as the outbreak period. In every yearly survey, the proportion of foliage that had been lost to defoliation in each stand was estimated and classified into one of four classes (undetectable, 0%; light, 1-25%; moderate, 26-65%; severe, 66-100%), which have been defined by the Forest Insect and Disease Survey (FIDS) program of the Canadian Forest Service. The cumulative area that was defoliated during this last outbreak reached about 1.4 million hectares, with a total defoliated extent in 2001 of nearly 1 million hectares (Bordeleau, 2011).

3.4.2 Data collection

Field data were obtained in August 2009. We selected twelve mixedwood stands that had experienced a range of defoliation regimes over the period 1999-2002. These stands were homogeneous in terms of overstory composition (trembling aspen basal area $\geq$ 50% of total basal area) and tree density (Table 3.1). These twelve stands were also similar in terms of understory vegetation type, particularly for the shrub species component (height and density). We were careful in selecting stands where shrub competition was low so to emphasize the effect of gaps on tree regeneration. For each stand, the mean defoliation intensity was calculated as the four-year average of the aerial defoliation survey class midpoints. Stand characteristics (composition, basal area, and stem density) were estimated using the data from two 400 m^2 inventory plots that had been established under closed canopy in each stand. Diameter at breast height (DBH, 1.3 m) and species of all living trees ≥ 9 cm were recorded. In addition, 2 cores were taken at breast-height from 5 dominant trembling aspen and 5 dominant balsam fir or white spruce to determine maximum ages.

In each stand, one transect was established to evaluate the percentage of canopy openings. Transects varied in length from 500 to 800 m (for a total of 7.4 km). The starting point for each transect was randomly assigned after applying a 50-metre wide buffer to any open area. At every metre along the transects, the forest canopy was visually inspected and classified as closed if a live tree crown was present, or open in the presence of one or more mature dead trees (Kneeshaw & Bergeron, 1998). A canopy opening at the stand level was subsequently calculated as the relative frequency of open canopy to the total length of transect (Runkle, 1992). To confirm that canopy openings were not influenced by gaps the formation of which pre-dated the most recent FTC outbreak, we used pre-disturbance aerial photos (1994-1995) to verify that pre-existing gap areas were within the range of natural variability of undisturbed stands (5-10%, following Kneeshaw & Bergeron, 1998; Moulinier *et al.*, 2011).

Gap characterization was performed in each stand on the first third of the total transect length, resulting in a subsample of 112 (out of 378) gaps. A canopy gap is created by the death of an individual or small cluster of trees and is defined as the vertical projection upward from the ground surface of the canopy opening (Runkle, 1982). For circular-shaped gaps, measures of the longest and shortest perpendicular axes of both the canopy and extended gaps were recorded. Multiple extra axis measurements were performed in the case of irregular-shaped gaps. Dead trees within the gaps, which were referred to as gap makers, were counted, identified, and classified as either standing dead, snapped, uprooted, or crown damaged (crown or branch dieback).

Regeneration was inventoried in the 112 subsampled gaps. An exhaustive count of regeneration by species was achieved in the smaller gaps (area < 100 m^2), whereas two 2-metre wide transects (north, south) that were perpendicular to the north-south axis were used for larger gaps. Regeneration was categorized into one of three height classes for each species: suckers (< 1 m), saplings (1-2 m) and large saplings (2-4 m) for trembling aspen; and seedlings (< 0.5 m), saplings (0.5-2 m) and large saplings (2-4 m) for conifers. The density of the regeneration was calculated by species for the entire gap (total density) and for each of the three height classes. Because trembling aspen and balsam fir represented 99% and 85% of deciduous and coniferous regeneration, respectively, we only considered the abundance of these two species. The remaining 1% of deciduous and 15% of conifer regeneration were white birch and white spruce, respectively. Regeneration density under forest cover was quantified in two 10 m^2 subplots, which were sampled in each 400 m^2 plot that had been used to describe stand characteristics.

Apical growth of balsam fir was quantified along the gradient of mean defoliation intensity in gaps of different size and under forest cover. In each of the 12 investigated stands, from 5 to 42 balsam fir trees were sampled among 3 height classes, for a total of 247 stems (75 seedlings, 80 saplings and 92 large saplings). To determine apical growth before, during, and after the outbreak, we measured internodes length for each fir stem from its apex to the base until those internodes could no longer be identified. We subsequently were able to measure apical growth from 1994 to 2009. Apical growth measurements were not attempted for aspen since internodes are less pronounced, and frequent apical stem mortality can lead to errors.

3.4.3 Data analysis

Canopy opening, mean gap area, number of gap makers per gap, and the proportion of gap maker types were each analyzed by linear regression to determine stand-level changes in these gap characteristics in relation to defoliation intensity. Log-transformation was performed on gap area prior to analysis, and the residuals from all four regressions were examined to ensure that statistical assumptions of normality and homoscedasticity had been met.

Gaps were grouped into classes of 25 m^2 increments of surface area, with upper class limits ranging from 0 (under forest cover) to 475 m^2. Comparisons of gap size-class distributions between defoliation regimes were performed using Kolmogorov-Smirnov tests. As we applied multiple comparisons, Bonferroni corrections were performed to adjust the significance level from α (0.05) to α/n (0.004), with n (12) being the number of comparisons.

A linear mixed-effects model (Pinheiro & Bates, 2000; Pinheiro *et al.*, 2008) was performed to analyze regeneration density of trembling aspen and balsam fir. Stand was considered as a random effect in this analysis. We used model selection methods to assess which factors significantly affected gap regeneration density. We formed a set of plausible models to identify which of the predictor variables and their interactions might explain patterns of regeneration density. The fit of the global model was assessed for this analysis and models were compared using the second-order Akaike Information Criterion (AIC_c) and the information theoretic approach that was presented by Burnham & Anderson (1998, 2002). We considered models with ΔAIC_c values ≤ 2 to have strong support; we also calculated model weights from the AICc values to indicate the level of support for each of the models that were considered (Burnham & Anderson, 2002). Regeneration density was categorized in two classes (< 0.1 stems.m^{-2} vs > 0.1 stems.m^{-2}). The threshold of 0.1 stems.m^{-2} was used to discriminate between minimally and poorly regenerated gaps, following

MRNQ regeneration survey guidelines. Density data from minimally regenerated gaps was analyzed with mixed logistic regression to test effects of defoliation intensity, gap area, species, height class and three interactions, viz., [defoliation intensity×height class], [gap area×height class], and [species×height class]. Stand and gap were considered as random effects in the model. Model selection analysis was also performed, and only one model with a ΔAIC_c value ≤ 2 was used to predict height class regeneration density.

Apical growth of balsam fir was analyzed with a linear mixed-effect model. We defined four periods of growth: prior to the outbreak (1994-1998), during the outbreak (1999-2002), immediately following the outbreak (2003-2006), and 5-7 years after the outbreak (2007-2009). We also determined the height class of the stems in 1998 to test which height class at the inception of the FTC outbreak responded to different defoliation intensities. The same height classes as previously described were used: seedlings [0-0.5m], saplings [0.5-2m], and large saplings [2-4m]. Apical growth was analyzed as a function of defoliation intensity, gap area, height class in 1998, growth period, and two interactions, i.e., [defoliation intensity×period] and [height class×period].

All statistical analyses were performed in R (version 2.10.1, R development Core Team, Vienna, Austria).

3.5 RESULTS

3.5.1 Canopy and gap characteristics

The proportion of canopy opening increased significantly from 11.3% to 46.8% with the increase in mean defoliation intensity, the index that combines defoliation severity and duration over the four-year period of the forest tent caterpillar outbreak (Fig. 3.1a). Mean gap area also showed a significant positive relationship ($r = 0.81$, $P < 0.01$) with mean defoliation intensity and increased at a rate of about 1 m^2 per percent of mean defoliation intensity across the gradient of defoliation (Fig. 3.1b).

The number of gap makers increased significantly with defoliation intensity for trembling aspen ($r = 0.86$, $P < 0.01$), but not for balsam fir (Fig. 3.1c). Among the 521 dead trembling aspen that were sampled in the gaps, 72.1% were classified as snapped, 22.5% as standing dead, 3.5% as uprooted, and 1.9% as crown-damaged. Among the 172 coniferous gap makers, 47.7% were snapped, 39.5% were uprooted, 12.2% were standing dead, and 0.6% were crow- damaged. In contrast to coniferous gap maker which did not exhibit any relationship with mean defoliation intensity (data not shown), the proportion of snapped trembling aspen increased significantly with mean defoliation intensity, while the proportion of trees standing dead decreased marginally (Fig. 3.1d). The proportions of crown-damaged and uprooted aspen trees were not significantly related to defoliation intensity (Fig. 3.1d).

Patterns of gap size distributions showed that gap size frequency did not differ between mean defoliation intensities (Bonferroni-corrected $P > 0.004$). However, this result revealed an increase in the proportion of 100 m^2 gaps in stands that had been defoliated three or four years (mean defoliation intensities $\geq$ 43%, Fig. 3.2).

3.5.2 Regeneration

Analysis of regeneration density by height class showed that only one of the 9 models that was considered had strong support, with an AIC_c weight of 0.78 (Table 3.2). This model showed that the density of balsam fir was higher than that of trembling aspen ($\beta = 0.64$, $P < 0.01$). Density of small-sized regeneration (seedlings for balsam fir, suckers for trembling aspen) was higher than that of saplings ($\beta = -1.11$, $P < 0.01$) and large saplings ($\beta = -2.06$, $P < 0.01$). The density of fir seedlings and aspen suckers decreased more strongly with increasing gap area than did the density of saplings in both species ($\beta = 0.24$, $P = 0.06$, Fig. 3.3a,b), while large sapling density was not affected by gap area in either species ($\beta = -0.01$, $P = 0.97$, Fig. 3.3a,b). There was a significant and positive effect of defoliation intensity on regeneration density ($\beta = 0.01$, $P = 0.01$), principally for fir seedlings and saplings

(Fig. 3.3c), which increased more than did aspen suckers and saplings (Fig. 3.3d). Overall, our analysis showed a significant effect of defoliation intensity on small and intermediate regeneration for both species and a less important effect of gap size on regeneration patterns.

In stands containing white spruce in the understory, the mean density of white spruce regeneration (data not shown) was similar between gaps and under forest cover along the gradient of defoliation intensity (about 200 ± 40 stem.ha^{-1}), except in the stand that had been defoliated for four consecutive years and in which mean density reached 400 ± 200 stem.ha^{-1}. The seedling class represented 52% of total white spruce regeneration, while sapling and large sapling classes represented 43% and 5%, respectively.

3.5.3 Balsam fir apical growth

Mixed-effects regression analysis (Table 3.3) showed that mean apical growth of balsam fir increased significantly with gap area ($\beta = 0.07$, $P < 0.01$). Apical growth was greater in gaps ≥ 100m^2 (13.2 ± 0.8 cm.year^{-1}) than in gaps < 100m^2 (11.1 ± 0.4 cm.year^{-1}) and under forest cover (9.4 ± 0.4 cm.year^{-1}). The interaction [defoliation intensity×period] had a significant and positive effect on mean apical growth ($P < 0.01$). This result meant that mean apical growth increased more with defoliation intensity directly after the outbreak (2003-2006, $\beta = 0.43$) and during the most recent period (2007-2009, $\beta = 0.48$) than actually during the outbreak (1999-2002, $\beta = 0.26$). Mean apical growth of balsam fir observed between 1994 and 1998 was consistent between stands before the outbreak (Fig. 3.4a). Mean apical growth by height class in 1998 (Fig. 3.4b) showed that, before the outbreak, large saplings grew more than did saplings and seedlings. After the outbreak, apical growth of saplings and seedlings was greater than that of large saplings. Apical growth of seedlings increased by 180% between 1998 and 2009, and during the same period, growth of saplings and large saplings increased by 60% and decreased by 22%, respectively.

Increases in apical growth during the outbreak period did not statistically differ among seedlings, saplings and large saplings ($P = 0.901$ for saplings; $P = 0.662$ for large saplings; Table 3.3). However, apical growth during both of the periods after the outbreak increased more for seedlings than for either saplings ($P \leq 0.01$) or large saplings ($P \leq 0.05$, Table 3.3), compared to apical growth during the outbreak. Thus, patterns of apical growth clearly showed that seedlings were more positively affected by the outbreak than were saplings and large saplings, although saplings exhibited the highest apical growth (Fig 3.4b).

3.6. DISCUSSION

3.6.1 Canopy, gaps and gap makers

This study showed a close relationship between canopy opening (due to tree mortality) and FTC defoliation intensity in the mixedwood boreal forest of the northwestern Quebec Clay Belt (Fig. 3.1a). The observed range in canopy opening (from 11.3% to 46.8% across the disturbance gradient) is wider than the 24.4 to 35.3% range reported by Kneeshaw & Bergeron (1998) for similar mixedwood stands of Quebec. In the latter case, canopy openings resulted from the mortality of fir trees following a spruce budworm outbreak. The wider range observed for mixedwoods in our study may be due to the generally larger size of aspen compared to fir trees (Kneeshaw & Bergeron, 1998). The increase in canopy opening that we observed in our twelve sampled stands was also comparable to results that have been reported in twenty stands dominated by trembling aspen, where canopy openness increased from 12.3% in undefoliated stands to 43.7% after 3 years of severe FTC defoliation (Moulinier *et al.*, 2011). Compared to these deciduous stands (Moulinier *et al.*, 2011), canopy opening rates in mixedwood stands have appeared to be slightly lower for equivalent defoliation intensities (20.8 and 37.5% in mixedwood stands; 23.7 and 43.7% in deciduous stands after 1 and 3 years of severe FTC defoliation, respectively). These differences can be attributed to residual trees, principally the dominant and intermediate conifers such as balsam fir, which are exposed to increase light when dominant trembling aspen trees die, thereby reducing gap size and limiting connections between neighbouring gaps.

Patterns of gap size are also consistent with the effects of FTC defoliation on canopy openings reported in pure poplar stands (Moulinier *et al.*, 2011). Gap size increased significantly with defoliation intensity (Fig. 3.1b) and gaps > 100 m^2 were only present in stands that had been defoliated over three consecutive years (Fig. 3.2). These results revealed that the structure of mixedwood stands was not significantly affected by one year of severe FTC defoliation, while three consecutive years of moderate to severe FTC defoliation tended to alter gap size frequency distribution and significantly increased the level of canopy opening.

Gap size distribution was directly related to the increase in the number of trembling aspen gap makers per gap, which doubled from one to three years of FTC defoliation (Fig. 3.1c). Snapped gap makers increased with defoliation intensity and dominated in all stands (Fig. 3.1d). Proportions of snapped trembling aspens corroborated the observation that high densities of such gap makers constitute one of the most conspicuous footprints of severe FTC defoliations (Moulinier *et al.*, 2011). The decreasing proportion of up-rooted trembling aspen showed that windstorm events were not associated with trembling aspen mortality. However, up-rooted balsam fir represented a large proportion of the coniferous gap makers (40 %, data not shown), which could be attributed to the greater wind vulnerability of such species (Ruel, 2000).

3.6.2 Response of understory trees

Contrary to our expectation, recruitment of trembling aspen in the twelve sampled stands was not improved by FTC defoliation intensity (Fig. 3.3b), while recruitment of balsam fir was favoured and appeared more dependent upon defoliation regimes than influenced by gap size. The low density of trembling aspen suckers and saplings that was observed in stands defoliated for three years (Fig. 3.3d) was consistent with the response of trembling aspen regeneration that was observed after an FTC outbreak in mixed stands of northeastern Ontario (Man & Rice, 2010). However, our results did not compare well with patterns reported after FTC outbreak in pure trembling aspen stands in which trembling aspen recruitment increased with the number of years of severe FTC defoliation (Man & Rice, 2010) and with gap size (Moulinier *et al.*, 2011). This difference may have resulted from competition that is provided by residual coniferous trees (Peterson & Peterson, 1992), which contribute to reduced understory light penetration (Messier *et al.*, 1998) and to increased organic soil layer thickness (Laganière *et al.*, 2009) and reduced soil temperature (Bonan & Shugart, 1989). These conditions are not adequate for trembling aspen root suckering and sucker survival (see Frey *et al.*, 2003).

The density of fir seedlings significantly increased with mean defoliation intensity and significantly decreases with gap size (Fig. 3.3a,c). Balsam fir has been reported of mast seeding every other year in the study area (Messaoud *et al.*, 2007) and 2006, three years before our sampling, was an exceptional mast year (Robert *et al.* 2012), suggesting that the observed patterns in fir seedlings is largely associated with the last FTC disturbance in those mixed stands. These patterns suggest that FTC defoliation created conditions that favoured balsam fir seedlings establishment at the stand, but not at the gap, level: (1) the increase in gap size and canopy opening with mean defoliation intensity enhanced light conditions sufficiently to improve balsam fir seed production (Greene *et al.*, 2002); (2) the dispersion over short distances of the large seeds of balsam fir (Asselin *et al.*, 2001) restricted colonisation in large gaps, and thus, limited seedlings establishment to the understory and close to mast trees; (3) the combination of the effects of FTC defoliation on canopy opening and balsam fir seed production resulted in an increase in seedling density with mean defoliation intensity and not with gap size. The decreasing abundance of balsam fir regeneration with increasing gap size (Fig. 3.3a) was also reported in mixedwood stands by Kneeshaw and Bergeron (1998).

Given that balsam fir can take 62 years to reach a height of 1.3 m (McCarthy & Weetman 2006), most fir saplings (0.5-2 m), and most likely all large sapling (2-4 m), in our study were advanced regeneration, present prior to the last FTC outbreak. The density of large fir saplings was low and not affected by gap size or by mean defoliation intensity, while the density of saplings tended to increase with defoliation intensity (Fig. 3.3C). This increase in balsam fir saplings density may have resulted from the apical growth response of seedlings established prior to the outbreak.

In fact, apical growth of balsam fir seedlings and saplings (Fig. 3.4b) increased during and after the last FTC outbreak, corroborating effects of increased understory light availability (Parent & Messier, 1995) and patterns of balsam fir growth and survival that were reported by Arbour and Bergeron (2011). The absence of large sapling growth responses could result from variation in resource allocation, mainly because taller balsam fir regeneration generally assigns higher priority to root diameter than to apical and radial growth after partial canopy removal (Claveau *et al.*, 2006).

3.6.3 Gap dynamics and forest stand succession

In stands that had been defoliated for one year, only few co-dominant trees died following the FTC outbreak. In other studies, those trees are usually the smallest (Moulinier *et al.*, 2011) and least vigorous ones (Man & Rice, 2010). Canopy opening rates revealed that gaps were more frequent after one year of severe defoliation than following light to moderate defoliation, but the former were not larger or more aggregated than the latter. Small changes in the canopy that were generated by low mortality rates should allow over-topped and intermediate trees (mainly conifers) to access the canopy more rapidly and, thus, should only slightly modify stand composition and forest succession. In stands disturbed by three consecutive years of moderate or severe FTC defoliation, small and medium gaps, together with the forest matrix surrounding gaps, should favour balsam fir recruitment and alter succession from trembling aspen-balsam fir to balsam fir-trembling aspen. In contrast, large gaps in which trembling aspen generally best regenerates and survives (Kneeshaw & Bergeron, 1998; Coates, 2002), should potentially contribute to maintaining a younger and mixed structure at the gap- and stand-level (Bergeron, 2000; Cumming *et al.*, 2000; Namroud *et al.*, 2005). However, our results indicate that recruitment of aspen in large gaps is likely insufficient to completely close the canopy in years ahead.

Competition from shrubby species such as mountain maple (*Acer spicatum* Lamarck), speckled alder (*Alnus incana* subsp. *rugosa* [Du Roi] R.T.Clausen), black or European alder (*Alnus glutinosa* L.), beaked hazel (*Corylus cornuta* Marshall), and raspberry (*Rubus idaeus* L.) was low in our study. Shrub competition, when present, should however be considered in assessing large gap trajectories, mainly because growth of such species generally increases after an FTC outbreak and where overstory mortality is very high (Batzer *et al.*, 1985; Kneeshaw & Bergeron, 1998; Man & Rice, 2010).

In the mixed matrix surrounding gaps, trembling aspen should continue to share dominance in canopy composition after an FTC outbreak until a new disturbance or natural tree senescence modifies canopy dominance. At the stand-level, stand structure should evolve from an even-aged to uneven-aged distribution because of the dynamics within gaps. In the case of repeated FTC outbreak events, exclusion of trembling aspen is expected to be exacerbated, with the transition of stands to coniferous forests strongly hastened.

Interestingly, effects of FTC outbreak on mixed trembling aspen-balsam fir stand dynamics produce the opposite pattern found following spruce budworm outbreak in mixedwood stands, where repeated defoliations contributed to increase balsam fir mortality, reducing fir component to the benefit of trembling aspen (Kneeshaw & Bergeron, 1998; Nealis & Régnière, 2004; Bouchard et al. 2007).

3.7 CONCLUSION

This study is complementary to previous work, which aimed at describing the effects of natural disturbances such as fire and spruce budworm outbreaks on boreal mixedwood forest succession. Our results clearly showed that FTC outbreaks leave a unique footprint on mixedwood stands that are dominated by trembling aspen. Variability in FTC outbreak severity and duration creates a range of canopy stand structures and modifies patterns of understory regeneration. The main difference between the responses of mixed *versus* deciduous stands to FTC defoliation lies in tree recruitment, which depends more upon defoliation intensity and canopy opening in mixedwood stands than on gap size in deciduous stands (Moulinier *et al.*, 2011). From a successionnal viewpoint, less disturbed stands should conserve their trajectories, while the transition from trembling aspen- to balsam fir-dominated mixedwoods should accelerate after repeated FTC defoliation, which increases trembling aspen mortality. However, further monitoring of such disturbed mixedwood stands is required to evaluate the response of residual canopy trees and to assess the consistency of regeneration patterns and forest succession pathways over the long-term.

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Table 3.1 Description of the twelve mixedwood stands from plots measured under closed canopies in 2009, including defoliation regime during the last outbreak (1999, 2000, 2001, 2002), mean defoliation intensity (mean percent of foliage annually lost), maximum tree age at breast height diameter (DBH), basal area (mean ± SE, $m^2.ha^{-1}$), tree density (mean ± SE, stem.ha^{-1}), and proportion of trembling aspen basal area (%).

Stand	Defoliation Regime	Mean Defoliation	Trembling aspen			Conifers			% BA Aspen
			Age	Basal	Density	Age	Basal	Density	
1	0,1,1,0	6.5	47	11.2±2.5	300±62	70	8.4±1.8	450±112	57,1
2	0,0,2,0	11	57	17.2±3.7	337±63	54	8.6±1.0	325±25	66,7
3	0,0,2,0	11	79	13.5±0.5	263±13	92	12.3±1.0	550±25	52,3
4	0,0,3,0	21	104	24.0±2.0	338±69	79	8.7±1.8	400±100	73,4
5	0,0,3,0	21	102	15.3±6.5	213±63	80	14.7±4.6	450±100	51,0
6	0,0,3,0	21	58	20.3±0.8	338±63	54	8.6±3.6	363±63	70,2
7	2,2,3,0	43	60	14.4±3.4	288±63	50	10.7±3.4	450±100	57,4
8	2,2,3,0	43	54	17.7±4.0	713±187	69	11.9±1.0	600±75	59,8
9	2,3,3,0	53	59	10.2±1.7	388±38	48	7.2±0.8	338±38	58,6
10	2,3,3,0	53	53	10.9±2.8	313±88	54	8.0±3.4	363±153	57,7
11	2,3,3,0	53	59	11.6±6.5	238±110	60	8.2±4.7	425±200	58,6
12	3,3,3,1	65	78	14.4±0.8	263±63	67	10.1±2.4	400±75	58,8

Note: Def = defoliation, 0 = no defoliation, 1 = low, 2 = moderate, 3 = severe; BA = basal area; density: of trees with DBH $\geq$ 9 cm.

Table 3.2 Top-ranking models for mixed-effects analysis of total density and density by height class of trembling aspen and balsam fir regeneration, which was sampled in 2009 from mixedwood stands that were defoliated for 1 to 4 years during the last FTC outbreak. This last outbreak occurred in northwestern Québec between 1999 and 2002. For brevity, only the five first models are shown for each response variable.

Model	K[*]	AIC$_c$[†]	ΔAIC$_c$[‡]	w_i[§]
Total density				
Gap+Species+[Gap×Species]	6	455.1	0.00	0.46
Def+Gap+Species+[Gap×Species]	7	455.7	0.61	0.34
Species	4	458.1	2.99	0.10
Def+Gap+Species+[Def×Species]	7	458.8	3.72	0.07
Def+Species+[Def×Species]	6	460.4	5.28	0.03
Height class density				
Def+Gap+Hc+Species+[Gap×Hc]	9	814.79	0.00	0.78
Def+Gap+Hc+Species+[Species×Hc]	9	818.45	3.65	0.12
Def+Gap+Hc+Species+[Def×Hc]+[Species×Hc]	10	818.98	4.19	0.10
Hc+Species+[Species×Hc]	7	825.46	10.66	0.00
Def+Hc+[Def×Hc]	7	829.16	14.36	0.00

[*] K = no. of parameters.

[†] AIC$_c$ = Akaike's Information Criterion corrected for small sample sizes.

[‡] ΔAIC$_c$ = AIC$_c$ relative to the most parsimonious model.

[§] w_i = AIC$_c$ model weight.

Note: Def = mean defoliation intensity calculated as the mean % removal of foliage per year over the 4 years of the last forest tent caterpillar outbreak (1999-2002); Gap = Gap area; Hc = Regeneration height classes (seedling for fir and sucker for aspen; sapling, and large sapling for both species); [×] = interaction.

Table 3.3 Parameter estimates and standard errors with *t*-values and *P*-values from linear mixed-effects model analysis describing balsam fir apical growth before, during and after the last forest tent caterpillar outbreak, which occurred in Quebec between 1999-2002, and considering [height classes×period] and [defoliation intensity×period] interactions. Tested levels are shown in parentheses for categorical covariates.

Variables	Estimate	SE	*t*-value	*P*-value
Def	-0.15	0.133	-1.174	0.26
Gap	0.07	0.015	4.379	**<0.01**
Hc (2)	0.78	0.093	8.423	**<0.01**
Hc (3)	1.06	0.189	5.617	**<0.01**
1999-2002	-0.53	0.184	-2.899	**<0.01**
2003-2006	-0.89	0.183	-4.883	**<0.01**
2007-2009	-0.85	0.183	-4.631	**<0.01**
Hc (2)×1999-2002	-0.01	0.085	-0.125	0.901
Hc (2)×2003-2006	-0.21	0.085	-2.447	**0.01**
Hc (2)×2007-2009	-0.51	0.085	-6.002	**<0.01**
Hc (3)×1999-2002	-0.07	0.174	-0.437	0.662
Hc (3)×2003-2006	-0.34	0.174	-1.973	**0.05**
Hc (3)×2007-2009	-0.56	0.174	-3.203	**<0.01**
Def×1999-2002	0.26	0.052	5.029	**<0.01**
Def×2003-2006	0.43	0.052	8.455	**<0.01**
Def×2007-2009	0.48	0.052	9.277	**<0.01**

Note: Parameter estimates in bold type correspond to terms with significant effect ($P \leq 0.05$). Def = defoliation intensity; Gap = Gap area; Hc = Regeneration height class; (2): sapling; (3): large sapling, [×] = interaction. Reference levels for height class = seedling (1), and for period = before the outbreak (1994-1998) did not appear in the Figure.

Figure 3.1 Relationship between mean defoliation intensity that was calculated with the mean percentage removal of foliage per year over the 4 years following the last forest tent caterpillar outbreak (1999-2002), which occurred in northwestern Quebec, versus (a) canopy opening (%), (b) mean gap area (m^2), (c) mean number of gap makers per gap and per species (i.e., number of trees from which gaps originated), and (d) the proportion of gap makers per status (only trembling aspen data are shown).

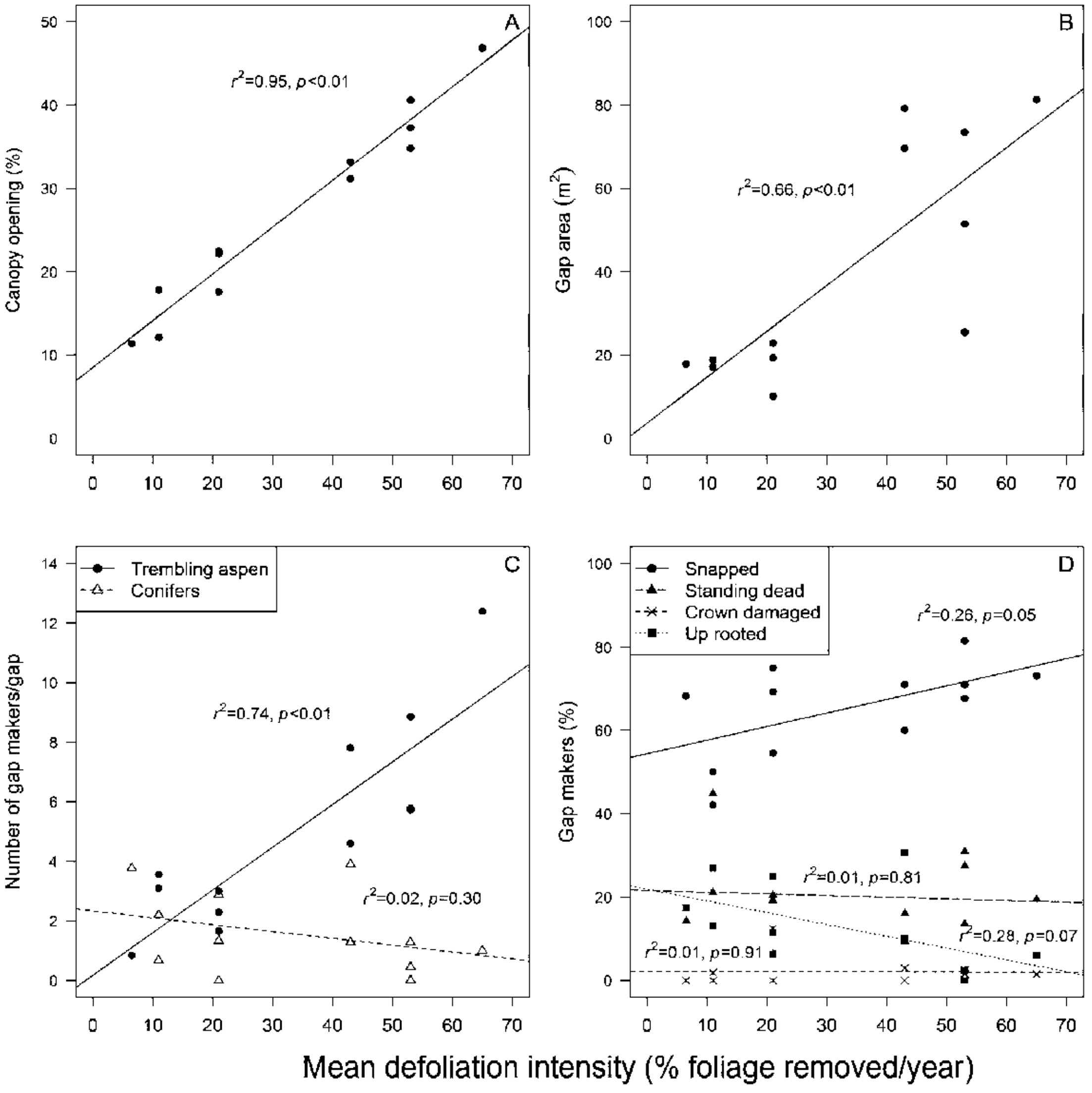


Figure 3.2 Relative frequency distributions of gap sizes in mixedwood stands that experienced increasing defoliation intensities during the last outbreak of forest tent caterpillar in northwestern Québec (1999-2002).

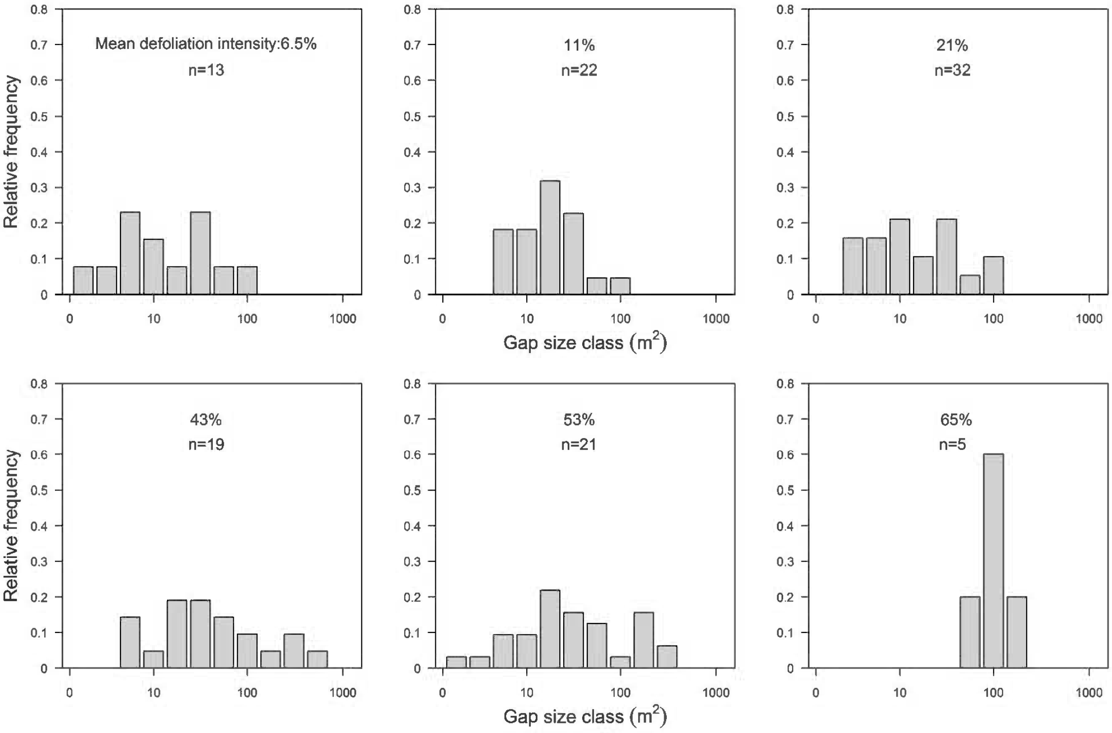
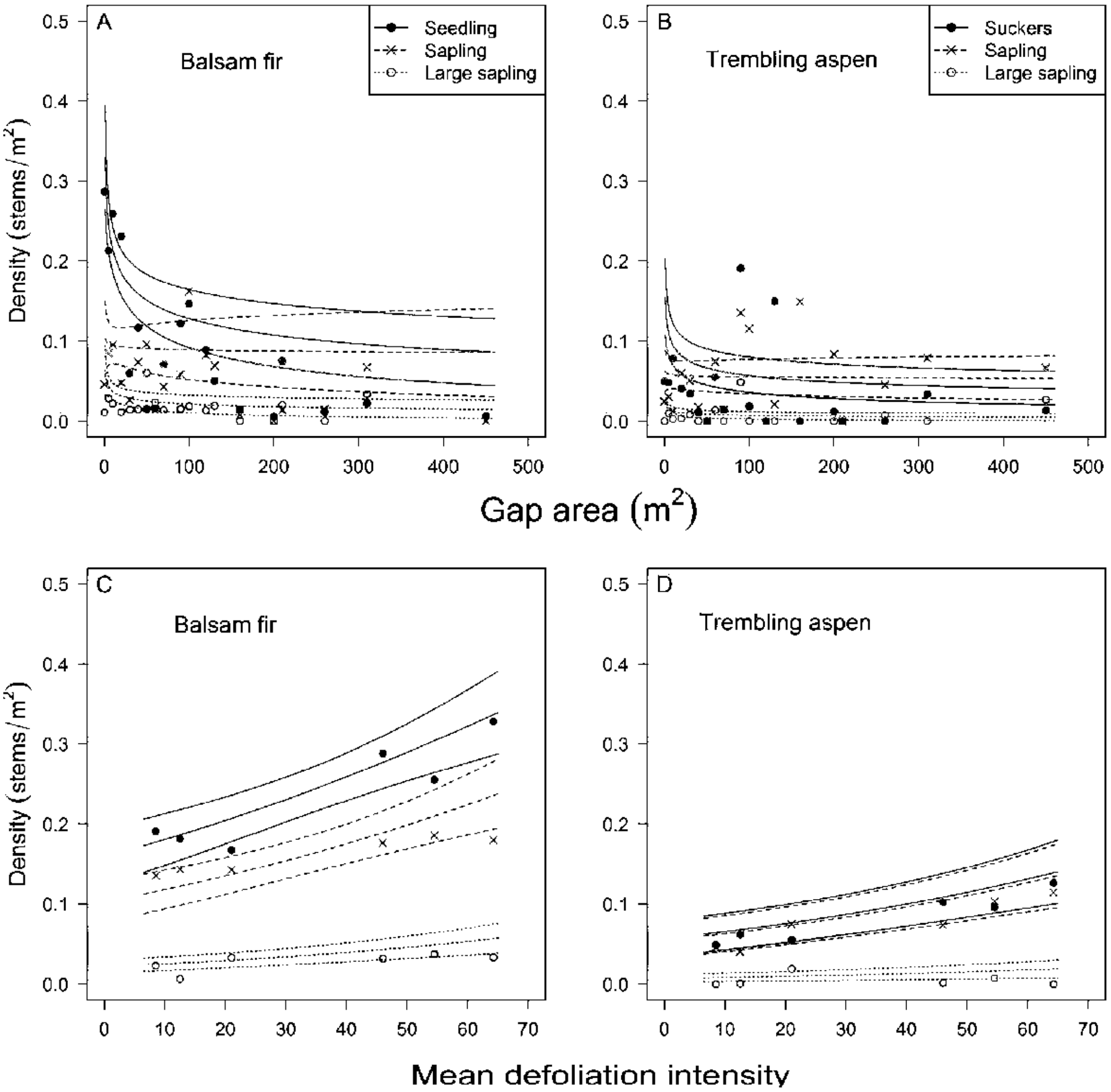
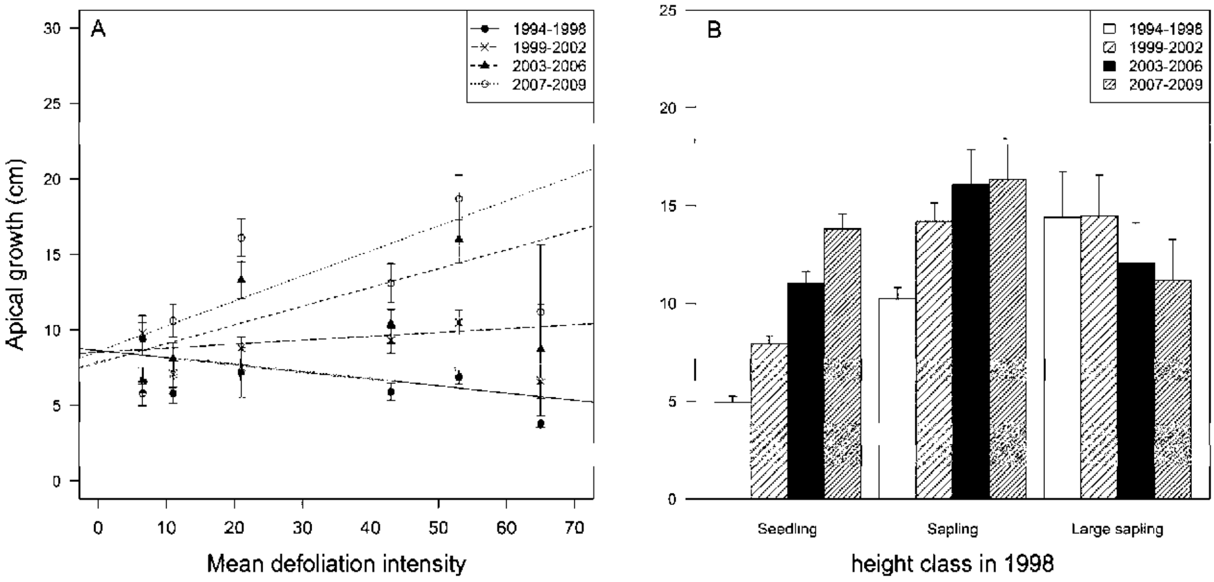


Figure 3.3 Effect of gap area and defoliation intensity on the density of balsam fir (A, C) and trembling aspen (B, D) regeneration in each of three height classes (model-averaged estimates with 95% confidence intervals).



Note: Regeneration height classes for trembling aspen: suckers (0-1 m) and sapling (1-2 m). Regeneration height classes for balsam fir: seedling (0-0.5 m); sapling (0.5-2 m). For both species: large sapling (2-4 m).

Figure 3.4 (a) Effect of defoliation intensity on balsam fir apical growth regeneration (mean±SE) for different periods, i.e., prior to (1994-1998), during (1999-2002), and two periods following (2003-2006, 2007-2009) the last forest tent caterpillar outbreak that occurred in northwestern Quebec. (b) Apical growth of balsam fir (mean±SE) for different height classes (based on height in 1998, just before the outbreak), i.e., seedling (< 0.5 m), sapling (0.5-2 m), and large sapling (2-4 m), during the four periods relative to the outbreak period.



CHAPITRE IV

GROWTH AND MORTALITY OF TREMBLING ASPEN (*POPULUS TREMULOIDES*) IN RESPONSE TO ARTIFICIAL DEFOLIATION: A THREE-YEARS EXPERIMENT AT THE STAND LEVEL

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4.1. ABSTRACT

To simulate effects of forest tent caterpillar (FTC) defoliation on trembling aspen growth and mortality, artificial defoliation was performed over three years in young aspen stands located in northwestern Quebec (Harricana Teaching and Research Forest). Defoliation plots measuring 15 x 15 m were established on three sites, together with associated control stands of pure trembling aspen. A 5 m buffer surrounded each defoliation plot was considered to evaluate leaf removal effects on neighbouring undefoliated trees. In 2007, root collar diameters were measured and positions of all trees were mapped prior defoliation. For three successive years (2007-2009), severe FTC defoliation was simulated by manually removing all leaves of most trees (90-95%) located in defoliation plots. Yearly surveys of growth and mortality were conducted until 2010 to evaluate defoliation effects on defoliated as well as surrounding undefoliated trees. In absence of other factors, growth and mortality of trembling aspen decreased and increased, respectively, after artificial defoliation. Our study further revealed that small-diameter trees died after one year of artificial defoliation, while larger-diameter trees died after repeated defoliations. Distributions of tree mortality tended to be aggregated at small scales (< 5 m), corroborating gap patterns observed in mature stands following FTC outbreaks. This experiment revealed that trembling aspen mortality can be directly attributed solely to defoliation. Further, repeated defoliations during FTC outbreaks could profoundly modify stand productivity and structure by reducing tree growth and increasing tree mortality.

Keywords: Forest tent caterpillar, trembling aspen, artificial defoliation, mortality.

4.2 RÉSUMÉ

Pour simuler les effets de la défoliation par la livrée des forêts (LDF) sur la croissance et la mortalité du peuplier faux-tremble, une expérimentation de défoliation artificielle a été réalisée pendant trois années dans de jeunes peuplements de peuplier situés dans le nord-ouest du Québec (Forêt d'enseignement et de recherche Harricana). Les parcelles de défoliation mesurant 15 x 15 m ont été installées dans trois sites et associées à des parcelles témoins de peuplier faux-tremble. Une zone tampon de 5 m entourant les parcelles était considérée pour évaluer l'effet de la défoliation sur les arbres voisins non défoliés. En 2007, le diamètre au collet et la position de tous les arbres ont été relevés avant défoliation. Durant trois années successives (2007-2009), des défoliations sévères de livrées des forêts ont été manuellement simulées en enlevant toutes les de presque tous les arbres (90-95%) des parcelles de défoliation. Des suivis annuels de croissance et de mortalité ont été réalisés jusqu'en 2010 afin d'évaluer les de la défoliation sur les arbres défoliés et les arbres non défoliés dans leur voisinage. En absence d'autres facteurs, la croissance et la mortalité du peuplier faux-tremble diminuait et augmentait respectivement après la défoliation artificielle. Notre étude a aussi révélé que les arbres de petits diamètres étaient morts après une année de défoliation artificielle alors que les arbres de plus gros diamètres étaient morts après des défoliations répétées. La distribution des arbres morts avait une tendance à l'agrégation à une petite échelle (< 5 m), ce qui corroborait les patrons de trouées observés dans les peuplements matures après épidémies de livrée des forêts. Cette expérimentation a révélé que la mortalité du peuplier faux-tremble pouvait être directement attribuée au seul effet de la défoliation. De plus, des défoliations répétées durant des épidémies de livrée des forêts pourraient profondément modifier la productivité et la structure des peuplements en réduisant la croissance des arbres et en augmentant leur mortalité.

Mots-clés: livrée des forêts, peuplier faux-tremble, défoliation artificielle, mortalité.

4.3. INTRODUCTION

In boreal deciduous and mixedwood forests of North America, the forest tent caterpillar (*Malacosoma disstria* Hübner) (FTC) is an important epidemic insect and voracious defoliator of various deciduous tree species, including trembling aspen (*Populus tremuloides* Michx.), which is its preferred host (Fitzgerald 1995). With recurrence every 9 to 13 years (Cooke and Lorenzetti 2006), FTC outbreaks last from 1 to 6 years (Cooke et al. 2009) and can occur as far as 54°N in Quebec (Huang et al. 2008). FTC defoliation reduces tree growth (Hildahl and Reeks 1960; Hogg et al. 2002a) and stand productivity (Bergeron and Charron 1994; Candau et al. 2002; Hogg and Schwarz 1999). Such defoliation generally induces reallocation of trembling aspen carbohydrate reserves to produce photosynthetic tissues such as new leaves (Hogg et al. 2002b; Jones et al. 2004; Reichenbacker et al. 1996). Tree mortality that follows repeated FTC defoliations has been more frequently associated with predisposing, inciting and contributing factors (see Frey et al. 2004), such as climate (Hogg et al. 2008), stand age (Brandt et al. 2003; Sutton and Tardif 2007), wildlife damage (Peterson and Peterson 1992), wood-boring insects (Hogg et al. 2002a) or fungal pathogens (Brandt et al. 2003), rather than with FTC defoliation itself (Brandt et al. 2003; Candau et al. 2002; Churchill et al. 1964; Man and Rice 2010; Moulinier et al. 2011).

Trembling or quaking aspen is the most widely distributed tree species in North America (Peterson and Peterson 1992), if not globally. It is a fast-growing species that dominates early successional stages following stand-replacing disturbance (Chen and Popadiouk 2002) and is both nutrient-demanding and shade-intolerant (Burns and Honkala 1990). Thus, trembling aspen is an important pioneer species in many boreal forest ecosystems, which provides wood products, wildlife habitat, carbon sequestration and many other appreciable resources and ecological services. Several studies have experimentally simulated insect defoliation in trembling aspen and hybrid poplars under controlled conditions to gain a better understanding of tree growth responses (Hodson 1981; Kosola et al. 2001; Osier and Lindroth 2004; Reichenbacker et al. 1996), effects on tree physiology including stomatal conductance, leaf water potential, hydraulic conductance, nitrogen uptake, root demography and white tree ring formation (Gálvez and Tyree 2009; Hart et al. 2000; Hogg et al. 2002b; Kosola et al. 2001), the effects of tree genotype (Osier and Lindroth 2004; Reichenbacker et al. 1996), and individual insect performance and insect population dynamics (Kaitaniemi et al. 1999; Parry et al. 2003). Yet, few experiments have examined the effects of repeated defoliation during successive years (Kaitaniemi et al. 1999; Kosola et al. 2001) and none has documented the corresponding tree mortality.

Following large-scale disturbance (i.e., fire or clear-cutting) or the removal of apical dominance (Farmer 1962), trembling aspen mostly regenerates via asexual reproduction through root suckering (Frey et al. 2004) from the residual root system of the previous stand. Suckers are produced on mother roots and, in turn, can develop their own roots to become independent trees (Brown and DeByle 1987). Otherwise, suckers can remain interconnected their whole life through the common parental root system which they share (DesRochers and Lieffers 2001a) and can interconnect with genetically different aspen clones through root grafting (Jelínková et al. 2009). Therefore, these clonal and physiological characteristics suggest that aspen stands could be considered as large physiological units of interconnected and genetically diversified trees (Jelínková et al. 2009) rather than individual trees or genetically uniform clones, as has been previously believed. Many would agree that interconnections between trees have great ecological significance (Graham and Bormann 1966), but few studies have clearly demonstrated the effects of root connections on tree physiology (see Tarroux and DesRochers 2011 on *Pinus banksiana*). A recent experimental study of Baret and DesRochers (2011) did show, however, that interconnected suckers of trembling aspen could physiologically interact through root connections and even exhibit compensatory photosynthesis to support respiration costs of artificially defoliated suckers. Further, the contributions made by aspen suckers that are produced after disturbance can support respiration costs of the large parental root system upon which they grow, but high sucker densities and leaf area are required to maintain such important underground biomass (DesRochers and Lieffers 2001b). When total leaf area of interconnected suckers becomes insufficient to compensate for respiratory costs of the communal root system (e.g., after defoliation), some suckers and a portion of the root system must therefore die off to balance the photosynthetic capacity of the aerial biomass (Desrochers et al. 2002; DesRochers and Lieffers 2001b). Given the dynamics associated with such interconnections in aspen stands, we investigated effects of simulated FTC defoliations on trembling aspen mortality and growth.

We postulated that, in absence of other influencing factors, differences in the response of mortality and growth that were observed between defoliated and control trees should be mostly attributable to defoliation itself. Our major hypothesis was that annual mortality of trembling aspen should increase, while growth should decrease from the first to subsequent years of artificial defoliation. Defoliation was also expected to affect the response of undefoliated trees that were situated close and potentially interconnected to defoliated ones. Because of compensatory photosynthesis, such undefoliated trees were expected to exhibit better growth after the first year of artificial defoliation. However, repeated defoliation should severely increase the imbalance between aerial and underground biomass of interconnected trees and should negatively affect undefoliated trees. As was the case for defoliated trees, we predicted that growth and mortality of undefoliated and surrounding trees should decrease and increase respectively after multiple years of artificial defoliation. Finally, based on the distance between trees, we determine whether the potential interconnection of trees through clonal establishment or root grafting could lead to aggregative mortality, as suggested from canopy gap formation that has been described in mature stands (Kneeshaw and Bergeron 1998; Moulinier et al. 2011).

Our related hypothesis was that spatial mortality of trembling aspen observed following artificial defoliation should tend to be aggregative and, therefore, spatially correlated as opposed to random. To achieve these objectives, we conducted a three-year-long field experiment in young aspen stands.

4.4 MATERIALS AND METHODS

4.4.1 Study area

This study was conducted in the Harricana Teaching and Research Forest, which is located 50 km northeast of Amos, northwestern Quebec (48°76'N, 77°83'W). Located on clay soils that originated from lacustrine deposits of the proglacial lakes Barlow and Ojibway (Vincent and Hardy 1977), the study area is characterised by a flat landscape and low elevations (300 m). The continental climate has cold, dry winters and short, mild summers. The vegetation consists of discontinuous mixedwood forest that is dominated by trembling aspen, white birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.) and jack pine (*Pinus banksiana* Lamb.).

4.4.2 Experimental design

Three 8-year-old pure stands of healthy aspen were selected at the onset of the 2007 growing season. They were similar in terms of soil type, topography, drainage class, tree age and density, and had originated from clear-cuts made in December 1998. All stands that had regenerated from these cuts were manually cleared in 2006 to remove competitive vegetation (mostly *Alnus* spp.), thereby minimising effects of interspecific competition on future growth and mortality of aspen. The three stands were spaced about 600 m apart.

One 'artificial defoliation' plot (ArtDefol) and one control plot (CtrlPlot) were assigned to each of the three stands, with the paired plots forming a statistical block (Fig. 1). The plots were about 25 m apart and measured 15 by 15 metres (225 m^2).

One edge of the plots was next to the logging road and facing south to allow for similar light incidence in each block. The three remaining sides of the plots were formed by the regenerated stands, with no change in stem densities and which acted as a buffer zone. On three sides of the ‘artificial defoliation’ plots, the first 5 m of the buffer zone was considered as an additional undefoliated control (CtrlBuff; Fig. 1).

The artificial defoliation treatment was repeated over three successive years (2007, 2008, 2009), and consisted of clipping the leaves from all but 7-10% of the trees. The latter were considered as control trees in the defoliated areas (CtrlTrees; Fig. 1). Artificial defoliation were completed during the last two weeks of June, about when leaves had reached full expansion, which is consistent with the timing of maximum food intake by FTC under natural conditions (Hodson 1941). To further mimic natural defoliation by the insect, petioles were left intact on branches. Clipped leaves were removed and discarded. Under natural conditions, undigested leaf material would normally return to the ground as frass, which serve a source of microbial inoculum and nutrients that can promote soil processes and plant growth (Frost and Hunter 2004; Kagata and Ohgushi 2012). Given that the clipped material had not undergone processing through insect guts, we considered its presence on site as a potential risk favouring unwanted fungal proliferation in the plots.

The experiment was considered a randomised block design with repeated measures (years) and four treatments within each block: ’artificial defoliation’ plots (ArtDefol); control undefoliated trees within ‘artificial defoliation’ plots (CtrlTrees); control undefoliated trees in the buffer zone of ‘artificial defoliation’ plots (CtrlBuff); and a control plot (undisturbed trees in an adjacent plot within a block; CtrlPlot).

4.4.3 Data collection and analyses

Root collar diameter of all trees was measured in the plots at the onset of each growing season in 2007, 2008, 2009, and 2010. These measurements allowed us to calculate root collar diameter growth for 2007, 2008 and 2009 for all trees that were alive in the subsequent year. All dead trees were noted, measured, and mapped each year.

Linear mixed-effect models (Pinheiro et al. 2008; Pinheiro and Bates 2000) were performed to analyse annual mortality rate, root collar diameter growth, and root collar diameter of dead trees as a function of treatment, year, and their interaction, i.e., treatment×year. Log-transformation was performed on the response variables (annual mortality rate, root collar diameter growth, and root collar diameter of dead trees) to satisfy assumptions of normality and homoscedasticity. Block (or site) was considered as a random effect in the annual mortality model, and trees were considered as nested within blocks for the growth and diameter models. Mixed models were fitted in R (version 2.10.1 (R Development Core Team 2010), using the *lme* function of the *nlme* (Pinheiro et al. 2008) and the *lmer* function of the *lme4* (Bates 2008) packages, respectively.

To determine spatial patterns of tree mortality in defoliated plots (ArtDefol), the positions of all trees within the treatments were recorded to the nearest 10 cm at the onset of the experiment. We then used the linearised form L(r) of Ripley's K-function (Ripley 1976) which is widely used in spatial point pattern analyses (Haase et al. 1996; Pélissier and Goreaud 2001; Ripley 1981; Schroff et al. 2006). Based on point-to-point distances, the K-function allows the analysis of spatial distributions without explicit knowledge of the process driving them. The $K(r)$ function calculates the density of points in a circle of a given radius (r) centered on each point (trees) (Ripley 1976). The prediction of a random distribution (null hypothesis of complete randomness) is tested by simulating a random process with the Monte Carlo method (Dale 1999). K-functions can be extended to describe point patterns with two types of points (e.g., trees dying in different years); the bivariate correlation function $K_{12}(r)$ and its linearised form $L_{12}(r)$ estimate the expected density of points of pattern 2 at a distance r from an arbitrary point of pattern 1. In the present study, we used this modified procedure of bivariate point pattern analysis to test spatial associations between years of mortality (2007-2008, 2008-2009, 2007-2009). Plot edge effects were accounted for using Ripley's local correction method (Goreaud and Pélissier 1999). Spatial analyses were conducted in R, using the ADS package (Chessel et al. 2004; Dray et al. 2007).

4.5 RESULTS

During three years of treatment, annual mean temperature at the closest meteorological station (Berry Lake; 48°85'N, 78°38'W) was consistent among years (1.05°C, 1.29°C, and 1.1°C in 2007, 2008 and 2009, respectively; Environment Canada 2010) but was higher than the mean for the previous 30 years (0.73 ± 0.21°C, 1977-2006). Total annual precipitation in the second (2008) and third (2009) years of treatment (867 and 911 mm, respectively; Environment Canada 2010) was consistent with the mean of the previous 30 years (886 ± 20 mm) but was higher than the annual total of 2007 (729 mm).

4.5.1 Tree mortality

The mortality survey showed dead tree numbers that were observed following each artificial defoliation were higher in artificial defoliation (Artdefol) plots than in all other treatments (Table 1). This survey also reported that only one undefoliated tree of the 67 individuals situated in the defoliation plots (CtrlTrees) died in 2009, after three years of artificial defoliation (Table 1).

Analysis of annual tree mortality demonstrated that mortality in artificially defoliated plots (ArtDefol) was higher than in control plots (Ctrlplot), the control buffer, (CtrlBuff), and control trees (CtrlTrees) since the first year of artificial defoliation (Table 2, Fig. 2a). Annual mortality of defoliated trees increased significantly after the second ($P < 0.01$) and third ($P < 0.01$; Table 2) years of artificial defoliation. Mortality of undefoliated trees that were situated in defoliated plots (CtrlTrees) was negligible in 2007 and 2008, and significantly lower than in control plots (Table 2, Fig. 2a), while mortality in the buffer zones (CtrlBuff) was similar to that in the control plots for each year of the experiment (Fig. 2a).

Cumulative mortality rates (Fig. 2b) that had been observed after 3 years of mortality in CtrlPlot (10.1%) and CtrlBuff (7.7%) were more similar than after one year in artificial defoliation plots (ArtDefol, 8.4%)., A cumulative mortality rate of 37% was achieved after two successive years of artificial defoliation, and almost doubled (72%) after a third year of artificial defoliation.

4.5.2 Tree growth

In all treatments, mean root collar diameter growth was higher in 2008 than in 2007 and 2009, except in Ctrltrees, where 2008 and 2009 growth was similar (Fig. 3). For each year, the growth of trees that had been artificially defoliated (Artdefol) was lower than in all of the other treatments (Table 3, Fig. 3) and was the lowest reported after three successive years of artificial defoliation (0.11 cm). Root collar diameter growth after the first year of artificial defoliation was 30-40% lower in defoliated plots than in all of the other treatments, and decreased from 60% to 75% after the second and third years of defoliation. Root collar diameter growth in buffer plots (CtrlBuff) was similar to that in control plots (CtrlPlot) but tended to be greater in the first (2007) and second (2008) years of the experiment (Fig. 3). Control trees (CtrlTrees) exhibited higher root collar diameter growth, which was 35 and 60% more important in 2008 (0.78 cm) and 2009 (0.77 cm) than in control plots (Fig. 3).

4.5.3 Dead tree diameter

Root collar diameter of trees that were dead in 2007 did not differ between all control treatments (ArtDefol, CtrlPlot and CtrlBuff; Fig. 4, Table 4). The root collar diameter of dead trees increased significantly after the second and third years in artificially defoliated trees (ArtDefol) from 1.8 cm (2007) to 2.5 cm (2008) and 3.3 cm (2009) (Table 4, Fig. 4), while was consistent between years (1.6 to 2 cm) in CtrlPlot and CtrlBuff treatments. Trees that were dead in 2008 and 2009 after the second and third years of artificial defoliation that exhibited larger diameters were already larger at the onset of the experiment (Fig. 4). Finally, the sole dead tree in the CtrlTrees treatment had a root collar diameter of 2.8 cm (data not shown).

4.5.4 Spatial mortality patterns

Maps of defoliation plots (Fig. 5; Appendix 1 and 2) illustrate the distribution of dead trees for each year of treatment as well as live ones in 2010. Mortality in artificial defoliation plot 1 (ArtDefol 1) showed a significant and positive association (statistical attraction) between 2007 and 2008 at 3-4.5 m, and between 2008 and 2009 at 1.5-3 m and 4.5-5 m (Fig. 6a). Patterns of mortality in ArtDefol plot 2 (Fig. 6b) also showed a positive association between years of mortality at scales ≤ 2 m (1-1.5 m between 2007 and 2008, 0.5-1 m between 2008 and 2009, 1.5-2 m between 2007 and 2009). Tree death in ArtDefol plot 3 (Fig. 6c) was spatially randomly distributed among years, except between 2008 and 2009 for which a trend of positive association at 2-3.5 m was observed.

4.6 DISCUSSION

Artificial defoliation had a clear and significant decreasing effect on trembling aspen growth. During each of the three successive years of artificial defoliation, trees had been deprived of their photosynthetic structures and consequently suffered from short growing seasons. Such short growing seasons that are caused by early defoliation have been reported to decrease tree growth and xylem production (Jones et al. 2004). Reduction of root collar diameter growth that was observed after the first year of artificial defoliation was more pronounced than has been previously observed for radial and diameter growth in artificial defoliation studies (Jones et al. 2004; Kosola et al. 2001; Reichenbacker et al. 1996). Such differences in growth may result from variation in defoliation intensity in contrast to complete defoliation (this study); partial defoliation has been shown to increase the photosynthetic rate of residual leaves and compensate for the loss of foliage (Bassman and Dickman 1982 ; Hart et al. 2000; Reichenbacker et al. 1996). Root collar diameter growth reduction that was observed after the second and third years of artificial defoliation, however, compares well with radial growth reductions that have been reported after repeated defoliation during FTC outbreaks in mature trembling aspen stands (Hildahl and Reeks 1960; Hogg et al. 2002a; Hogg et al. 2008; Man et al. 2008). Our experiment confirmed growth reduction in trembling aspen as early as the first year of defoliation, and corroborated that FTC outbreaks, depending on their severity, duration and extent, can represent an important contributor to productivity loss at both the tree- and stand-level (Bergeron and Charron 1994; Hogg et al. 2002a; Man and Rice 2010).

The increase in the growth of undefoliated trees that were located within defoliated plots (CtrlTrees) was contrary to expectation and suggested that defoliation could have a beneficial effect. Such increases in growth could result from an increase in canopy opening and light availability that is incurred with leaf removal, and which could contribute to improved overall photosynthetic activity and carbohydrate production (Pothier and Prévost 2002) of the remaining undefoliated trees within defoliation plots. This positive growth response of undefoliated trees could also be due to compensatory photosynthesis that is induced through root connections with defoliated trees (Baret and Desrochers 2011). Compensatory photosynthesis of undefoliated trees is expected to support the respiratory cost of the parental root system shared by trees. Such mechanisms enhance carbohydrate availability for interconnected trees (connected undefoliated and defoliated neighbours) and could confer advantage to undefoliated trees, particularly if defoliated trees and part of the common parental root system died following defoliation (DesRochers and Lieffers 2001b). Furthermore, tree mortality induced by defoliation could enhance resource uptake by undefoliated and connected trees if the roots of dead trees continue to occupy the soil and maintain their activity (DesRochers and Lieffers 2001a). Such effects might also explain the response of growth of buffer trees (CtrlBuff) during the first two years of the experiment that exhibited higher growth rates than undefoliated trees grouped in control plots (CtrlPlot).

Although aspen mortality following FTC defoliation has been generally associated with predisposing, inciting and contributing factors (Frey et al. 2004; Hartmann and Messier 2008; Kosola et al. 2001), our study clearly showed a strong relationship between artificial defoliation and aspen mortality in the absence of other co-factors. Our results revealed that tree mortality occurred after only one year of artificial defoliation in young and healthy stands under unstressed environmental conditions. The pronounced rates of trembling aspen mortality observed after repeated artificial defoliation may result from the incapacity of interconnected trees to sustain respiratory requirements of the total aerial and underground biomass (Desrochers et al. 2002; DesRochers and Lieffers 2001b). The diameter and proportion of dead trees that were observed after the first year of defoliation were comparable to those measured for three years in control (CtrlPlot) and buffer (CtrlBuff) treatments, suggesting that mortality of small diameter trees tended to be exacerbated directly after the first year of defoliation. Conversely, 2007 diameters of trees that were dead after the second (2008) and third (2009) years of artificial defoliation confirmed that those trees were already larger at the beginning of the experiment (Fig. 4). These increases in aspen mortality rates and dead tree diameter with repeated defoliation were consistent with patterns of tree mortality that have been reported after consecutive years of moderate to severe FTC defoliation in mature aspen stands (Churchill et al. 1964; Man and Rice 2010; Moulinier et al. 2011) and corroborated that repeated FTC defoliation can reduce stand density by more than 50% (Churchill et al. 1964; Man and Rice 2010).

Contrary to expectation, mortality of undefoliated trees that were situated in artificial defoliation plots (CtrlTrees) was almost negligible and did not increase with repeated defoliation. Undefoliated trees were expected to support the large energetic costs of the common parental root system (Shepperd and Smith 1993) that they share with defoliated trees (Baret and Desrochers 2011; DesRochers and Lieffers 2001b). Defoliation-induced foliage loss and mortality should have contributed to exacerbating the imbalance between leaf area and root biomass, and to demands upon undefoliated trees, which should lead some to die. However, low mortality of undefoliated trees suggested that these trees did not suffer from the effects of defoliation of neighbouring trees but likely benefited from their deaths. Like for growth, we speculate that benefit may result from the combination of several mechanisms: a new equilibrium that is established between leaf area and live root biomass (DesRochers and Lieffers 2001b) through the death or integration of part of the common root system (DesRochers and Lieffers 2001a; Jelínková et al. 2009), compensatory photosynthesis induced through root connections (Baret and Desrochers 2011), and increases in photosynthetic activity in response to canopy opening and increased light availability (Pritchard and Comeau 2004).

The positive association observed between years for trembling aspen mortality was weaker than expected, but spatial patterns suggested that tree mortality tended to be aggregated at a small scale (< 5 m). The mechanism of mortality observed after artificial defoliation was likely enhanced by the imbalance between above- and below-ground biomass of interconnected trees (DesRochers and Lieffers 2001b). Interconnected trees that originated from root suckering are closely situated on the same parental root system, which *a priori* contributed to the production of aggregated patterns. Our results confirmed aggregative mortality patterns that have been described in mature stands (Kneeshaw and Bergeron 1998) and from which gaps emerge following FTC outbreaks (Kneeshaw and Bergeron 1998; Moulinier et al. 2011). The absence of aggregative mortality at distances over 5 m was not expected, however. The genetic structure of our young stands possibly mitigated the strength of the aggregative tree mortality response, principally because genotypes have been more frequently reported to be mixed (Wyman et al. 2003) rather than spatially segregated (Namroud et al. 2005) in young aspen stands. Moreover, root grafts probably played a less important role than expected in our study, perhaps because they have been more frequently observed between stumps and suckers rather than between suckers in young aspen stands (DesRochers 2000). Therefore, the mixed spatial genetic structure likely contributed to reducing the probability of having neighbours with same genotype at distances over 5 m.

4.7 CONCLUSION

Root collar diameter growth reductions and augmented mortality of trembling aspen that were observed after artificial defoliation were consistent with patterns of growth and mortality reported after FTC defoliation. The increase in root collar diameter of dead trees with repeated defoliation confirmed natural patterns of dead tree diameters that have been reported after FTC outbreaks. Our results also showed that undefoliated trees in defoliated areas could have benefitted directly or indirectly from foliage loss of their neighbours. It is known, however, that in extreme situations where all trees are defoliated, defoliation-induced mortality can affect all trees (Man and Rice 2010), thereby causing stand-wide collapse (DesRochers and Lieffers 2001a). Aggregative mortality of trembling aspen observed following artificial defoliation corroborated gap formation that is routinely observed in natural stands after FTC outbreak. Rather than merely reporting trembling aspen mortality following artificial defoliation, this study allowed us to infer that short-duration outbreaks (1 year) tended to accelerate natural exclusion (self-thinning) of suppressed and small diameter trees, while long-duration outbreaks (2+ years) should more profoundly alter stand structure by removing both small and large diameter trees (Moulinier et al. 2011). Finally, further research is required to increase our understanding of FTC defoliation effects, particularly in the role of root connections in young and mature stands and how they affect patterns of growth and mortality of trembling aspen in a context of an outbreak.

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Table 4.1 Summary data for the number of trembling aspen sampled in each block and associated treatments, and percentage of dead trees for each year of defoliation (2007, 2008, 2009 in parentheses).

Block	ArtDefol	CtrlTrees	CtrlBuff	CtrlPlot
1	290 (12,43,62)	31 (0,0,3)	469 (3,3,3)	350 (3,3,5)
2	258 (7,27,52)	18 (0,0,0)	438 (3,3,3)	339 (2,4,7)
3	200 (4,22,50)	18 (0,0,0)	285 (2,1,1)	266 (1,3,3)

Note: ArtDefol, artificial defoliation; CtrlBuff, control buffer; CtrlPlot, control plot; CtrlTrees, control trees.

Table 4.2. Parameter estimates and associated standard errors with *t*- and *p*-values from linear mixed-model analysis describing annual mortality of trembling aspen. The models considered the effects of treatment and year, and the interaction between these two factors. *P*-values in bold are associated with parameters significant at $P < 0.05$.

	Value	SE	DF	t-value	p-value
Intercept	1.098	0.224	22	4.893	**<0.01**
ArtDefol	1.027	0.242	22	4.240	**<0.01**
CtrlTrees	-1.097	0.242	22	-4.536	**<0.01**
CtrlBuff	0.235	0.242	22	0.972	0.34
2008	0.325	0.243	22	1.343	0.19
2009	0.638	0.243	22	2.634	**0.01**
ArtDefol x 2008	0.981	0.342	22	2.865	**<0.01**
CtrlTrees x 2008	-0.584	0.342	22	-1.707	0.11
CtrlBuff x 2008	-0.325	0.342	22	-0.950	0.35
ArtDefol x 2009	1.264	0.324	22	3.693	**<0.01**
CtrlTrees x 2009	-0.780	0.324	22	-2.277	**0.03**
CtrlBuff x 2009	-0.157	0.324	22	-0.460	0.65

Note: ArtDefol: artificial defoliation, CtrlBuff: control buffer, CtrlTrees: control trees, CtrlPlot: control plot. Reference level: Control plot and year 2007.

Table 4.3 Summary of the linear mixed-model regression analysis of annual root collar diameter growth. Treatment and year, and the interaction between the two factors were considered as explanatory factors.

	Value	SE	DF	t-value	p-value
Intercept	0.275	0.026	7572	10.45	**<0.01**
ArtDefol	-0.101	0.011	7572	-9.81	**<0.01**
CtrlTrees	0.095	0.026	7572	3.67	**<0.01**
CtrlBuff	0.075	0.009	7572	8.24	0.64
2008	0.139	0.007	7572	19.62	**<0.01**
2009	0.044	0.007	7572	6.12	**<0.01**
ArtDefol x 2008	-0.098	0.011	7572	-8.27	**<0.01**
CtrlTrees x 2008	0.030	0.023	7572	1.39	**<0.01**
CtrlBuff x 2008	-0.039	0.009	7572	-4.19	0.34
ArtDefol x 2009	-0.138	0.015	7572	-8.96	**<0.01**
CtrlTrees x 2009	0.120	0.028	7572	4.32	**<0.01**
CtrlBuff x 2009	-0.068	0.009	7572	-7.06	0.56

Note: ArtDefol: artificial defoliation, CtrlBuff: control buffer, CtrlTrees: control trees, CtrlPlot: control plot. Reference level: Control plot and year 2007.

Table 4.4 Summary of linear mixed-model regression analysis of dead tree root collar diameter. Treatment and year, and the interaction between the two factors were considered as explanatory factors.

	Value	SE	DF	t-value	p-value
Intercept	1.042	0.047	718	21.83	**<0.01**
ArtDefol	-0.018	0.048	718	-0.38	0.70
CtrlBuff	-0.047	0.053	718	-0.89	0.37
2008	-0.021	0.055	718	-0.39	0.69
2009	0.056	0.051	718	1.11	0.26
ArtDefol x 2008	0.233	0.061	718	3.81	**<0.01**
CtrlBuff x 2008	0.090	0.073	718	1.24	0.22
ArtDefol x 2009	0.367	0.058	718	6.39	**<0.01**
CtrlBuff x 2009	0.011	0.07	718	0.15	0.87

Note : ArtDefol, artificial defoliation; CtrlBuff, control buffer; CtrlPlot, control plot. Reference level: Control plot and year 2007.

Figure 4.1 Plan of the experimental block: a defoliated plot (15mx15m, 225m^2) surrounded by a 5 m wide buffer (control buffer: 11x25m^2, 275m^2) and a separate control plot within the same stand (15mx15m, 225m^2). Manual defoliation was repeated over 3 consecutive years (2007 to 2009), except for 7-10% of trees, which are considered control trees within defoliation plot (triangular points). All stems were mapped and root collar diameters measured in 2007 before the first artificial defoliation (last two weeks of June). Annual mortality and diameter growth measurements were repeated in 2008, 2009 and 2010.

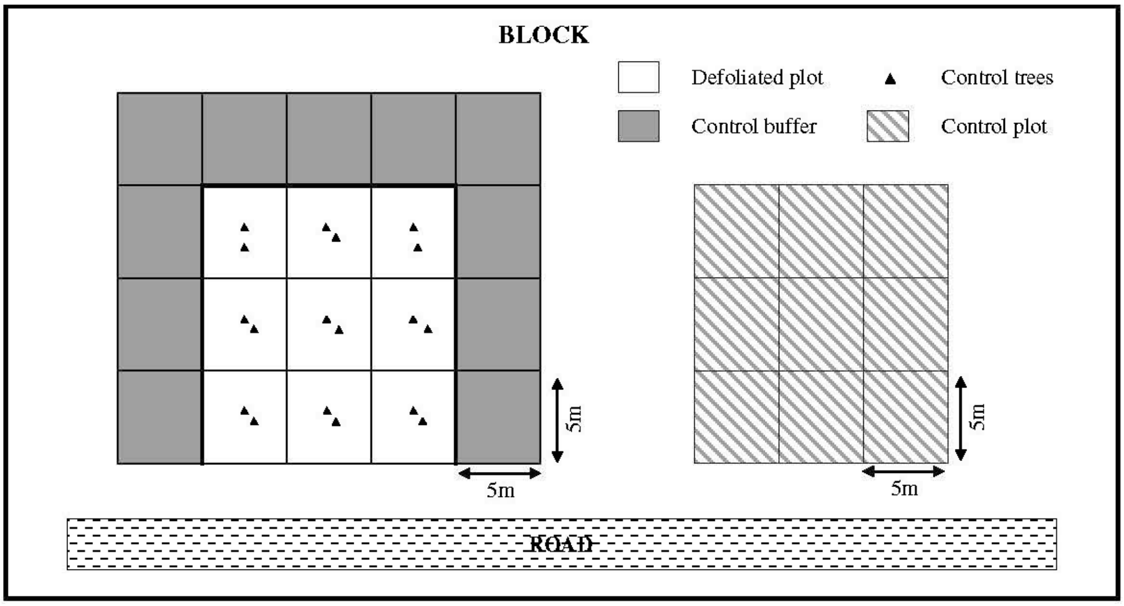
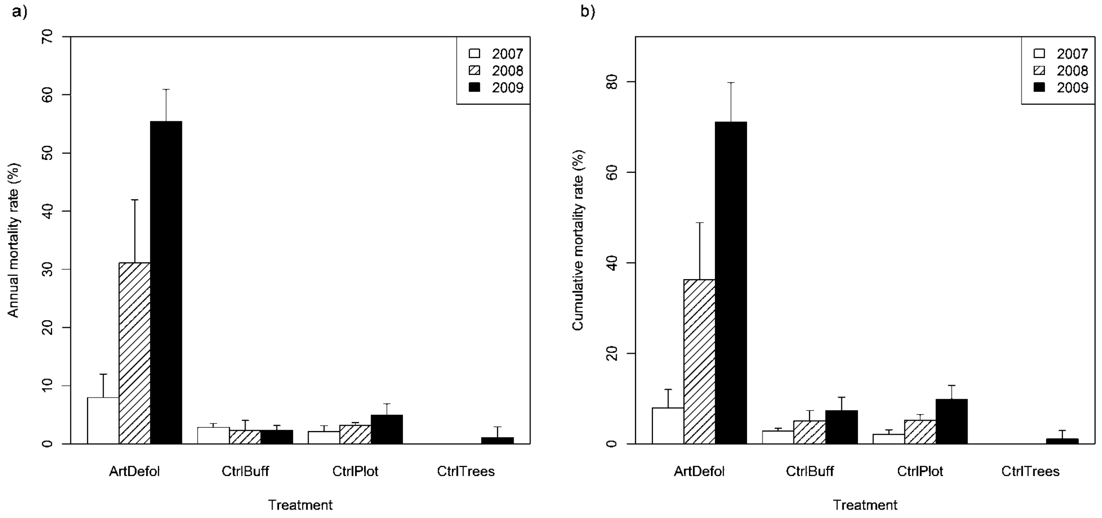
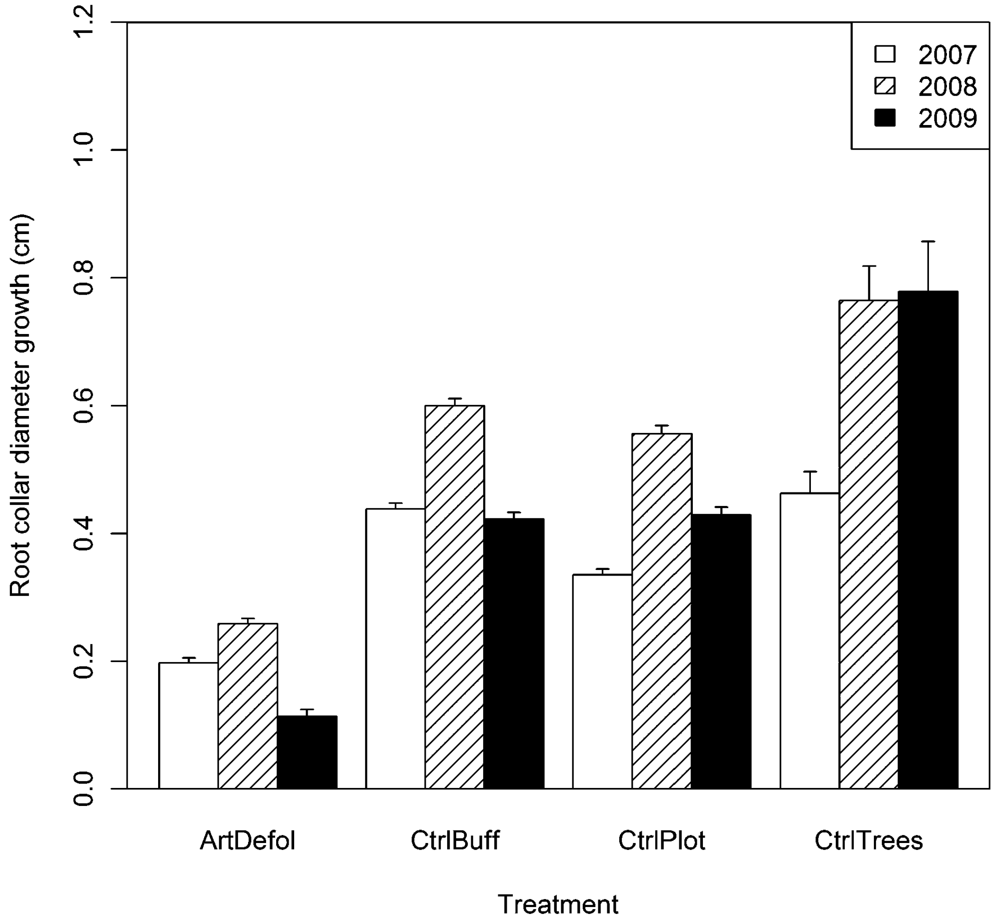


Figure 4.2 Log-transformed annual mortality rate (a) and cumulative mortality rate (b) (mean ± SE) of trembling aspen during 3 successive years of artificial defoliation (2007, 2008, 2009) in each of the four experimental treatments.



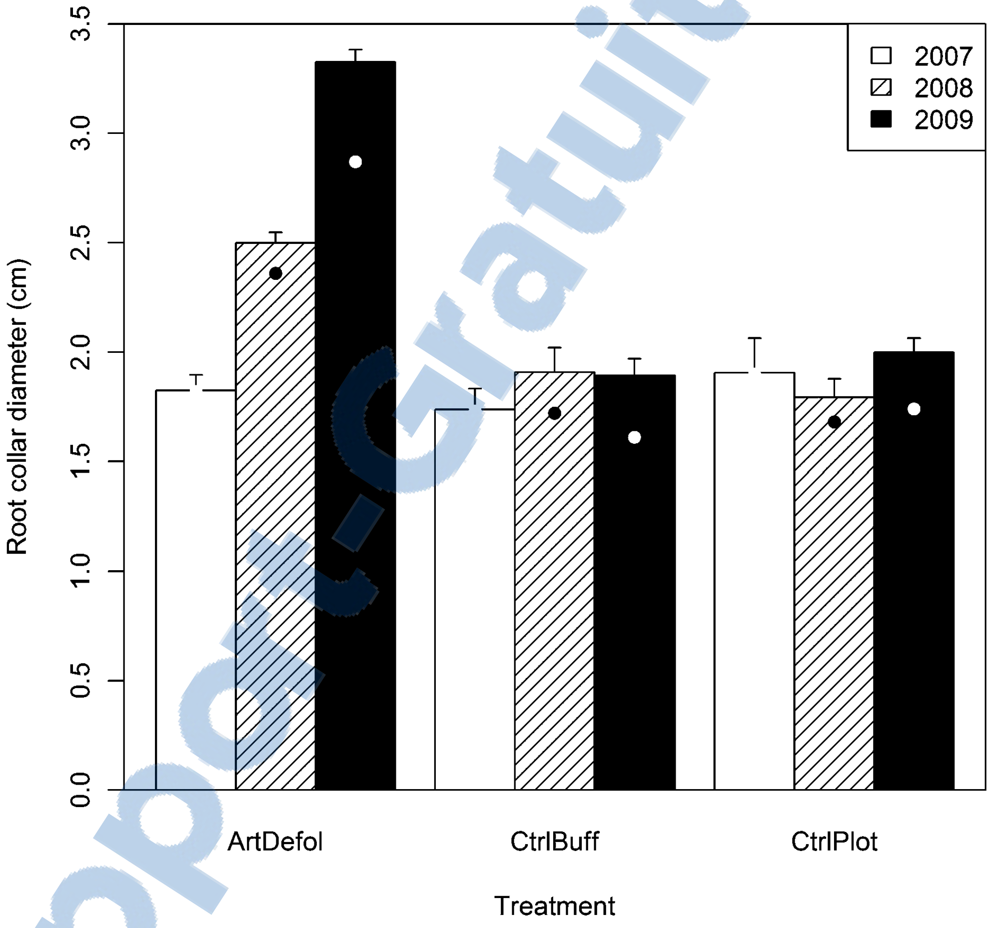
Note: ArtDefol, artificial defoliation; CtrlBuff, control buffer; CtrlPlot, control plot; CtrlTrees, control trees.

Figure 4.3 Trembling aspen root collar growth (mean ± SE) in 2007, 2008 and 2009 for all living trees in each of the four experimental treatments.



Note: ArtDefol, artificial defoliation; CtrlBuff, control buffer; CtrlPlot, control plot; CtrlTrees, control trees.

Figure 4.4 Root collar diameter (mean ± SE) of dead trees in 2007, 2008 and 2009 for each of the three experimental treatments. Dots (grey, black and white) represent the 2007 root collar diameter of trees that were dead in 2007, 2008 and 2009.



Note: ArtDefol, artificial defoliation; CtrlBuff, control buffer; CtrlPlot, control plot; CtrlTrees, control trees.

Figure 4.5 Example of trembling aspen distribution in artificially defoliated plot 1 (ArtDefol Plot1) (20 m x 25 m). Trees were categorised as dead in 2007 (open circles), 2008 (grey circles), 2009 (black circles), or alive in 2010 (open triangles). The undefoliated trees within the defoliation plot are marked by an x. Hatched lines indicate the buffer zone.

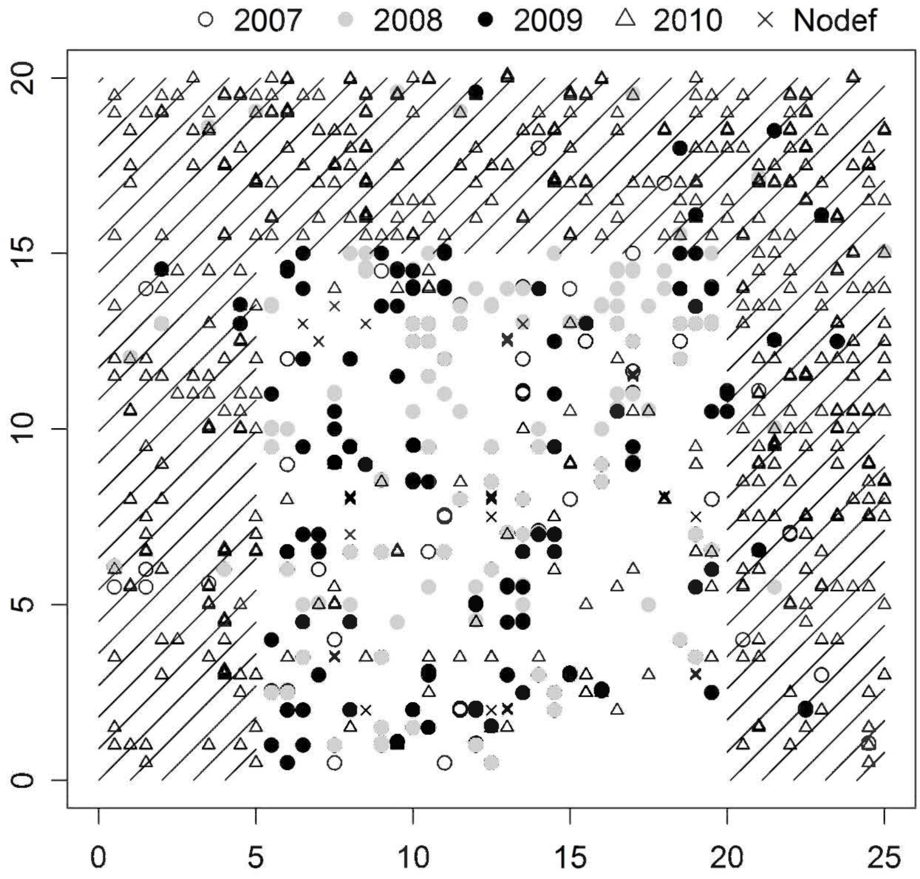


Figure 4.6 Linearised form $L_{12}(r)$ of the Ripley's $K_{12}(r)$ function (solid lines) illustrating the relationship between the spatial distribution of dead trees observed in the 'artificial defoliation' plots between 2007-2008, 2008-2009, and 2007-2009. Dashed lines are the upper and lower 99% confidence intervals (CI) based on Monte Carlo simulation (1000 simulations). $L_{12}(r)$ values above the CI suggest a clumped distribution whereas values below the CI a dispersed distribution. Values within the CI suggest randomness or no spatial pattern.

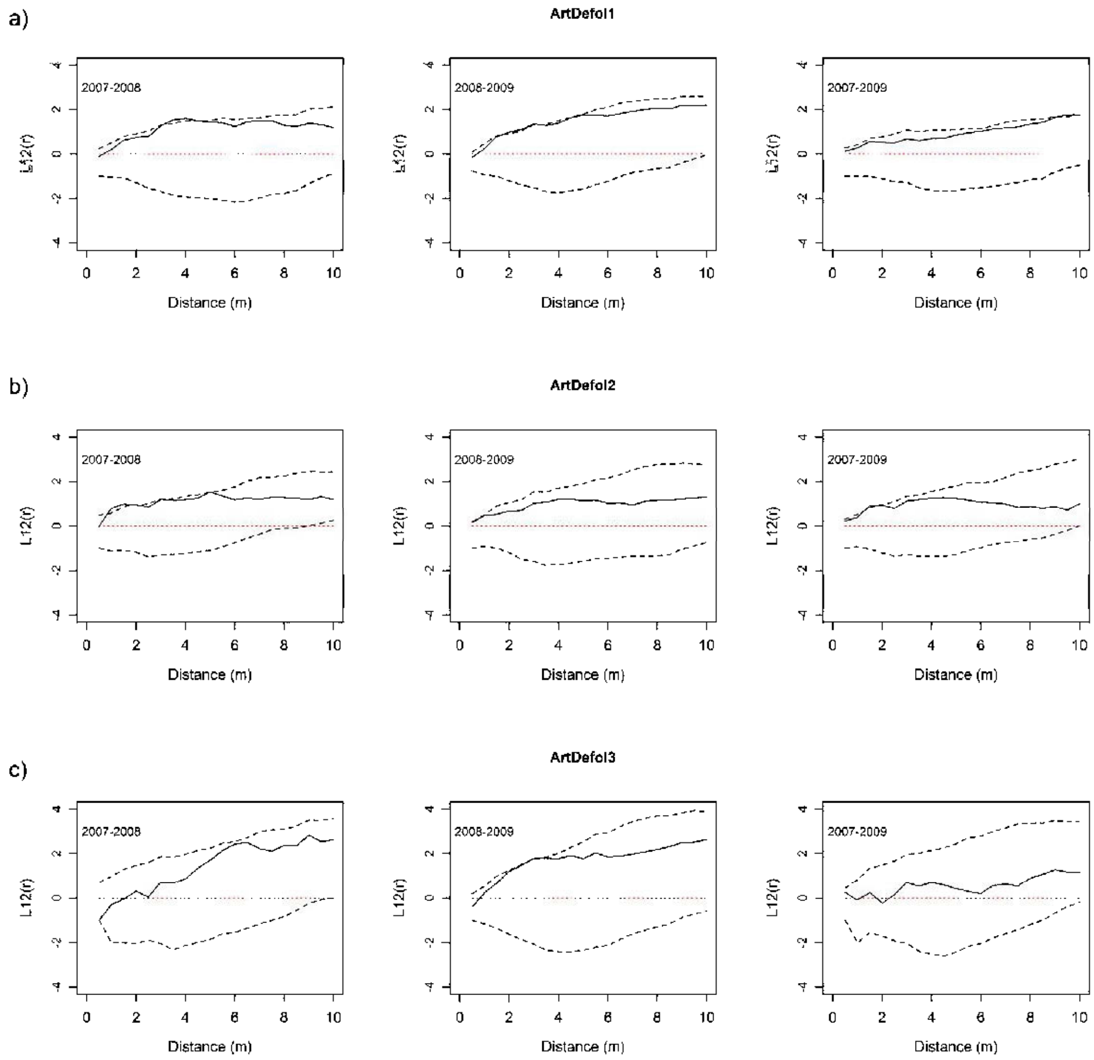


Figure 4.7 Appendix 1. Trembling aspen distribution in artificially defoliated plot 2 (ArtDefol Plot2) (20 m x 25 m). Trees were categorised as dead in 2007 (open circles), 2008 (grey circles), 2009 (black circles) or alive in 2010 (open triangles). The undefoliated trees within the defoliation plot are marked by an x. Hatched lines indicate the buffer zone.

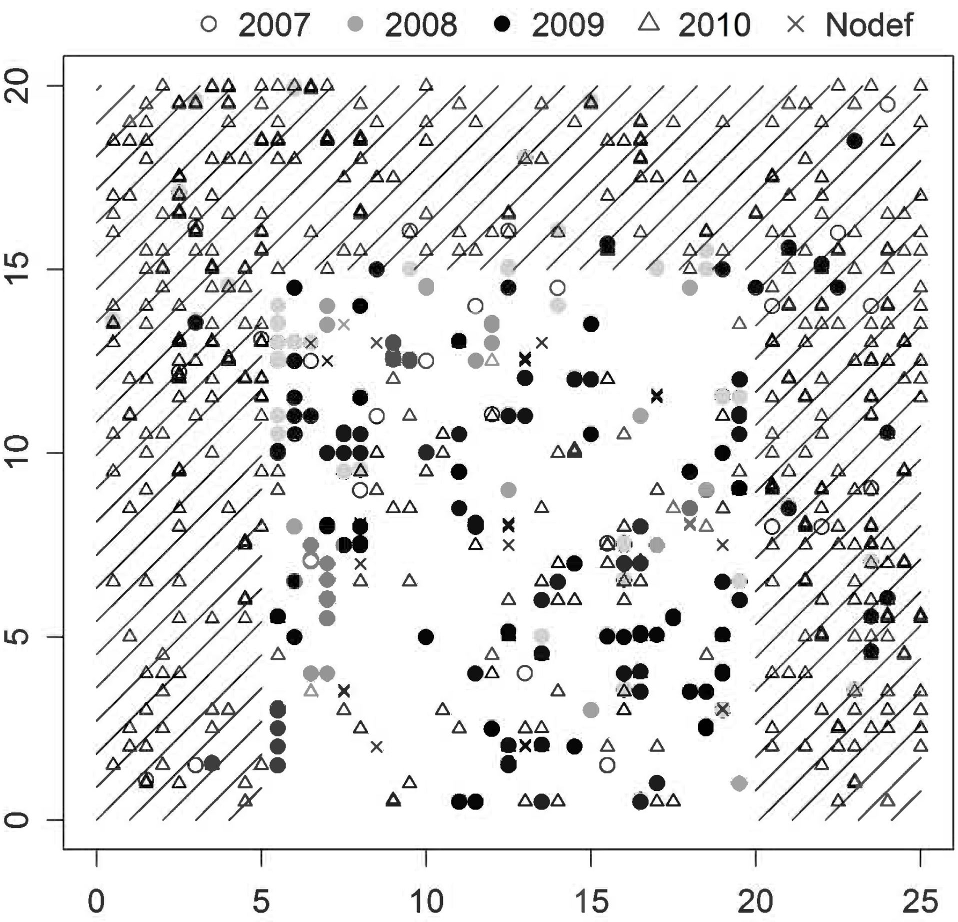
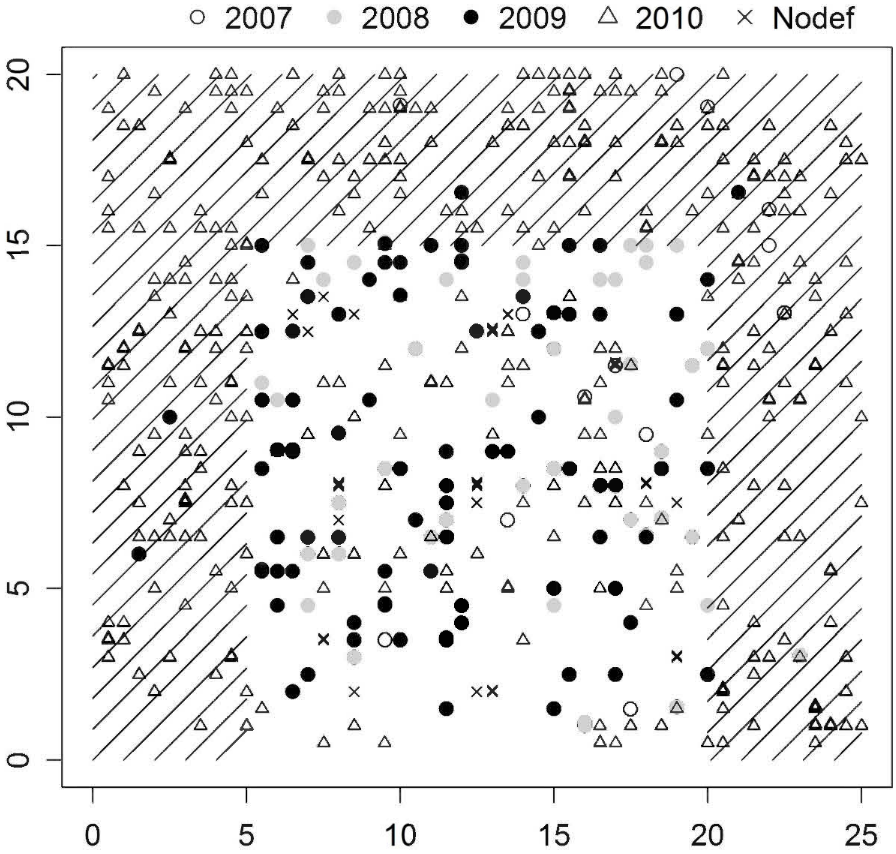


Figure 4.8 Appendix 2. Trembling aspen distribution in artificially defoliated plot 3 (ArtDefol Plot3) (20 m x 25 m). Trees were categorised as dead in 2007 (open circles), 2008 (grey circles), 2009 (black circles) or alive in 2010 (open triangles). The undefoliated trees within the defoliation plot are marked by an x. Hatched lines indicate the buffer zone.



CONCLUSION GÉNÉRALE

Au cours des dernières décennies, l'intérêt grandissant pour les effets des activités anthropiques passées et actuelles sur le fonctionnement des écosystèmes forestiers a conduit à un important enjeu d'acquisition de connaissances sur la dynamique de végétation des forêts naturelles. En effet, pour mieux appréhender et prévenir les risques liés à l'aménagement forestier en zone boréale, il est primordial de bien comprendre les régimes de perturbations naturelles qui régissent la dynamique de succession des peuplements forestiers. L'orientation vers de nouveaux modes d'exploitation forestière qui vise à réduire les écarts entre les paysages naturels et les paysages aménagés en s'inspirant des régimes de perturbations naturelles suscite d'autant plus d'intérêt pour la dynamique de succession naturelle que les effets de l'aménagement forestier ont déjà commencé à en altérer les patrons (Cyr *et al.* 2009). Dans cette thèse, je me suis intéressé aux effets de la perturbation par la livrée des forêts sur la mortalité des arbres en m'attachant plus spécifiquement à décrire les répercussions sur la dynamique forestière des peuplements feuillus et mixtes dominés par le peuplier faux-tremble de la forêt boréale méridionale de l'ouest du Québec. Bien que de nombreuses études aient déjà caractérisé la mortalité du peuplier faux-tremble suite à la défoliation par la livrée des forêts (Duncan et Hodson 1958; Churchill *et al.* 1964; Hogg *et al.* 2002a; Brandt *et al.* 2003; Man et Rice 2010), peu d'études ont cherché à discriminer les facteurs environnementaux associés aux patrons de mortalité que l'on observe à l'échelle d'un paysage perturbé par ce type d'épidémie. De la même façon, peu d'études ont décrit l'influence d'une épidémie de livrée des forêts sur les trajectoires successionnelles des peuplements feuillus et mixtes dominés par le peuplier faux-tremble (Man et Rice 2010) et aucune n'a cherché à caractériser les effets d'une telle perturbation sur la dynamique par trouées en forêt boréale (Kneeshaw et Bergeron 1998). Finalement, peu d'expérimentations ont testé les effets d'une défoliation artificielle sur le peuplier faux-tremble (Hogg *et al.* 2002b; Jones *et al.* 2004) et aucune n'a évalué les effets de la défoliation sur les patrons spatiaux et temporels de mortalité du peuplier faux-tremble. Dans cette conclusion, je présente les principaux résultats de chacun des quatre chapitres de cette thèse, et je discute de leurs implications écologiques dans un contexte de gestion écosystémique des peuplements de la forêt boréale méridionale de l'ouest du Québec dominés par le peuplier faux-tremble.

Les patrons de mortalité des espèces feuillues hôtes observés à l'échelle d'un paysage perturbé par la livrée des forêts (Chapitre I) ont permis de démontrer que certains peuplements forestiers étaient plus vulnérables aux épidémies que d'autres. En effet, tel qu'il est rapporté dans la littérature, la probabilité de mortalité des arbres hôtes a fortement augmenté après 2 à 3 années de défoliation par la livrée des forêts (Churchill *et al.* 1964; Candau *et al.* 2002; Man *et al.* 2008). L'abondance des espèces hôtes était aussi fortement associée aux patrons de mortalité, ce qui se manifestait par une plus grande probabilité de mortalité dans les peuplements purs et mixtes dominés par les essences feuillues. Contrairement à nos attentes, les vieux peuplements de 70 ans et plus, généralement perçus comme plus vulnérables, présentaient des probabilités de mortalité plus faibles que les peuplements d'âge moyen de 50 ans. Les résultats de ces travaux réalisés dans la forêt méridionale du nord-ouest du Québec suite à la dernière épidémie de livrée des forêts (1999-2002) ont permis de montrer que les peuplements à dominance feuillus de 50 ans qui avaient subi 2 à 3 années de défoliation modérée et sévère présentaient une plus grande probabilité de mortalité que tout autre type de peuplements. Bien que cette étude de cas ne permette pas de transposer les résultats à d'autres paysages forestiers tant les dynamiques de défoliation et de mortalité peuvent varier en fonction des attributs du paysage et du peuplement (Roland 1993; Cooke et Roland 2000; Frey *et al.* 2004; Charbonneau *et al.* 2012), elle pourrait aider à réduire les pertes de volumes ligneux associées aux épidémies de livrée des forêts en permettant de mieux cibler les peuplements à forte vulnérabilité potentielle et en facilitant la mise en place de plans de récupération prioritaire.

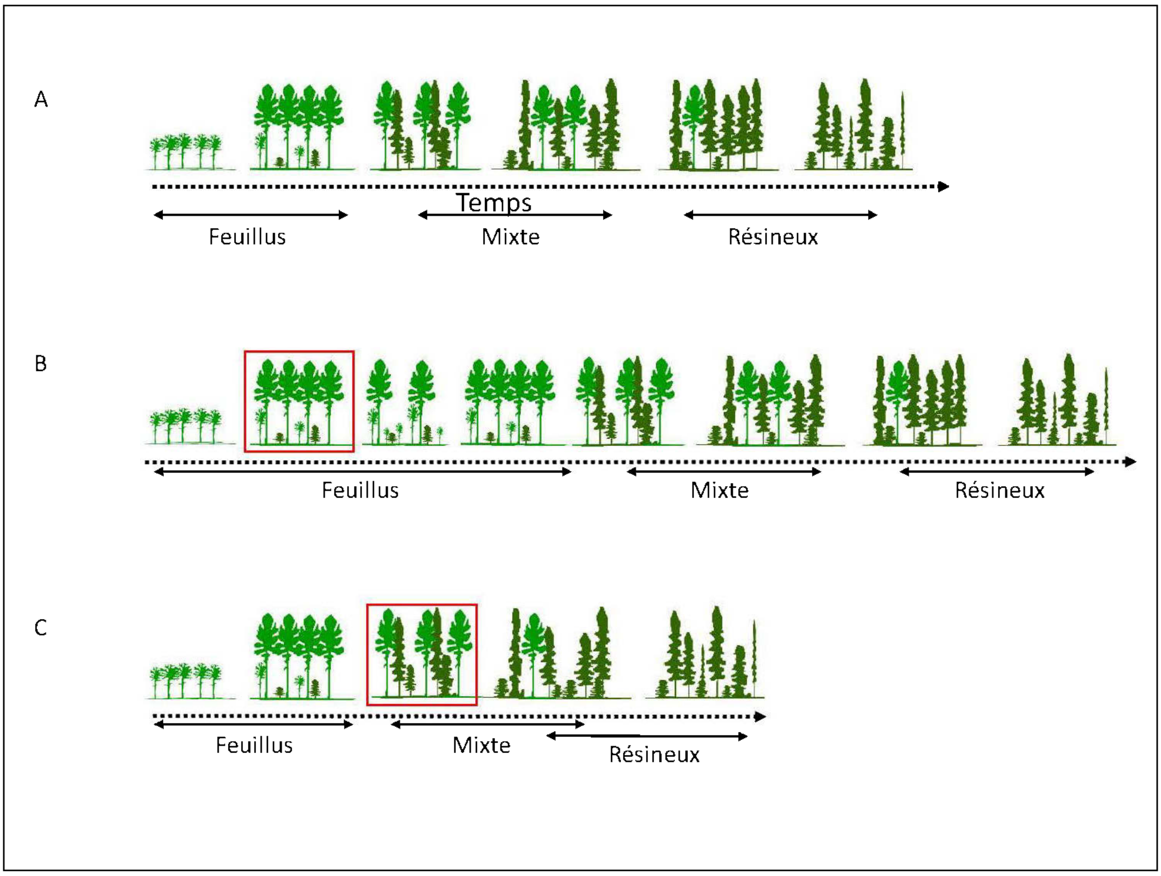
À l'échelle du peuplement (Chapitre II et III), la mortalité du peuplier faux-tremble résultant de la défoliation par la livrée des forêts génère des trouées qui modifient les conditions environnementales (lumière, température, humidité, espace) en sous couvert forestier (Kneeshaw et Bergeron 1998; Messier *et al.* 1998; Messier *et al.* 1999; McCarthy 2001). Les patrons de formation des trouées (e.g., le taux d'occupation, la taille) sont généralement fonction du synchronisme et de l'ampleur de la mortalité (Kneeshaw et Bergeron 1998). Au cours de mes travaux (chapitres II et III), j'ai pu observer que l'augmentation du taux d'ouverture du couvert forestier des peuplements feuillus et mixtes approchait 50% après 3 années de défoliation, alors qu'ils étaient proches de 10% dans les peuplements témoins et légèrement défoliés. L'utilisation de photographies aériennes (chapitre III) a permis de vérifier que les taux d'ouverture de la canopée ou taux d'occupation des trouées des peuplements échantillonnés étaient bien inférieurs en 1994 et 1995 à ceux observés après épidémie et se situaient dans la gamme de la variabilité naturelle (Kneeshaw et Bergeron 1998; Hill *et al.* 2005). Cette réponse du taux d'ouverture du couvert forestier à l'intensité de la défoliation était directement liée à l'altération des patrons de taille des trouées qui se manifestait par une augmentation de la taille moyenne des trouées et de la proportion des trouées de grande taille. La taille moyenne des trouées après 3 années de défoliation était plus importante dans les peuplements feuillus ($87{,}5\pm5{,}7m^2$) que dans les peuplements mixtes ($52{,}3\pm6{,}1m^2$), probablement due à la présence de conifères en canopée qui limitaient l'expansion des trouées en peuplements mixtes. Les faibles proportions d'arbres déracinés et de résineux morts ont permis de confirmer que la mortalité observée résultait bien de l'effet de la défoliation et non d'un autre type de perturbation, tel que le vent (Ruel 2000). Finalement, l'augmentation du diamètre des arbres morts avec l'intensité de la défoliation a permis de corroborer les résultats de Churchill et al (1964) qui rapportaient une plus grande proportion d'arbres dominants et co-dominants morts dans les peuplements défoliées plusieurs années consécutives. Les effets de la défoliation par la livrée des forêts sur la mortalité des arbres et la réponse du couvert forestier démontrent clairement que la livrée des forêts constitue un important agent de formation des trouées capable d'entrainer de profondes modifications de la structure des peuplements feuillus et mixtes dominés par le peuplier faux-tremble. Ces patrons montrent aussi que les épidémies de livrée des forêts tendent à générer des structures équiennes dans les peuplements faiblement affectés et une large gamme de structures inéquiennes dans les peuplements fortement défoliés.

Les suivis qualitatifs et quantitatifs de la régénération sont indispensables à la compréhension des trajectoires de succession des peuplements forestiers. Dans le cadre de mes travaux, j'ai pu observer que la variabilité dans les patrons de régénération des peuplements affectés par la livrée des forêts était fortement reliée à l'intensité de la défoliation. En effet, les peuplements feuillus peu affectés par la livrée des forêts avaient généralement peu de régénération en sous couvert forestier, alors que les peuplements défoliés plusieurs années consécutives présentaient de fortes densités de drageons de peuplier faux-tremble. Cette différence notable a été attribuée à l'effet de l'ouverture de la canopée et à la formation des trouées (principalement les trouées de grandes tailles) qui ont amélioré les conditions de lumière et de température au niveau du sol, créant ainsi des conditions favorables au drageonnement du peuplier faux-tremble (Frey *et al.* 2003). De plus, la défoliation et la mortalité du peuplier faux-tremble ont causé la perte de la dominance apicale qui a aussi favorisé le drageonnement chez cette espèce (Farmer 1962). En effet, la perte de dominance apicale entraîne une altération des mécanismes hormonaux à l'échelle de l'arbre qui se traduit par un déséquilibre entre la quantité d'auxine produite au niveau foliaire qui inhibe le drageonnement (Schier *et al.* 1985) et la quantité de cytokinine produite au niveau racinaire qui favorise le drageonnement (Hungerford 1988). La mortalité synchrone des arbres dans les trouées de grandes tailles a contribué à augmenter la température du sol qui favorise la dégradation de l'auxine et participe à réduire le rapport auxine/cytokinine et à améliorer le drageonnement (Schier *et al.* 1985). Ces patrons de régénération observés dans les peuplements feuillus révèlent que les épidémies de livrée des forêts de faible intensité n'affectent que très légèrement les patrons de régénération, alors que les épidémies de forte intensité entraînent le recrutement d'une nouvelle cohorte de peuplier faux-tremble.

Dans les peuplements mixtes, la strate en régénération était dominée par le sapin baumier alors que le peuplier faux-tremble n'était présent qu'en faible densité dans tous les types de trouées et tous les types de peuplements qu'ils aient été légèrement ou sévèrement affectés par la livrée des forêts. Les résultats montrent que la densité de sapin baumier en régénération a augmenté avec l'intensité de la défoliation, mais elle n'a pas augmenté avec la taille des trouées. Ce patron de régénération peut s'expliquer par la distribution des sapins semenciers et la distribution des trouées. En effet, les trouées de grandes tailles se sont formées dans des zones dominées par le peuplier faux-tremble et où le sapin baumier était absent au moment de l'épidémie. Les sapins dominants et semenciers étaient donc distribués en périphérie des grandes trouées, soit sous couvert forestier et à proximité des petites trouées. Ces arbres ont bénéficié de l'effet de l'ouverture de la canopée et de l'amélioration des conditions de lumière qui améliorent la production de graines (Greene *et al.* 2002). L'importance de la taille des graines du sapin baumier et leur faible capacité de dispersion (Asselin *et al.* 2001) ont contribué à un ensemencement plus important sous couvert forestier et dans les trouées de petite taille plutôt que dans les grandes trouées. Les semis de sapin baumier présents en sous couvert forestier au moment de l'épidémie ont profité de l'amélioration des conditions de lumière. Les patrons de croissance ont clairement montré une augmentation de la croissance apicale des sapins avec l'augmentation de l'intensité de défoliation, particulièrement pour les semis (<0,5m) et les gaulis (0,5-2m).

Du point de vue de la succession forestière, la dynamique naturelle en forêt boréale méridionale (Figure 1, A) est généralement initiée par des peuplements monospécifiques dominés par le peuplier faux-tremble qui s'installent après feu (Bergeron 2000). Avec le temps, l'établissement d'essences résineuses, telle que le sapin baumier, entraîne les peuplements feuillus vers des stades transitoires de mixité. En absence de perturbation, ces peuplements mixtes évoluent vers des stades résineux dominés par le sapin baumier, puis ensuite dominés par des espèces plus longévives, telles que l'épinette blanche (*Picea glauca* (Moench) Voss.), l'épinette noire (*Picea mariana* (Mill) B.S.P.) et le thuya occidental (*Thuya occidentalis* L.). Touefois, le peuplier faux-tremble peut rester présent en faible proportion dans ces peuplements résineux de fin de succession grâce à la formation de trouées de grandes tailles (Kneeshaw et Bergeron 1998). Les patrons de régénération observés suite aux épidémies de livrée des forêts de fortes intensités dans les peuplements de début de succession suggèrent que l'installation d'une nouvelle cohorte de peupliers devrait permettre le maintien de la composition initiale et le rétablissement du couvert forestier des peuplements purs de peupliers faux-tremble (Man et Rice 2010; Reinikainen *et al.* 2012). Les épidémies de livrée des forêts pourraient donc permettre un allongement de la durée de la phase feuillue et ainsi favoriser le rajeunissement du couvert forestier (Figure 1, B). À l'inverse, les patrons de régénération observés en peuplements mixtes suggèrent que les effets des épidémies de livrée des forêts devraient contribuer à accélérer la succession forestière et la conversion du couvert vers des stades dominés par les essences résineuses (Man et Rice 2010; Reinikainen *et al.* 2012) (Figure 1, C). Toutefois, il est important de se rappeler que les caractéristiques du peuplement avant la perturbation, telles que la composition, l'état de la banque de graines, la situation géographique, la vigueur et l'état sanitaire vont conditionner la dynamique de succession post-perturbation, et que l'intensité de la perturbation va influencer la trajectoire de succession.

Figure 1: Schéma de la dynamique naturelle de succession forestière de la sapinière à bouleau blanc de l'ouest du Québec (A), et répercussions des effets d'une épidémie de livrée des forêts de forte intensité (carré rouge) sur la dynamique des peuplements feuillus (B) et mixtes (C) dominés par le peuplier faux-tremble.



Des travaux menés en parallèle de mon doctorat m’ont permis d’étudier des peuplements qui illustrent une dynamique de succession atypique. En effet, ce projet qui ne figure pas dans ma thèse a été réalisé avec les industries Norbord (qui œuvrent principalement dans la production de panneaux de fibres orientées) et visait à tester l’efficacité de différents traitements sylvicoles sur la remise en production de peupleraies dégradées. Ce projet a permis de constater que l’état de dégradation des peuplements dominés par le tremble jumelé à la défoliation par la livrée des forêts pouvait conduire à un blocage de la succession forestière dans certains sites. En effet, bien que les effets de la végétation compétitrice sur la dynamique de succession n’aient pas été étudiés dans mes travaux de doctorat, ils ont été contrôlés par la sélection de sites homogènes en termes de densité, recouvrement et hauteur moyenne de la végétation en sous couvert forestier. Toutefois, certaines tremblaies dégradées (avec de forts taux d’ouverture du couvert) situées sur des sols mal drainés présentent des espèces arbustives telles que l’aulne rugueux qui peut dominer la strate en sous couvert forestier. La présence d’une telle végétation compétitrice contribue à retarder la succession forestière en réduisant la quantité de lumière et le recrutement d’espèces arborescentes (Kneeshaw et Prévost 2007). De plus, un lent processus de dépérissement et de mortalité du peuplier faux-tremble dominant la canopée pourrait limiter le drageonnement et bloquer l’établissement d’espèces forestières arborescentes. Finalement, certaines observations ont conduit à émettre l’hypothèse que la diminution de l’évapotranspiration causée par la combinaison de la défoliation et de la mortalité du peuplier faux-tremble pourrait entraîner une remontée de la nappe phréatique dans les sites moins bien drainés. Ce phénomène pourrait subséquemment engendrer l’asphyxie racinaire des arbres dominants, aggravant ainsi la mortalité du peuplier faux-tremble et annihilant la capacité de drageonnement. Ces observations et hypothèses sont la démonstration que certains aspects de la mortalité du peuplier faux-tremble et de la dynamique naturelle de succession des tremblaies sont encore mal connus et restent à être documentés.

Pour certains, l'absence d'analyse dendrochronologique des arbres formant les trouées dans les peuplements étudiés dans cette thèse pourrait représenter une faiblesse puisqu'elle aurait pu permettre de dater la mortalité des arbres et de la corroborer aux années de défoliation par la livrée des forêts. Toutefois, suffisamment de preuves indirectes sont apportées pour affirmer que la défoliation par la livrée des forêts constitue à elle seule un facteur responsable de la mortalité du peuplier faux-tremble. L'expérimentation de défoliation artificielle réalisée en conditions contrôlées dans de jeunes peuplements purs et sains de peuplier faux-tremble (Chapitre IV) conforte d'ailleurs cette idée. Cette expérimentation a clairement montré qu'en absence de facteurs prédisposant et contribuant (Frey *et al.* 2004), 8 et 72% des arbres sont morts après 1 et 3 années de défoliation respectivement, alors que seulement 3 et 10% de mortalité naturelle a été observé après 1 et 3 années d'expérimentation dans les sites témoins. Bien que ces peuplements soient généralement peu ou moins vulnérables à la livrée des forêts que les peuplements matures (chapitre I), une défoliation totale répétée 3 années successives a pourtant été suffisante pour entraîner d'importants taux de mortalité. Cette expérimentation a aussi permis de vérifier plusieurs patrons observés dans les peuplements naturels suite à une épidémie de livrée des forêts. La mortalité pouvait survenir dès la première année de défoliation et augmentait significativement après les deuxième et troisième années de défoliation par rapport aux peuplements témoins (chapitres II et III). Cette expérimentation a aussi confirmé l'augmentation du diamètre des arbres morts avec l'intensité de défoliation observée dans le chapitre II et a permis de corroborer les résultats de Churchill et al (1964) sur la mortalité des individus dominants. Finalement, les tendances d'agrégation spatiale de la mortalité observées dans cette étude rappellent à une moindre échelle les patrons de mortalité décrits lors de la formation des trouées en peuplements naturels (chapitres II et III).

À la lumière des résultats de cette thèse, il apparaît pertinent d'émettre des recommandations quand à l'aménagement forestier des peuplements dominés par le peuplier faux-tremble. En effet, depuis le début des années 1990, de nouvelles approches intégrées ont été proposées pour améliorer l'aménagement des forêts boréales mixtes (Hunter 1993; Lieffers et Beck 1994; MacDonald 1995; Bergeron et Harvey 1997; Coates et Burton 1997; Harvey *et al.* 2002; Gauthier *et al.* 2008). Basées sur les patrons régionaux des perturbations naturelles, les classifications des écosystèmes forestiers et la dynamique des peuplements forestiers, ces approches visent, entre autre, au maintien de la diversité de structure et de composition à l'échelle du peuplement et du paysage. En promouvant des modalités d'aménagement qui s'inspirent des perturbations et des processus naturels, ces approches écosystémiques ont pour objet de réduire les écarts entre les forêts aménagées et les forêts naturelles (Chen et Popadiouk 2002). La coupe totale est le traitement inspiré des feux de forêt le plus communément utilisé en forêt boréale mixte, alors que les coupes partielles sont généralement employées pour imiter les effets des épidémies d'insectes et des chablis. Dans cette section, je m'attarde à comparer les connaissances sur les effets des épidémies de livrée des forêts ainsi que des coupes partielles sur la structure et la composition des peuplements feuillus et mixtes de la forêt boréale méridionale. Je discute ensuite de modalités de coupes susceptibles d'atteindre les cibles d'aménagement recherchées à l'échelle du peuplement.

Les résultats de différentes expérimentations de coupes partielles (Prevost et Pothier 2003; Brais *et al.* 2004; MacDonald *et al.* 2004; Harvey et Brais 2007; Man *et al.* 2008; Prevost *et al.* 2010) se comparent assez bien aux effets des épidémies de livrées rapportés dans cette thèse (voir aussi Man et Rice 2010). En effet, les coupes partielles qui prélèvent de 30 à 70% de la surface terrière reflètent généralement la gamme de variabilité des taux de mortalité observés après épidémie de livrée des forêts (23 à 61%, Man et Rice 2010). De la même façon, les taux d'ouverture du couvert qui varient de 15 à 30% après 30 à 40% de prélèvement de la surface terrière correspondent à la variabilité observée après une année de défoliation (12 à 32% d'ouverture, chapitre II et III). Après 50% et plus de prélèvement de la surface terrière, les taux d'ouverture du couvert varient de 25 à 50% et concordent avec la variabilité naturelle rapportée après 3 années de défoliation modérées et sévères par la livrée des forêts (28 à 48%, chapitre II et III). Ces données montrent que les taux de prélèvements peuvent être ajustés pour imiter l'effet de l'intensité de la défoliation par la livrée des forêts sur la perte de volume de ligneux et les taux d'ouverture de la canopée. Les travaux de Gendreau-Berthiaume *et al.* (2012) ont aussi montré que certains types de coupes partielles permettaient de reproduire une diversité structurelle (distribution diamétrale des tiges résiduelles vivantes et volume des débris ligneux au sol), une composition des espèces en régénération, et une croissance des arbres résiduels et du sapin baumier en régénération comparable à celles observées dans les peuplements soumis à un régime de perturbation naturelle. Toutefois, les coupes partielles ne permettent pas de maintenir une quantité équivalente de chicots à celle observée en peuplements naturels (Harvey et Brais 2007) ou après épidémies de livrées des forêts (chapitre II voir aussi Gendreau-Berthiaume *et al.* 2012). Un autre défi de taille de l'aménagement écosystémique réside dans la gestion des effets du prélèvement sur les conditions de lumière et la réponse de la régénération. En modélisant les effets de l'intensité du prélèvement et de la distribution spatiale des coupes (et des arbres résiduels) sur la quantité de lumière sous le couvert forestier, Beaudet *et al.* (2011) ont montré que l'augmentation du taux de prélèvement avait plus d'impacts sur la quantité de lumière dans les coupes par trouées que dans les coupes uniformes et par bandes. Ainsi, les scénarios montraient qu'un prélèvement de 60% de la surface terrière était suffisant pour favoriser le drageonnement du peuplier faux-tremble, alors qu'un prélèvement de seulement 30% générait des conditions de lumière intermédiaires plus propices aux essences tolérantes à l'ombre.

Dans les peuplements feuillus monospécifiques à structure équienne, le traitement généralement prescrit actuellement est la coupe totale. À l'exception des accidents de régénération, la coupe totale est généralement un bon traitement qui maximise le prélèvement en favorisant la réponse de drageonnement du peuplier faux-tremble (Schier *et al.* 1985; Brais *et al.* 2004) et qui optimise le rétablissement de la structure équienne de la canopée. Cependant, les résultats de cette thèse suggèrent qu'une proportion des peuplements dominés par le peuplier faux-tremble devrait être aménagée par coupes partielles afin de reproduire des structures de peuplements feuillus sévèrement affectés par la livrée des forêts (soit environ 7 à 10% des peuplements feuillus de l'aire d'étude). Parmi la gamme de coupes partielles qui existe, la coupe par trouées semble tout à fait appropriée pour recréer les patrons de mortalité observés dans les peuplements perturbés. Les trouées d'une surface minimale de 1000 m^2 (comprenant un minimum de 40 à 50 arbres) pourraient occuper de 50 à 60% du couvert, offrant ainsi suffisamment de ressource lumineuse pour favoriser le recrutement d'une nouvelle cohorte de peuplier faux-tremble (Beaudet *et al.* 2011). Afin d'améliorer l'effet de la température sur la réponse de drageonnement et la croissance des drageons (Farmer 1963) et de réduire l'effet de la dominance apicale des peupliers faux-tremble situés en périphérie des trouées (Farmer 1962), un prélèvement variable du couvert résiduels (qui ne devrait pas excéder 30% des arbres des inter-trouées) pourrait être envisagé. L'augmentation du taux d'ouverture du couvert de 50% après épidémie à 60-70% après récolte par trouées devrait permettre d'optimiser les chances de remise en production des peuplements dominées le peuplier faux-tremble (drageonnement et survie des drageons) et de maximiser la récolte de bois tout en diminuant les différences de structure et de composition entre les peuplements défoliés et aménagés. Les arbres résiduels laissés sur pieds devraient présenter une diversité diamétrale représentative du peuplement et pourraient ainsi permettre d'assurer une connectivité du couvert forestier et de fournir des arbres de gros diamètre nécessaire au maintien de la biodiversité des réseaux d'excavateurs et d'utilisateurs de cavités (Gasse 2007; Cadieux 2011). De la même façon, ce mode d'aménagement par coupes partielles par trouées devrait laisser sur pieds un maximum d'arbres morts et de chicots qui sont une empreinte caractéristique des épidémies de livrée des forêts (chapitre II) nécessaire au réseau d'espèces cavicoles (Cadieux 2011).

Dans le cas des peuplements mixtes, les coupes partielles ont été généralement proposées afin de limiter la progression des espèces feuillues après coupes totales et d'améliorer la croissance et le recrutement des espèces résineuses en maintenant les principales structures et fonctions des écosystèmes non aménagés (Lieffers et Beck 1994; Lieffers *et al.* 1996; Bergeron et Harvey 1997; Harvey *et al.* 2002). Tout comme dans les peuplements feuillus, la coupe partielle par trouées pourrait s'avérer être le traitement adéquat pour simuler les effets des épidémies de livrée des forêts en peuplements mixtes. Toutefois, pour favoriser la régénération résineuse préétablie, ce traitement devrait maximiser la protection de cette dernière. Cette modalité d'aménagement pourrait concerner une partie du territoire correspondant à la proportion de forêts mixtes sévèrement affectées par la livrée des forêts et présentant de la mortalité (soit 4 à 5 % sur notre territoire d'étude). Les trouées de 500 m^2 et moins (soit de 20 à 25 arbres) pourraient occuper de 30 à 40% du couvert. Les taux de prélèvement en peuplier faux-tremble pourraient être ajustés en fonction de la proportion du couvert et du sous couvert occupé par les essences résineuses et selon les objectifs de maintien ou de changement de la composition. Le prélèvement du peuplier faux-tremble par la création de trouées de moyenne dimension devrait améliorer les conditions de lumière et favoriser la croissance des résineux présents en sous couvert, mais il ne devrait pas être suffisant pour encourager la réponse de drageonnement du peuplier faux-tremble (Beaudet *et al.* 2011). Ces prélèvements par trouées devraient aussi se concentrer sur le dégagement des résineux dominants afin d'améliorer les chances d'ensemencement, d'installation et de survie des semis de résineux. En plus d'accélérer la conversion du couvert en hâtant l'exclusion du peuplier faux-tremble et en améliorant le recrutement et la croissance des résineux, la coupe par trouées devrait permettre le maintien de la composition mixte en conservant une certaine proportion de peuplier faux-tremble dans partie non aménagée du peuplement. Finalement, ces coupes partielles devraient contribuer au maintien d'une proportion d'arbres de gros diamètre vivants et morts et ainsi que de chicots qui sont importants pour la biodiversité (Drapeau *et al.* 2009).

Finalement, un des principaux défis de l'aménagement forestier écosystémique réside dans le déploiement des interventions dans le temps. En effet, compte tenu que les épidémies de livrée des forêts ont une récurrence décennale, il apparait important de déterminer comment planifier les interventions de récolte dans le temps afin d'imiter les effets de la livrée des forêts à l'échelle du paysage. Bien que cette thèse ne se soit intéressée à répondre à un tel objectif, les données qu'elle présente combinées aux données de travaux préliminaires peuvent toutefois apporter des éléments de réponse. Sur la base des données de Cooke et Lorenzetti (2006, issues des Relevés des Insectes et Maladies des Arbres), il faut remonter dans les années 1950 pour observer une épidémie comparable à celle observée entre 1998 et 2003 (en termes de proportion du paysage affectée pendant 3 années de défoliation). Par conséquent, avec un intervalle de retour de 50 ans (pour une épidémie de 3 années de défoliations sévères susceptible d'entrainer des taux de mortalité significatifs, chapitres I à IV), il faudrait planifier une récolte par coupes partielles d'environ 0,2% des peuplements feuillus et 0,1% des peuplements mixtes par année pour atteindre 10 % de forêts feuillus et 5 % de forêts mixtes aménagées sur une période de 50 ans correspondant aux proportions de peuplements présentant de la mortalité suite à la dernière épidémie de livrées des forêts (le reste des peuplements étant conventionnellement aménagés par coupes totales ou coupes avec protection de la régénération et des sols pour imiter l'effet des feux de forêts). Ces chiffres sont d'ordre indicatif et ne constituent en rien les résultats d'analyses approfondies mais ils apportent une dimension temporelle au déploiement opérationnel des coupes visant à imiter les effets des épidémies de livrée des forêts. Finalement, compte tenu de la variabilité dans la sévérité et la durée des épidémies de livrée des forêts, il sera important de suivre l'évolution des futurs cycles épidémiques afin d'adapter les calculs d'intervalle de retour et d'améliorer la planification des récoltes.

Pour conclure, bien que les traitements de coupes partielles proposés précédemment puissent paraître acceptables pour imiter les effets des épidémies de livrées des forêts et recréer une diversité de structure et de composition des peuplements à l'intérieur de la gamme de la variabilité naturelle, la reproduction de certains attributs et processus resteront des défis d'envergure pour les aménagistes. En effet, bien que les coupes partielles réduisent les écarts entre les peuplements naturels et les peuplements aménagés par coupes totales, de nombreuses études rapportent différents niveaux de changements à courts termes dans le cycle des nutriments (Brais *et al.* 2004) et entre les communautés d'oiseaux et de petits mammifères (Steventon *et al.* 1998), d'arthropodes (Work *et al.* 2004; Schowalter *et al.* 2005), d'espèces de sous-bois (Haeussler *et al.* 2007; Fenton *et al.* 2008), de bryophytes (Fenton et Bergeron 2007), et de lichens (Boudreault *et al.* 2003). La raréfaction du bois mort sur pied et du bois mort de gros diamètre au sol constitue aussi un important enjeu écologique, qui selon Harvey et Brais (2007) devrait faire l'objet de prescription sylvicoles spécifiques. Actuellement, aucune donnée concernant les effets des épidémies de livrées des forêts sur de tels attributs des peuplements forestiers n'est disponible. Des études à long terme devront améliorer les connaissances des effets des épidémies de livrées des forêts et des coupes partielles sur la dynamique des peuplements feuillus et mixtes dominés par le peuplier faux-tremble. Ces études devront vérifier si les tendances observées à court terme se maintiennent et si les trajectoires de succession des peuplements aménagés convergent avec les trajectoires des peuplements soumis aux perturbations naturelles.

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