Dynamique du chablis en forêt boréale irrégulière et aménagement écosystémique

Thèse

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Résumé

La mise en place d'un aménagement forestier écosystémique passe par une meilleure connaissance des régimes de perturbations naturelles. En forêt boréale canadienne, le feu est la perturbation naturelle la plus été étudiée. Cependant, dans les régions où le cycle de feu est long, d'autres perturbations, comme le chablis, sont importantes. La description du régime de chablis dans la forêt boréale de l'est du Québec a été effectuée en tenant compte de ses caractéristiques intrinsèques, temporelles et spatiales, ainsi que ses conséquences sur l'écosystème forestier. D'abord, les caractéristiques de station et géoclimatiques influençant la susceptibilité d'un peuplement au chablis à l'échelle du paysage ont été étudiées. La base de données SIFORT a été utilisée, permettant une profondeur temporelle d'environ 30 ans. Deuxièmement, les caractéristiques spatiales du chablis et des coupes ont été analysées à l'échelle du paysage et de la perturbation, dans trois zones de la pessière de 5000 ha. Finalement, à l'échelle du peuplement, les principaux attributs clés présents en pessière suite au chablis ont été recensés et comparés à ceux retrouvés après coupe de récupération. Ces trois approches complémentaires ont permis de dresser un portrait du chablis en forêt boréale irrégulière. Les variables ayant le meilleur pouvoir prédictif de la susceptibilité au chablis sont le topex, l'épaisseur du dépôt et la pente. Les chablis sont surtout partiels et couvrent 0.23% du territoire annuellement. Les chablis partiels présentent une variété de tailles plus importante que les chablis totaux, qui eux, sont plus petits. Les chablis partiels possèdent, en moyenne, plus de 60% de leur superficie couverte par des arbres vivants. Les coupes de récupération modifient les attributs post-chablis. La quantité de bois mort est réduite et les stades de dégradation ne sont pas tous représentés. Les lits de germination et la présence de bryophytes sont aussi affectés par les opérations de récolte. Dans un contexte d'aménagement écosystémique, ces résultats démontrent l'importance de la mise en place de traitements sylvicoles inéquiennes afin de mieux reproduire les caractéristiques après chablis. De plus, il en découle des recommandations de saines pratiques d'aménagement pour que les coupes de récupération assurent le maintien d'attributs clés.

Abstract

The implementation of ecosystem management involves a better understanding of natural disturbance regimes. In the boreal forest of Canada, fire is the most studied natural disturbance. However, in areas where the fire cycle is long, other natural disturbances, such as windthrow, are important. Thus, the description of windthrow regime of the eastern boreal forest of Quebec was performed considering its intrinsic, temporal and spatial characteristics, and also its consequences on the forest ecosystem. Firstly, site and stand characteristics affecting windthrow susceptibility were studied. The SIFORT database was used, allowing a 30 year temporal coverage. Secondly, windthrows and cutblocks spatial characteristics were analysed at landscape and polygons (or disturbance) levels, in three areas of 5 000 ha. Finally, at the stand level, the main key attributes or biological legacies in the black-spruce forest after windthrow episodes were measured and compared to salvaged windthrows. These three complementary approaches provided a global picture of the windthrow regime in the irregular boreal forest. Results showed that the variables having the best predictive capacity of a stand susceptibility to windthrow are topex, surface deposit thickness and slope. Windthrows, mainly partial, annually affects 0.23% of the study area with a return interval of approximately 450 years at a given location. At the landscape level, partial windthrows have a higher variability in their size than total windthrows, which are smaller. Partial windthrow polygons have a mean of 60% of their area in residual living trees, and total windthrow polygons have 15% of their cover in residual trees. Salvage logging changes many post-windthrow key stand structure, microsite and vegetation attributes. Salvage logging causes a reduction in the quantity of downed coarse woody debris and snags and all the decay classes are not present in salvaged windthrows. Furthermore, forest floor heterogeneity and bryophytes cover are affected by salvage logging operations. These results highlight the importance of uneven-age silvicultural treatments in the irregular boreal forest. Furthermore, salvage logging operations should be designed to ensure the maintenance of key attribute.

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Avant-propos

Insertion d’articles

La présente thèse est composée de quatre chapitres dont je suis l’auteure principale. Chaque chapitre a été rédigé en anglais sous forme d’article scientifique. Pour chaque chapitre, j’ai établi les objectifs de recherche et formulé les hypothèses, réalisé les analyses statistiques, l’interprétation des résultats ainsi que de la rédaction de l’article scientifique. De plus, j’ai planifié et supervisé la collecte de données sur le terrain. Jean-Claude Ruel et Sylvie Gauthier sont coauteurs de tous les chapitres de la thèse puisqu’ils ont supervisé les travaux, et ont commenté et bonifié les articles. Philippe Goulet est coauteur du second chapitre puisqu’il a participé à la mise en place du protocole et a réalisé les travaux de photo-interprétation. Finalement, Louis De Grandpré et Chris J. Peterson sont coauteurs du quatrième chapitre puisqu’ils ont été des collaborateurs importants. Ils ont commenté et bonifié l’article et ont donné des conseils statistiques.

Chapitre I

Waldron, K., Ruel, J.-C., and Gauthier, S. 2013. The effects of site characteristics on the landscape-level windthrow regime in the North Shore region of Quebec, Canada. Forestry 86: 159-171.

Chapitre II

Waldron, K., Ruel, J.-C., Gauthier, S., and Goulet, P. Windthrow characteristics in the eastern boreal forest of Canada at two spatial levels.

L’article sera soumis sous peu.

Chapitre III

Waldron, K., Ruel, J.-C., and Gauthier, S. 2013. Forest structural attributes after windthrow and consequences of salvage logging. Forest Ecology and Management 289: 28-37.

Chapitre IV

Waldron, K., Ruel, J.-C., Gauthier, S., De Grandpré, L., and Peterson, C.J. Effects of windthrow and salvage logging on microsites, plant composition and regeneration.

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Introduction générale

En forêt boréale, les perturbations naturelles sont fréquentes et font partie de l'écosystème, qui lui, est résilient face à ces perturbations. Les perturbations naturelles sont en partie responsables de la biodiversité et de la diversité des cycles biogéochimiques retrouvés dans une région donnée. En effet, les régimes de perturbations créent des attributs clés et legs biologiques permettant le maintien de la biodiversité. Ces attributs concernent la composition et la structure forestière, la matière organique du sol ainsi que le bois mort sur pied et au sol (Gauthier et al. 2008). Le fait que les perturbations naturelles fassent partie intégrante des écosystèmes forestiers boréaux et qu'elles soient à la base de plusieurs caractéristiques essentielles au bon fonctionnement de ces écosystèmes nous démontre l'importance de s'inspirer des régimes de perturbation dans la gestion des forêts boréales. Les perturbations naturelles font donc partie de cette intégrité écologique et contribuent au maintien de la biodiversité sur lesquels l'aménagement forestier écosystémique est fondé.

Le feu a longtemps été considéré comme étant la perturbation naturelle dominante en forêt boréale. Cependant, dans les écosystèmes boréaux, d'autres perturbations naturelles peuvent participer à la régulation de la dynamique forestière (Bergeron et al. 1998). La Côte-Nord est une de ces régions caractérisées par la prépondérance de perturbations dites secondaires comme les épidémies de tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)) et le chablis (De Grandpré et al. 2000; Pham et al. 2004). En effet, la durée du cycle de feu dans cette région se situe entre 300 et 600 ans alors qu'il est de 50 à 150 ans dans la pessière de l'ouest du Québec. Ce taux relativement faible de feux de forêt dans la forêt boréale de l'Est est principalement dû au climat maritime qu'on y retrouve. Ce climat favoriserait le sapin baumier (*Abies balsamea*) contrairement aux pessières des régions plus à l'ouest, où les pessières pures sont dominantes. En effet, comme le sapin est une espèce mal adaptée au feu, son établissement et sa croissance sur un site sont favorisés lorsque le cycle de feu est long (Bergeron et Leduc 1998; Boucher et al. 2003; Bouchard et Pothier 2008). De plus, la tordeuse des bourgeons de l'épinette et le chablis créent des ouvertures dans la canopée permettant la croissance de nouvelles tiges. La forêt boréale de l'Est est donc caractérisée par sa structure forestière complexe (Boucher et al. 2003) et par la grande proportion de vieux peuplements, qui forment plus de 70% de la superficie forestière résineuse (De Grandpré et al. 2008).

Le chablis est une perturbation naturelle se définissant comme étant un « *arbre, ou groupe d'arbres, déraciné ou rompu par le vent ou brisé sous le poids de la neige, de la glace ou de l'âge* » (Ordre des ingénieurs forestiers du Québec 2003). Les épisodes de chablis sont parfois suivis de coupes de récupération, qui peuvent entraîner des coûts de récolte importants (Ruel et al. 2010) et dont certaines conséquences écologiques ont été documentées (Rumbaitis del Rio 2006; Peterson et Leach 2008; Jonásová et al. 2010). La pessière à mousses de l'est du Québec a subi deux épisodes de chablis majeurs au cours des dernières années, soit en 2006 et en 2008. Ces épisodes de chablis ont mené à la mise en place d'un plan de récupération massif, menant à la récolte d'un plus grand volume après chablis qu'après feu pour les années 2006 et 2007 (Ruel et al. 2010).

Au Québec, la littérature sur le chablis demeure relativement rare, et ce, malgré son importance écosystémique et économique (Ruel et Benoit 1999; Ruel et al. 2010; Vaillancourt 2008). La description globale du chablis passe par la description des facteurs influençant le risque de perturbation et les conséquences écosystémiques de cette perturbation. De plus, la description spatiotemporelle et la compréhension des caractéristiques intrinsèques de la perturbation, c'est-à-dire de la sévérité, permettent de dresser un portrait global du chablis. La section qui suit a donc comme objectif de dresser le portrait global de cette perturbation naturelle.

Caractéristiques spatio-temporelles et intrinsèques du chablis

La connaissance de la dynamique spatio-temporelle d'une perturbation naturelle permet une meilleure compréhension de la structure et des patrons de succession forestière à l'échelle du peuplement et du paysage (Kramer et al. 2001). En connaissant les caractéristiques spatiales, temporelles et intrinsèques d'une perturbation, il est possible de déterminer la plage de variabilité naturelle de cette dernière (Landres et al. 1999). Pour se rapprocher des régimes de perturbations naturelles, l'aménagement forestier devrait se rapprocher de cette variabilité naturelle des perturbations. La forêt boréale de l'est du Québec est caractérisée par une structure complexe, avec une proportion importante de vieux peuplements. Cependant, on assiste actuellement à un rajeunissement de la matrice forestière et à une surreprésentation des peuplements équiennes dans certaines zones (Bouchard et Pothier 2011). Une meilleure connaissance du cycle des perturbations naturelles et de leur répartition spatiale permettrait, entres autres, d'avoir une meilleure idée de la proportion du territoire à aménager de manière équienne et du taux de récolte à privilégier (De Grandpré et al. 2008).

Caractéristiques temporelles

On définit le cycle d'une perturbation naturelle comme étant le temps requis pour qu'une perturbation donnée affecte la totalité d'un territoire (Vaillancourt et al. 2008). Une autre caractéristique temporelle des perturbations naturelles est la proportion moyenne du territoire affectée annuellement (aussi nommée fréquence ou taux de chablis), qui se veut être l'inverse du cycle. La connaissance du taux de chablis de différentes sévérités dans un territoire donné peut servir à déterminer la proportion que devraient représenter différents traitements sylvicoles dans le paysage forestier (Vaillancourt et al. 2008). De plus, en connaissant la dynamique à long terme du chablis, les opérations forestières pourraient être effectuées en respectant les processus et fonctions de l'écosystème (Kramer et al. 2001).

Caractéristique spatiale du chablis

Le chablis est une perturbation ayant une grande hétérogénéité spatiale, autant à l'échelle du paysage que de la perturbation (Mitchell 2013). Un chablis peut être décrit de par sa forme, sa taille ou encore, à une échelle plus grande, de par la répartition des différents peuplements affectés dans le paysage forestier. Les études portant sur les caractéristiques spatiales du chablis sont rares. Lindemann et Baker (2001), ont dressé un portrait spatial complet d'un épisode de chablis, ce qui est difficile à trouver dans la littérature actuelle. Cependant, une généralisation de leurs résultats serait risquée puisqu'ils décrivent un épisode de chablis ponctuel. D'autres études sur les caractéristiques spatiales du chablis dans d'autres écosystèmes forestiers seraient donc de mise (Lindemann et Baker 2001). En effet, les caractéristiques spatiales du chablis influenceront la disposition des legs biologiques post-chablis dans le peuplement et le paysage, ainsi que la structure interne des peuplements et la structure d'âge des forêts à l'échelle du paysage.

Caractéristiques intrinsèques du chablis: sévérité et spécificité

Au Québec, le chablis est cartographié opérationnellement en deux catégories, soit le chablis total (plus de 75% de la surface terrière affectée) et le chablis partiel (entre 25 et 75% de la surface terrière affectée) (Létourneau et al. 2009). Cette classification demeure grossière puisque ce qui est caractérisé comme étant chablis partiel est très large comparativement à ce qu'on identifie comme chablis total. Bon nombre d'études sur le chablis effectuées à l'extérieur du Québec ont utilisé une autre catégorisation de la sévérité du chablis (Ilisson et al. 2006; Pauli et al. 2006; Lain et al. 2008).

Les chablis catastrophiques, qui sont des phénomènes rares affectant de grandes superficies, sont généralement causés par des évènements météorologiques extrêmes, tels que des tornades, ouragans ou rafales de vent violent (Foster et al. 1998; Elliott et al. 2002). Le Québec peut être soumis à des épisodes de vent violent qui affecteront de grandes superficies (Ruel et Benoit 1999; Doyon et Bouffard 2008; Ruel et al. 2010).Cependant, dans les écosystèmes forestiers où ces évènements météorologiques extrêmes sont inhabituels, les chablis sévères ou catastrophiques demeurent relativement rares (Lorimer et White 2003; Bouchard et al. 2009).

Évidemment, la description de la sévérité d'un chablis dépendra de l'échelle spatiale qui est considérée, puisqu'un chablis peut affecter localement la totalité des arbres tout en étant considéré comme partiel sur une surface plus importante. La sévérité du chablis influencera les legs biologiques et attributs clés, tout comme la structure d'âge des peuplements à l'échelle du paysage et la structure interne des peuplements. Un chablis affectant la totalité des arbres d'un peuplement résultera en un peuplement de première cohorte (voir Bergeron et al. 2002). D'un autre côté, un peuplement où une faible proportion des arbres est affectée par le chablis possèdera une quantité importante d'arbres vivants résiduels et aura, par le fait même, une structure diamétrale plus complexe qu'après un chablis total (De Grandpré et al. 2008; Mitchell 2013).

En plus de la sévérité, le chablis possède comme caractéristique intrinsèque une certaine spécificité. En effet, certaines espèces d'arbre, structures de peuplement ou encore caractéristiques géoclimatiques influenceront l'occurrence du chablis. Cette spécificité est un phénomène important à considérer dans la mise en place d'approches visant à réduire les risques de chablis après intervention sylvicole dans un peuplement. La section qui suit décrit quelques facteurs influençant le risque de chablis ainsi que sa sévérité.

Facteurs influençant le risque de chablis

Le chablis est un phénomène complexe, influencé par l'interaction de plusieurs caractéristiques à l'échelle de l'arbre, du peuplement et du paysage, ainsi que des facteurs édaphiques et géographiques (Ruel 1995; Mitchell 2013). Les principaux facteurs influençant le chablis peuvent être séparés en deux catégories, soit les facteurs géoclimatiques ainsi que les facteurs reliés à l'arbre et au peuplement.

Facteurs géoclimatiques

La susceptibilité d'un peuplement au chablis dépendra du site sur lequel il se trouve, principalement du type de sol, de la topographie et du régime de vent. L'influence du vent est intimement liée aux caractéristiques topographiques d'un site. Les effets de la topographie et du couvert forestier peuvent entraîner des rafales, donc des variations locales dans la vitesse du vent. Ces rafales sont des phénomènes très complexes et variables (Savill 1983). Malgré le fait que certains auteurs aient constaté une meilleure estimation de la susceptibilité au chablis en incluant la vitesse moyenne du vent dans leurs modèles (Meng et al. 2008), l'emploi de la vitesse moyenne du vent comme indice de susceptibilité au chablis demeure difficile (Ruel 1995; Ruel et Benoit 1999).

La susceptibilité au chablis augmente généralement avec l'altitude (Ruel 1995; Mitchell 2013). La présence d'une vallée influencera aussi le régime du vent. En effet, des différences dans la direction du vent pourront être observées selon la forme de la vallée (Ruel et al. 2002). De plus, la provenance du vent pourra aussi influencer sa vitesse et, par le fait même, son impact sur les arbres (Ruel 1995; Ruel et al. 1998). Le topex est un indice ayant été mis sur pied dans le but de caractériser l'exposition topographique d'un site donné. Cet indice, qui est décrit plus en détail au premier chapitre, a été reconnu dans plusieurs études comme étant une bonne variable prédictive du risque de chablis (Ruel et al. 1997; Quine et White 1998; Ruel et al. 2002). Bref, les endroits les plus à risque aux dommages par le vent sont des zones où les variations régionales de vitesse de vent sont importantes, c'est-à-dire des zones en altitude, des zones ayant une forte exposition ou encore des zones situées à proximité d'une grande masse d'eau (Miller 1985).

L'influence du sol sur le risque de chablis est intimement liée à la relation entre le sol et le système racinaire des arbres. L'aération du sol, sa capacité à retenir l'eau, l'épaisseur du dépôt et la résistance du sol à la pénétration des racines en sont des exemples (Ruel 1995). Si les propriétés physiques du sol permettent une bonne pénétration racinaire, les risques de chablis diminueront. Par exemple, les racines ont plus de difficulté à pénétrer dans un sol possédant un mauvais drainage que dans un sol bien drainé. Ainsi, de façon générale, les peuplements se situant sur des sols mal drainés sont plus susceptibles au chablis que ceux se trouvant sur sols bien drainés (Savill 1983; Ruel 1995; Dobbertin 2002). L'épaisseur du sol influence aussi la susceptibilité des arbres au chablis, mais les études à ce sujet ont des résultats qui sont parfois contradictoires. En effet, bien qu'intuitivement, on puisse penser que les arbres poussant sur sols épais devraient être moins susceptibles au déracinement, plusieurs études reliant l'épaisseur du sol au risque de chablis ont prouvé le contraire (Dobbertin 2002; Bouchard et al. 2009; Stueve et al. 2011).

Facteurs à l'échelle de l'arbre et du peuplement

À l'échelle du peuplement, mais aussi à l'échelle de l'arbre, plusieurs facteurs sont cités dans la littérature comme étant reliés aux risques de chablis. À l'échelle de l'arbre, on constate qu'une augmentation dans la hauteur entraînera une augmentation de la susceptibilité au chablis (Savill 1983; Ruel 1995; Canham et al. 2001). La relation existant entre la hauteur de l'arbre et son diamètre est un facteur qui est, lui aussi, déterminant. Meunier et al. (2002) ont démontré que le ratio hauteur/DHP influençait la susceptibilité des arbres au chablis. En effet, plus ce ratio est élevé, plus ces derniers seront propices au renversement (Ruel 1995; Meunier et al. 2002). Cependant, cette relation entre le ratio hauteur/DHP et le chablis semble varier selon les espèces (Canham et al. 2001).

La structure du peuplement a aussi été rapportée dans la littérature comme étant un facteur influençant la susceptibilité au chablis (Everham et Brokaw 1996). Les peuplements réguliers seraient plus affectés par le vent que ne le sont les peuplements irréguliers. En effet, la présence de gaules en peuplement irrégulier diminuerait la charge de vent sur les arbres formant la canopée (Gardiner et al. 2005; Lavoie et al. 2012). Ce constat est en contradiction avec la relation entre l'âge d'un peuplement et sa susceptibilité au chablis. En effet, en forêt boréale, les peuplements irréguliers sont généralement plus vieux que les peuplements réguliers. Un peuplement plus vieux pourrait avoir tendance à avoir plus d'arbres infectés par la carie, ce qui le rendra, de façon générale, plus propice au chablis qu'un jeune peuplement (Ruel 1995; Ruel et Benoit 1999).

La composition du peuplement peut aussi être reliée au chablis. Les différentes espèces n'ont pas toutes la même susceptibilité face à ce type de perturbation (Canham et al. 2001; Rich et al. 2007; Nolet et al. 2012), les feuillus étant généralement moins propices au déracinement que ne le sont les résineux (Savill 1983; Ruel 1995). En forêt boréale, les essences ayant une plus forte prédisposition à la carie auront tendance à être plus affectées par le chablis (Savill 1983; Ruel 1995). Cette affirmation est en accord avec le fait que le sapin baumier est considéré comme une essence plus propice au chablis que ne l'est l'épinette (Ruel 2000; Rich et al. 2007). La forme de la tige des arbres et la composition en espèces ne sont pas les seuls facteurs d'un peuplement pouvant être reliés à la susceptibilité au chablis. On peut aussi citer, entres autres, la forme de la canopée et la répartition spatiale du peuplement (présence de trouées, effet de bordure) (Quine et Gardiner 2007).

Conséquences du chablis sur l'écosystème forestier

Le chablis, comme toute autre perturbation naturelle, génèrera dans l'écosystème forestier plusieurs attributs clés et legs biologiques (Franklin et al. 2007; Gauthier et al. 2008). On définit un attribut clé comme étant un élément de l'écosystème qui lui permettra de demeurer résilient face aux perturbations et aux stress ultérieurs. Les legs biologiques sont des caractéristiques présentes dans un peuplement perturbé qui proviennent de la forêt précédente et qui influenceront la trajectoire de succession post-perturbation (Gauthier et al. 2008). Ces deux notions sont donc fortement liées entre elles. Un peuplement post-chablis compte plusieurs de ces attributs clés et legs biologiques, dont les principaux sont: le bois mort sur pied et au sol, la présence d'arbres vivants résiduels, la microtopographie en monticules et en cuvettes et l'hétérogénéité des lits de germination, la régénération ainsi que la biodiversité des plantes de sous-bois (Beatty et Stone 1986; Schaetzl et al. 1989; Ulanova 2000).

Bois mort

Le lien existant entre la biodiversité et la présence de bois mort a été démontré à plusieurs reprises au cours des dernières années (Berg et al. 1994; Müller et Bütler 2010). La raréfaction du bois mort est d'ailleurs responsable de la présence de plusieurs espèces sur la liste rouge des espèces menacées en Scandinavie (Jonsell et al. 1998; Jonsson et al. 2005). Après chablis, les peuplements affectés contiennent une forte concentration de bois mort debout et au sol et ce, à différents stades de décomposition (Bouget et Duelli 2004). En effet, le positionnement des arbres au sol, la taille de ces derniers, l'essence ainsi que les conditions environnementales influenceront la rapidité de dégradation du bois mort et le temps de persistance de ce dernier à travers les différents stades de dégradation (Vanderwel et al. 2006; Angers 2009). On peut aussi retrouver une quantité relativement importante de souches et de chicots si les arbres ont cassé sous l'effet du vent. Évidemment, le volume de bois mort au sol et la densité de chicots dépendront du type de peuplement, mais aussi de la sévérité et de la variabilité temporelle des perturbations (Aakala et al. 2007). Cette variété de stades de dégradation et de tailles du bois mort revêt une importance écologique puisque les organismes utilisateurs de bois mort ne possèdent pas tous les mêmes besoins et certains utiliseront le bois mort à des stades de dégradation spécifiques ou encore à des tailles particulières (Angers 2009).

Arbres vivants résiduels

Un peuplement post-chablis, surtout partiel, est rarement homogène, puisque certaines parties du peuplement sont totalement affectées alors que d'autres ne le sont pas du tout (Lindemann et Baker 2001; Mitchell 2013). Ainsi, une certaine densité d'arbres vivants résiduels demeure présente dans les peuplements post-chablis. Ces arbres vivants, surtout ceux avec de forts diamètres, sont importants pour différentes espèces fauniques (Nilsson et al. 2002). De plus, ces arbres vivants sur pied contribuent à l'hétérogénéité structurale des peuplements suite à un chablis, qui joue un rôle majeur dans le maintien de la biodiversité (Spies 1998; McCarthy 2001). Évidemment, certains épisodes de chablis sévères ou catastrophiques peuvent affecter la totalité des arbres du peuplement (Peterson 2007; Xi et Peet 2011) mais ces épisodes demeurent relativement rares dans le contexte de la forêt boréale québécoise.

Microtopographie en monticules et en cuvettes

Le déracinement d'un arbre entraine la formation d'un monticule et d'une cuvette sur le parterre forestier. Cette microtopographie, qui est particulière aux environnements post-chablis (Ulanova 2000; McCarthy 2001), peut couvrir une proportion relativement élevée du territoire après une perturbation par chablis (Peterson et al. 1990; Ulanova 2000). La taille des monticules et des cuvettes est reliée à la taille de l'arbre déraciné et de son système racinaire (Peterson et al. 1990; Clinton et Baker 2000; Doyon et Bouffard 2008). Le déracinement des arbres entraine un brassage du sol, c'est-à-dire que les horizons de surface se mélangent avec les horizons plus profonds, augmentant ainsi la disponibilité en éléments nutritifs et la fertilité du sol (Beatty et Stone 1986; Ulanova 2000). Le retour au profil de sol initial peut prendre de 100 à 300 ans selon la profondeur qu'avait le système racinaire de l'arbre touché (Ulanova 2000). Cette microtopographie particulière exposera une variété de lits de germination, favorisant une plus grande diversité d'espèces végétales que le plancher forestier intact (Peterson et Campbell 1993; Ulanova 2000; McCarthy

2001). De plus, la régénération et la croissance de plusieurs espèces d'arbres sont influencées positivement par la microtopographie (Kuuluvainen et Juntunen 1998; de Chantal et al. 2009; Šebková et al. 2012).

Biodiversité végétale

En forêt feuillue et mixte, plusieurs études ont démontré le lien entre la microtopographie ou encore les conditions de lumière post-chablis et la richesse et diversité des plantes de sous-bois (Peterson et Campbell 1993; Peterson et Pickett 1995; von Oheimb et al. 2006). Cette richesse et cette diversité en espèces peuvent varier à une échelle très fine, c'est-à-dire entre les cuvettes et les monticules. Par exemple, Peterson et Pickett (1990) ont trouvé, dans une forêt dominée par le hêtre, une plus grande diversité de plantes et une densité de semis plus importante dans les cuvettes que sur les monticules. Cependant, en forêt boréale, les monticules et cuvettes ne possèdent pas les mêmes propriétés qu'en forêt tempérée. Le système racinaire superficiel des principales essences, le DHP plus faible des tiges ainsi que les propriétés du sol entrainent une diminution de la densité et de la taille des monticules et des cuvettes (Peterson et al. 1990; Clinton et Baker 2000). Bien que certaines études démontrent une augmentation de la richesse en espèces dans les peuplements post-chablis comparativement aux peuplements intacts (Ulanova 2000), le lien direct entre la diversité et l'abondance de la végétation de sous-bois et la présence de monticules et de cuvettes est plus difficile à établir dans ce type d'écosystème. Par contre, après chablis, on retrouve en forêt boréale une abondance et une variété accrues de bryophytes. En effet, la diversité des microsites, les conditions d'humidité et le volume important de bois mort sont des conditions favorisant l'établissement de plusieurs espèces de bryophytes (Jonsson et Esseen 1990).

Régénération

Le chablis est reconnu comme étant une perturbation naturelle créant plusieurs lits de germination favorables à l'établissement de la régénération. En effet, le bois mort décomposé ainsi que la microtopographie en monticules et en cuvettes ont souvent été caractérisés comme étant des sites propices à la régénération et à la croissance de plusieurs espèces (Ulanova 2000). En Finlande, Kuuluvainen et Juntunen (1998) ont démontré que 60% des semis et gaules de pins sylvestres (*Pinus sylvestris*) et 91% des semis et gaules de bouleaux (*Betula* spp.) se situaient sur les monticules et les cuvettes alors que ces derniers ne couvraient que 3,4% de la superficie du plancher forestier. Toujours en Finlande, le nombre de semis et de gaules de *Picea* après chablis était significativement plus élevé sur le bois mort au sol et sur les cuvettes et monticules que sur le plancher forestier intact (Kuuluvainen et Kalmari 2003). Dans la sapinière à bouleau blanc du Québec, Ruel et Pineau (2002) ont mis en évidence le lien positif existant entre le chablis et la régénération en épinettes blanches. D'autres études n'ont cependant pas obtenu de relation entre la microtopographie en monticules et en cuvettes et la régénération après chablis (Doyon et Bouffard 2008). La régénération préétablie est souvent peu affectée lors d'un épisode de chablis. En effet, plusieurs auteurs ont démontré que la régénération préétablie dominait les peuplements post-chablis (Wohlgemuth et al. 2002; Jonásová et al. 2010).

Perturbations anthropiques

Les coupes de récupération sont des récoltes effectuées après une perturbation naturelle (Lindenmayer et al. 2008). Les principales inquiétudes environnementales associées aux coupes de récupération proviennent du fait que ces dernières enlèvent une partie ou la totalité des legs biologiques ou attributs clés caractéristiques des environnements perturbés (Lindenmayer et al. 2004; Lindenmayer et al. 2008; Burton 2010). Ainsi, les coupes de récupération pourraient affecter la résilience de l'écosystème. De plus, les coupes de récupération ont comme particularité d'infliger à l'écosystème forestier une deuxième perturbation et ce, dans un court délai afin d'éviter une détérioration du bois causée par les insectes ou les champignons (Burton 2010; Nappi et al. 2011). Les impacts des perturbations en rafale sur les écosystèmes forestiers boréaux ont été documentés dans d'autres contextes (Paine et al. 1998; Payette et al. 2000) et demeurent une inquiétude majeure concernant les coupes de récupération (Lindenmayer et Noss 2006).

Les impacts écosystémiques des coupes de récupération ont fait l'objet de plusieurs études au cours des dernières années, particulièrement la récolte dans les forêts brulées (Nappi et al. 2004; Purdon et al. 2004; Greene et al. 2006; Schmiegelow et al. 2006). Bien que plus rares que les travaux effectués sur les feux, les études ayant évalué les impacts des coupes de récupération post-chablis sur l'écosystème forestier ont permis de mettre en évidence quelques impacts négatifs. La coupe de récupération, comme tout type de coupe, a comme objectif la récolte de matière ligneuse. Ainsi, elle affectera le volume et les dimensions du bois mort présent dans le peuplement post-chablis (Loeb 1999; Greenberg 2001). Certains auteurs ont observé une diminution de la diversité végétale ou un changement dans la composition en espèces (Ilisson et al. 2006; Rumbaitis del Rio, 2006; Nelson et al. 2008) ou encore une diminution de la variété de lits de germination suite à la récolte dans les peuplements post-chablis (Peterson et Leach 2008).

En plus des coupes de récupération, d'autres types de coupe sont effectués dans la pessière à mousses et la sapinière à bouleau blanc de l'Est. Bien que des coupes partielles y aient été pratiquées à des fins expérimentales (Cimon-Morin et al. 2010), la majorité de l'aménagement forestier effectué dans la région est équienne. Le type de coupe le plus répandu demeure la CPRS, ou coupe avec protection de la régénération et des sols. La CPRS vise la récolte de la totalité du volume marchand présent sur le parterre de coupe, tout en assurant le maintien de la régénération préétablie (Doucet et al. 2009).

La gestion majoritairement équienne effectuée dans la forêt boréale de l'est du Québec soulève quelques enjeux de biodiversité et de résilience de l'écosystème. Le rajeunissement de la matrice forestière et la simplification de la structure verticale des peuplements en sont des exemples (De Grandpré et al. 2008; Grenon et al. 2010). Dans un contexte où plus de 70% de la matrice forestière est composée de forêts à structure irrégulière (Boucher et al. 2003) et où les épidémies d'insectes et le chablis sont des perturbations naturelles dominantes (De Grandpré et al. 2000; Pham et al. 2004), la mise en place de traitements sylvicoles plus adaptés à ces conditions devient nécessaire.

Démarche méthodologique

La thèse combine trois approches complémentaires, permettant de tracer un portrait global de la dynamique du chablis dans la forêt boréale irrégulière de l'est du Québec tout en faisant le pont avec l'aménagement forestier écosystémique. L'objectif général de la thèse était de répondre à la question de recherche suivante :

Quelles sont les conséquences du chablis sur l'écosystème forestier et quels sont les principaux facteurs influençant le régime de perturbation par chablis à l'échelle de l'arbre, du peuplement et du paysage, qui doivent être considérés dans la mise en place de pratiques sylvicoles dans une optique d'aménagement forestier écosystémique?

Pour répondre à cette question, un premier volet porte sur le patron de perturbation par chablis à l'échelle du paysage. La base de données SIFORT (Pelletier et al. 1998; Pelletier et al. 2007) est le principal outil ayant été utilisé. Ce chapitre vise à déterminer quelles sont les caractéristiques de station influençant les probabilités de chablis. Les chablis partiels et totaux ont été considérés dans l'analyse qui couvre une période d'environ 30 ans. La zone d'étude de ce chapitre est vaste, couvrant la majorité de la région administrative de la Côte-Nord. Deux sous-domaines bioclimatiques sont donc inclus dans l'analyse, soit la pessière à mousses et la sapinière à bouleau blanc de l'Est. Cette étude, présentée au chapitre I, visait à faire ressortir les caractéristiques de station et les caractéristiques géoclimatiques ayant le meilleur pouvoir prédictif sur le risque de chablis. De plus, un cycle de chablis a pu être calculé sur le territoire couvert par l'étude.

Le second volet vise la description spatiale du chablis dans la pessière à mousses de l'Est et ce, à deux échelles, soit à l'échelle du paysage et à l'échelle de la perturbation. Les caractéristiques spatiales des chablis partiels et totaux, mais aussi des coupes présentes dans le territoire à l'étude ont été considérées. Les résultats de ce volet, présentés au chapitre II, permettent une description plus fine de la dynamique spatiale à l'intérieur des peuplements caractérisés comme chablis partiel ou total.

Le troisième volet vise la description des conséquences du chablis sur l'écosystème forestier à l'échelle du peuplement. Un dispositif expérimental a été mis sur pied dans la pessière à mousses de l'Est, dans le secteur du lac Saint-Pierre. L'échantillonnage réparti sur deux étés avait comme objectif de décrire les principaux attributs clés et legs biologiques après chablis de différentes sévérités. De plus, les mêmes données étaient récoltées dans des chablis ayant subi une coupe de récupération afin de vérifier si la récolte dans les chablis affectait les attributs clés. Les chapitres III et IV ont donc permis de caractériser les attributs post-chablis et les impacts des coupes de récupération. Le chapitre III se concentre sur les attributs structuraux, soit le bois mort sur pied et au sol, les arbres vivants résiduels ainsi que la microtopographie en monticules et en cuvettes. Le chapitre IV présente les attributs liés à la végétation, soit la régénération, la biodiversité végétale et les lits de germination.

Tous les chapitres de cette thèse font le pont entre la description du régime de chablis et son implication en aménagement forestier écosystémique. En conclusion, les liens entre les résultats de chaque chapitre et l'aménagement forestier écosystémique seront également tracés. Finalement, les implications et les perspectives des résultats présentés de cette thèse seront abordées.

Références

Aakala, T., Kuuluvainen, T., De Grandpré, L., and Gauthier, S. 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. Can. J. For. Res. 37: 50-61.

Angers, V.-A. 2009. L'enjeu écologique du bois mort – Complément au Guide pour la description des principaux enjeux écologiques dans les plans régionaux de intégré des ressources et du territoire, Québec, pour le ministère des Ressources naturelles et de la Faune, Direction de l'environnement et de la protection des forêts, Québec, Canada, 45 p.

Beatty, S.W., and Stone, E.L. 1986. The variety of soil microsites created by tree falls. Can. J. For. Res. 16: 539-548.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., and Weslien, J. 1994. Threatened plant, animal, and fongus species in Swedish forests: distribution and habitat associations. Conserv. Biol. 8(3): 718-731.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H., and Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests: Introduction. J. Veg. Sci. Special Feature: 464-468.

Bergeron, Y., and Leduc, A. 1998. Relationships between change in fire frequency and mortality due to spruce budworm outbreak in the southeastern Canadian boreal forest. J. Veg. Sc. 9: 492-500.

Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the boreal forest. Silva Fenn. 36(1): 81-95.

Bouchard, M., and Pothier, D. 2008. Simulations of the effects of changes in mean fire return intervals on balsam fir abundance, and implications for spruce budworm outbreaks. Ecol. Model. 218: 207-218.

Bouchard, M., and Pothier, D. 2011. Long-term influence of fire and harvesting on boreal forest age structure and forest composition in eastern Québec. Forest Ecol. Manage. 261: 811-820.

Bouchard, M., Pothier, D., and Ruel, J.-C. 2009. Stand-replacing windthrow in the boreal forests of eastern Quebec. Can. J. For. Res. 39: 1-7.

Boucher, D., De Grandpré, L., and Gauthier, S. 2003. Développement d'un outil de classification de la structure des peuplements et comparaison de deux territoires de la pessière à mousses du Québec. Forest. Chron. 79(2): 318-328.

Bouget, C., and Duelli, P. 2004. The effects of windthrow on forest insect communities: a literature review. Biol. Conserv. 7: 749-764.

Burton, P. J. 2010. Striving for sustainability and resilience in the face of unprecedented change: the case of the mountain pine beetle outbreak in British Columbia. Sustainability 2: 2403-2423.

Canham, C.D., Papaik, M.J., and Latty, E.F. 2001. Interspecific variation in susceptibility to windthrow as a function of tree size and storm severity for northern temperate tree species. Can. J. For. Res. 31: 1-10.

Cimon-Morin, J., Ruel, J.-C., and Darveau, M. 2010. Short term effects of alternative silvicultural treatments on stand attributes in irregular balsam fir-black spruce stands. For. Ecol. Manage. 260: 907-914.

Clinton, B.D., and Baker, C.R. 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. Forest Ecol. Manage. 126: 51-60.

de Chantal, M., Lilja-Rothsten, S., Peterson, C., Kuuluvainen, T., Vanha-Majamaa, I., and Puttonen, P. 2009. Tree regeneration before and after restoration treatments in managed boreal *Picea abies* stands. Appl.Veg. Sc. 12: 131-143.

De Grandpré, L., Gauthier, S., Allain, C., Cyr, D., Périgon, S., Pham, A.T., Boucher, D., Morissette, J., Reyes, G., Aakala, T., et Kuuluvainen, T. 2008. Vers un aménagement écosystémique de la forêt boréale de la Côte-Nord. Régime des perturbations et dynamique naturelle. *Dans*: Aménagement forestier écosystémique en forêt boréale. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpre, L., Kneeshaw, D.D., Morin, H., Drapeau, P., et Bergeron, Y. (eds), Presses de l'Université du Québec, Montréal, Canada, pp. 241–268.

De Grandpré, L., Morissette, J., and Gauthier, S. 2000. Long-term post-fire changes in the northeastern boreal forest of Quebec. J. Veg. Sc. 11: 791-800.

Dobbertin, M. 2002. Influence of stand structure and site factors on wind damage comparing the storms Vivian and Lothar. For. Snow Landsc. Res. 77, ½: 187-205.

Doucet, R., Ruel, J.-C., Jutras, S., Lessard, G., Pineau, M., Prégent, G., and Thiffault, N. 2009. Sylviculture appliquée. In : Manuel de foresterie. Ordre des ingénieurs forestiers du Québec. 2e éd., ouvrage collectif, Éditions MultiMondes, Québec, Canada, pp. 1147-1186.

Doyon, F., and Bouffard, D. 2008. Étude sur le bois mort, les microsites et la régénération après chablis catastrophiques dans les érablières du Témiscamingue. Institut Québécois d'Aménagement de la Foret Feuillue, Ripon, Québec Rapport technique, 37 p.

Elliott, K.J., Hitchcock, S.L., and Krueger, L. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. J. Torrey Bot. Soc. 129: 48-59.

Everham, E.M., and Brokaw, N.V.L. 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. 62(2): 113-185.

Foster, D.R., Knight, D.H., and Franklin, J.F. 1998. Landscape patterns and legacies resulting from large, infrequent forest disturbances. Ecosystems 1: 497-510.

Franklin, J. F., Mitchell, R. J., and Palik, B. J. 2007. Natural disturbance and stand development principles for ecological forestry. Gen. Tech. Rep. NRS-19. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, 44 p.

Gardiner, B., Marshall, B., Achim, A., Belcher, R., and Wood, C. 2005. The stability of different sylvicultural systems: a wind-tunnel investigation. Forestry 78(5): 471-484.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D., Drapeau, P., De Grandpré, L., Claveau, Y., et Paré, D. 2008. Aménagement forestier écosystémique. Origines et fondements. *Dans*: Aménagement forestier écosystémique en forêt boréale. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., et Bergeron, Y. (eds). Presses de l'Université du Québec, Montréal, Canada, p. 13-40.

Greenberg, C.H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. Forest Ecol. Manage. 148: 135-144.

Greene, D.F., Gauthier, S., Noël, J., Rousseau, M., and Bergeron, Y. 2006. A field experiment to determine the effect of post-fire salvage on seedbeds and tree regeneration. Front. Ecol. Environ. 4: 69-74.

Grenon, F., Jetté, J.-P., and Leblanc, M. 2010. Manuel de référence pour l’aménagement écosystémique des forêts au Québec – Module 1 - Fondements et démarche de la mise en œuvre. Centre d’enseignement et de recherche en foresterie de Sainte-Foy inc. et ministère des Ressources naturelles et de la Faune, Direction de l’environnement et de la protection des forêts, Québec, Canada, 51 p.

Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K., and Kurm, M. 2006. Vascular plant response to windthrow severity in Norway spruce – dominated Myrtillus site type forests in Estonia. Ecoscience 13: 193-202.

Jonásová, M., Vávrová, E., and Cudlín, P. 2010. Western Carpathian mountain spruce forest after a windthrow: natural regeneration in cleared and uncleared areas. Forest Ecol. Manage. 259: 1127-1134.

Jonsell, M., Weslien, J., Ehnstrom, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodivers. Conserv. 7: 749-764.

Jonsson, B.G., and Esseen, P.-A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. J. Ecol. 78: 924-936.

Jonsson, B.G., Kruys, N., and Ranius, T. 2005. Ecology of species living on dead wood – lessons for dead wood management. Silva Fenn. 39: 289-309.

Kramer, M.G., Hansen, A.J., Taper, M.L., and Kissinger, E.J. 2001. Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska. Ecology 82(10): 2749-2768.

Kuuluvainen, T., and Juntunen, P. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest. J. Veg. Sci. 9: 551-562.

Kuuluvainen, T., and Kalmari, R. 2003. Regeneration microsites of *Picea abies* seedlings in a windthrow area of a boreal old-growth forest in southern Finland. Ann. Bot. Fenn. 40: 401-413.

Lain, E.J., Haney, A., Burris, J.M., and Burton, J. 2008. Response of vegetation and birds to severe wind disturbance and salvage logging in a southern boreal forest. Forest Ecol. Manage. 256: 863-873.

Landres, P.B., Morgan, P., and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9(4): 1179-1188.

Lavoie, S., Ruel, J.-C., Bergeron, Y., and Harvey, B. 2012. Windthrow after group and dispersed tree retention in eastern Canada. Forest Ecol. Manage. 269: 158-167.

Létourneau, J.-P., Bard, A., Lambert, J., Lord, G., and Faucher, A. 2009. Normes de cartographie écoforestière. Troisième inventaire écoforestier. Ministère des Ressources naturelles et de la Faune, Direction des inventaires forestiers et Service aux citoyens, Québec, Canada, 95 p.

Lindemann, J.D., and Baker, W.L. 2001. Attributes of blowdown patches from a severe wind event in the Southern Rocky Mountains, USA. Lands. Ecol. 16: 313-325.

Lindenmayer, D.B., Burton, P.J., and Franklin, J.F. 2008. Salvage logging and its ecological consequences. Island Press (ed.), Washington, DC, USA, 227 p.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.K.A., and Perry, D. 2004. Salvage harvesting policies after natural disturbance. Science 303: 1303.

Lindenmayer, D. B., and Noss, R. F. 2006. Salvage logging, ecosystem processes, and biodiversity conservation. Conserv. Biol. 20(4): 949-958.

Loeb, S.C. 1999. Responses of small mammals to coarse woody debris in a southern pine forest. J. Mammal. 80: 460-471.

Lorimer, C.G., and White, A.S. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecol. Manage. 185: 41-64.

McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. Environ. Rev. 9: 1-59.

Meng, S.X., Huang, S., Lieffers, V.J., Nunifu, T., and Yang, Y. 2008. Wind speed and crown class influence the height-diameter relationship of lodgepole pine: Nonlinear mixed effects modeling. For. Ecol. Manage. 256: 570-577.

Meunier, S., Ruel, J.-C., Laflamme, G., and Achim, A. 2002. Résistance comparée de l'épinette blanche et du sapin baumier au renversement. Can. J. For. Res. 32: 642-652.

Miller, K.F. 1985. Windthrow hazard classification. Forestry Commission Leaflet No 85. Forestry Commission, Edinburgh, UK, 14 p.

Mitchell, S. J. 2013. Wind as a natural disturbance agent in forests: a synthesis. Forestry 86(2): 147-157.

Müller, J., and Bütler, R. 2010. A review of habitat thresholds for dead wood: a baseline for management recommendations in European forests. Eu. J. Forest Res. 129: 981-992.

Nappi, A., Drapeau, P., and Savard, J.-P.L. 2004. Salvage logging after wildfire in the boreal forest: is it becoming a hot issue for wildlife? Forest. Chron. 80(1): 67-74.

Nappi, A., Bujold, F., Chabot, M., Dumont, M.-C., Duval, J., Drapeau, P., Gauthier, S., Brais, S., Peltier, J., and Bergeron, I. 2011. La récolte dans les forêts brûlées – Enjeux et orientations pour un aménagement écosystémique. Ministère des Ressources naturelles et de la Faune, Direction de l'environnement et de la protection des forêts, Québec, 51 p.

Nelson, J.L., Groninger, J.W., Battaglia, L.L., and Ruffner, C.M. 2008. Bottomland hardwood forest recovery following tornado disturbance and salvage logging. Forest Ecol. Manage. 256: 388-395.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G., and Ranius, T. 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. Forest Ecol. Manage. 161: 189-204.

Nolet, P., Doyon, F. and Bouffard, D. 2012. Predicting stem windthrow probability in a northern hardwood forest using a wind intensity bio-indicator approach. Open Journal of Forestry 2(2): 77-87.

Ordre des ingénieurs forestiers du Québec. 2003. Dictionnaire de la foresterie. Édition spéciale du XII[e] Congrès forestier mondial, Québec, Canada, 744 p.

Paine, R.T., Tegner, M.J., and Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. Ecosystems 1: 535-545.

Pauli, J. N., Bedrosian, B. E., and Osterberg, N. 2006. Effects of blowdown on small mammal populations. Am. Midl. Nat. 156(1): 151-162.

Payette, S., Bhiry, N., Delwaide, A., and Simard, M. 2000. Origin of the lichen woodland at its southern range limit in eastern Canada: the catastrophic impact of insect defoliators and fire on the spruce–moss forest. Can. J. For. Res. 30: 288-305.

Pelletier, G., Dumont, Y., and Bédard, M. 2007. SIFORT, Système d'Information FORestière par Tesselle. Manuel de l'usager. Ministère des Ressources naturelles et de la Faune, Québec, 125 p.

Pelletier, G., Dumont, Y., Bédard, M., and Bergeron, J. 1998. SIFORT, un système hybride des modes vectoriels et matriciels pour une nouvelle approche de l'analyse forestière. Arpenteur-Géomètre 23(3): 8-9.

Peterson, C.J. 2007. Consistent influence of tree diameter and species on damage in nine eastern North America tornado blowdowns. Forest Ecol. Manage. 250: 96-108.

Peterson, C.J., and Campbell, J.E. 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. B. Torrey Bot. Club 120: 451-460.

Peterson, C.J., Carson, W.P., McCarthy, B.C., and Pickett, S.T.A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58: 39-46.

Peterson, C.J., and Leach, A.D. 2008. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. Forestry 81: 362-376.

Peterson, C.J., and Pickett, S.T.A. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. J. Veg. Sci. 1: 657-662.

Peterson, C.J., and Pickett, S.P.K., 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. Ecology 76: 763-774.

Pham, A.T., De Grandpré, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. 34: 353-364.

Purdon, M., Brais, S., and Bergeron, Y. 2004. Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. Appl. Veg. Sci. 7: 49-60.

Quine, C.P., and Gardiner, B.A. 2007. Understanding how the interaction of wind and trees results in windthrow, stem breakage, and canopy gap formation. *Dans*: Plant disturbance ecology. The process and the response. Edward A. J., and Miyanishi, K. (eds), Academic Press, Amsterdam, Netherlands, pp. 103-156.

Quine, C.P., and White, I.M.S. 1998. The potential of distance-limited topex in the prediction of site windiness. Forestry 71(4): 325-332.

Rich, R.L., Frelich, L.E., and Reich, P.B. 2007. Windthrow mortality in the southern boreal forest: effects of species, diameter and stand age. J. Ecol. 95: 1261-1273.

Ruel, J.-C. 1995. Understanding windthrow: Silvicultural implications. For. Chron. 71(4): 434-444.

Ruel, J.-C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. For. Ecol. Manage. 135: 169-178.

Ruel, J.-C., Achim, A., Raul, E.H., Cloutier, A., Brossier, B. 2010. Wood degradation after windthrow in a northern environment. Forest Prod. J. 60: 200-206.

Ruel, J.-C., and Benoit, R. 1999. Analyse du chablis du 7 novembre 1994 dans les régions de Charlevoix et de la Gaspésie, Québec, Canada. For. Chron. 75(2): 293-301.

Ruel, J.-C., Mitchell, S.J., and Dornier, M. 2002. A GIS based approach to map wind exposure for windthrow hazard rating. North. J. Appl. For. 19(4): 183-187.

Ruel, J.-C., Pin, D., and Cooper, K. 1998. Effect of topography on wind behavior in a complex terrain. Forestry 71(3): 261-265.

Ruel, J.-C., Pin, D., Spacek, L., Cooper, K., and Benoit, R. 1997. The estimation of wind exposure for windthrow hazard rating: comparison between strongblow, MC2, topex and a wind tunnel study. Forestry 70(3): 253-266.

Ruel, J.-C., and Pineau, M. 2002. Windthrow as an important process for white spruce regeneration. Forest. Chron. 78(5): 732-738.

Rumbaitis del Rio, C.M. 2006. Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. Can. J. For. Res. 36: 2943-2954.

Savill, P.S. 1983. Silvilculture in windy climates. Forestry abstract 44(8): 473-488.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., and Small, T.W. 1989. Tree uprooting: a review of impacts on forest ecology. Vegetatio 79: 165-176.

Schmiegelow, F.K.A., Stepnisky, D.P., and Stambaugh, C.A. 2006. Reconciling salvage logging of boreal forest with a natural-disturbance management model. Conserv. Biol. 20(4): 971-983.

Šebková, B., Samonil, P., Valtera, M., Adam, D., and Janik, D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. Forest Ecol. Manage. 280: 9-19.

Spies, T.A. 1998. Forest structure: a key to the ecosystem. USDA, Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA, 39 p.

Stueve, K.M., Perry, C.H., Nelson, M.D., Healey, S.P., Hill, A.D., Moisen, G.G., Cohen, W.B., Gormanson, D.G., and Huang, C. 2011. Ecological importance of intermediate windstorms rivals large, infrequent disturbances in the northern Great Lakes. Ecosphere 2(1), article 2: 1-21.

Ulanova, N.G. 2000. The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manage. 135: 155-167.

Vaillancourt, M.-A. 2008. Effets des régimes de perturbation par le chablis sur la biodiversité et les implications pour la récupération. Ministère des Ressources naturelles et de la Faune, Direction du développement socio-économique, des partenariats et de l'éducation et Service de la mise en valeur de la ressource et des territoires fauniques, Québec, 58 p.

Vaillancourt, M.-A., De Grandpré, L., Gauthier, S., Leduc, A., Kneeshaw, D., Claveau, Y., et Bergeron, Y. Comment les perturbations naturelles peuvent-elles constituer un guide pour l'aménagement forestier écosystémique? *Dans*: Aménagement forestier écosystémique en forêt boréale. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. et Bergeron, Y. (eds). Presses de l'Université du Québec, Montréal, Canada, p. 41-59.

Vanderwel, M.C., Malcolm, J.R., and Smith, S.M. 2006. An integrated model for snag and downed woody debris decay class transitions. Forest Ecol. Manage. 234: 48-59.

von Oheimb, G., Friedel, A., Bertsch, A., and Härdtle, W. 2006. The effects of windthrow on plant species richness in a Central European beech forest. Plant Ecol. 191: 47-65.

Wohlgemuth, T., Kull, P., and Wüthrich, H. 2002. Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990. For. Snow Lands. Res. 77: 17-47.

Xi, W., and Peet, R.K. 2011. The complexity of catastrophic wind impacts on temperate forests. In: Recent hurricane research – Climate, dynamics, and societal impacts. Lupo, A.R. (ed), InTech, pp. 503-534.

Chapitre I

THE EFFECTS OF SITE CHARACTERISTICS ON THE LANDSCAPE-LEVEL WINDTHROW REGIME IN THE NORTH SHORE REGION OF QUEBEC, CANADA[1]

[1] Version intégrale d'un article publié / Intergral version of a published paper:
Waldron, K., Ruel, J.-C., and Gauthier, S. 2013. The effects of site characteristics on the landscape-level windthrow regime in the North Shore region of Quebec, Canada. Forestry 86(2): 159-171.

Abstract

Understanding windthrow disturbance regime is essential for the implementation of ecosystem management, especially in forests with long fire return intervals. Our study describes windthrow dynamics at a landscape scale of the Quebec North Shore region, Canada, and evaluates the effect of some site (soil surface material thickness or deposit thickness, drainage, slope, topography and wind), and stand (dominant species, height and density) characteristics on windthrow probabilities. The SIFORT database, created by the Ministry of Natural Resources and Wildlife of Quebec, the Quebec forest fire control agency and the Quebec forest pest and disease control agency was used to perform a spatiotemporal analysis of windthrow, according to site and stand characteristics. Windthrow probabilities were influenced by topographic exposure (topex), slope classes and deposit thickness. Windthrow probabilities increased with topographic exposure. Windthrow occurrence was highest when deposits were thick (more than 1 meter) and slope class was medium (from 15% to 30%). This study has also shown the importance of partial windthrow at the landscape scale in the North Shore region. Our results suggest that from an ecosystem management perspective, clear-cutting must be partly replaced by partial cuts, in order to emulate the regional dynamics of partial windthrow.

Keywords: topex, deposit thickness, slope, partial windthrow, stand-replacing windthrow, windthrow cycle.

Résumé

Une meilleure compréhension du régime de chablis est essentielle à la mise en place de l'aménagement forestier écosystémique, particulièrement pour les forêts possédant un long cycle de feu. Notre étude décrit la dynamique du chablis sur la Côte-Nord, au Québec, à l'échelle du paysage. De plus, l'influence des caractéristiques de site (épaisseur du sol, drainage, pente, topographie et vent) et de peuplement (essences dominantes, hauteur et densité) sur les probabilités de chablis a été évaluée. La base de données SIFORT, mise sur pied par le Ministère des Ressources naturelles et de la Faune du Québec, la société de protection des forêts contre le feu (SOPFEU) et la société de protection des forêts contre les insectes et maladies (SOPFIM), a été utilisée pour effectuer une analyse spatio-temporelle du chablis en fonction des caractéristiques de station. Les probabilités de chablis étaient influencées par l'exposition topographique (topex), la classe de pente et l'épaisseur du dépôt. Les probabilités de chablis augmentaient avec l'exposition topographique. Les chablis étaient plus fréquents lorsque le dépôt était épais (plus d'un mètre d'épaisseur) et la classe de pente était intermédiaire (de 15 à 30%). Finalement, cette étude a démontré l'importance du chablis partiel à l'échelle du paysage sur la Côte-Nord. Ainsi, nos résultats suggèrent que dans une perspective d'aménagement forestier écosystémique, les coupes partielles devraient être priorisées au profit des coupes totales et ce, dans le but de mieux émuler la dynamique régionale de chablis partiels.

Mots clés: topex, épaisseur du dépôt, pente, chablis partiel, chablis total, cycle du chablis.

Introduction

For several years now, the preservation of biodiversity and the modification of forestry practices with a view to reducing their impacts on ecosystems have emerged as global concerns (FAO 2009). As a result, greater scrutiny has been directed at the potential consequences of logging, including the loss of mature and structurally complex forest stands, soil impoverishment, and reduced ecological legacies (Jetté et al. 2009). Ecosystem management is a forestry approach that is designed to bridge the gap between natural forests and managed forests in order to pr.eserve the ecological integrity and biodiversity of ecosystems (Gauthier et al. 2009). It is an approach whose popularity has been growing in Quebec, in the other provinces of Canada (Mitchell and Beese, 2002; Burton et al. 2003) and throughout the world (Fisher et al. 2006).

In boreal forests, disturbance regimes create characteristics that are responsible for the regional biodiversity, involving, in particular, forest composition and structure, soil organic matter, and standing and downed deadwood (Gauthier et al. 2009; Bauhus et al. 2009). Natural disturbances are not only an integral part of boreal forest ecosystems, they are also the basis of several biological legacies and key attributes that are vital to the functioning of these ecosystems – all of which serves to demonstrate the relevance of disturbance regimes for the management of boreal forests (Niemelä 1999; Vaillancourt et al. 2009). Thus, first and foremost, the success of ecosystem management will depend on improving our knowledge of forest ecosystems and their natural disturbances (Kuuluvainen 2009; Vaillancourt et al. 2009).

The fire cycle of Quebec's boreal forest follows an east-west gradient. The bioclimatic domains consisting of balsam fir-white birch stands and spruce-moss stands enjoy more of a maritime climate in the eastern portion of the province than do domains in the western portion (Bouchard et al. 2008). As fires are rarer in the eastern portion of this bioclimate, the stands located there are often overmature. These older stands are more vulnerable to spruce budworm (*Choristoneura fumiferana*) outbreaks or windthrow events (Ruel 1995; Ruel and Benoit 1999). Thus there is now an understanding that natural disturbances other than forest fires can have a significant impact on boreal forest ecosystems (Bergeron et al. 1998; McCarthy 2001; McCarthy and Weetman 2007).

In Quebec, there is as yet little literature concerning the characterization of windthrow disturbance regime, notwithstanding its importance in terms of both the economy (Ruel and Benoit 1999) and ecosystems (Vaillancourt 2008). Bouchard et al. (2009) examined the occurrence of stand-replacing windthrow of over 5 ha, finding that windthrow events were both rather infrequent and difficult to predict. However, they also stressed the important role that smaller windthrows might play in forest stand dynamics and thus in the gap dynamics typifying stands in this region. Generally speaking, medium-intensity disturbances tend to attract less attention even if stands are at risk of being affected by them at least once in their lifetime (Stueve et al. 2011). The study of these disturbances is of considerable importance for improving our understanding of forest dynamics, particularly in regions that are little affected by fire. From the perspective of the ecosystem management of boreal forests, a better understanding of this disturbance regime will make it possible to choose silvicultural treatments that are both appropriate and well suited to a given region (Bergeron et al. 2009). The overarching objective of the present study is to describe windthrow dynamics at a landscape scale, including both total windthrow and partial windthrow, in a region of the boreal forest characterized by a long fire cycle, and to determine the influence of site characteristics (e.g., wind regime, topography and edaphic factors) and stand (e.g., composition, height, density) on this disturbance. The specific objectives were to: 1) characterize the pattern of windthrow severity and 2) estimate both the annual windthrow rate and the windthrow cycle for Quebec's North Shore region.

Methods

Study area

The study area covered a considerable portion of the North Shore (Côte-Nord) administrative region of Quebec, Canada. It extended from the 49th to the 52nd degree of latitude north and from the 66th to 70th degree of longitude west. Two sub-bioclimatic domains were thus considered – namely, the eastern spruce-moss subdomain and the eastern balsam fir-white birch subdomain (Figure 1).

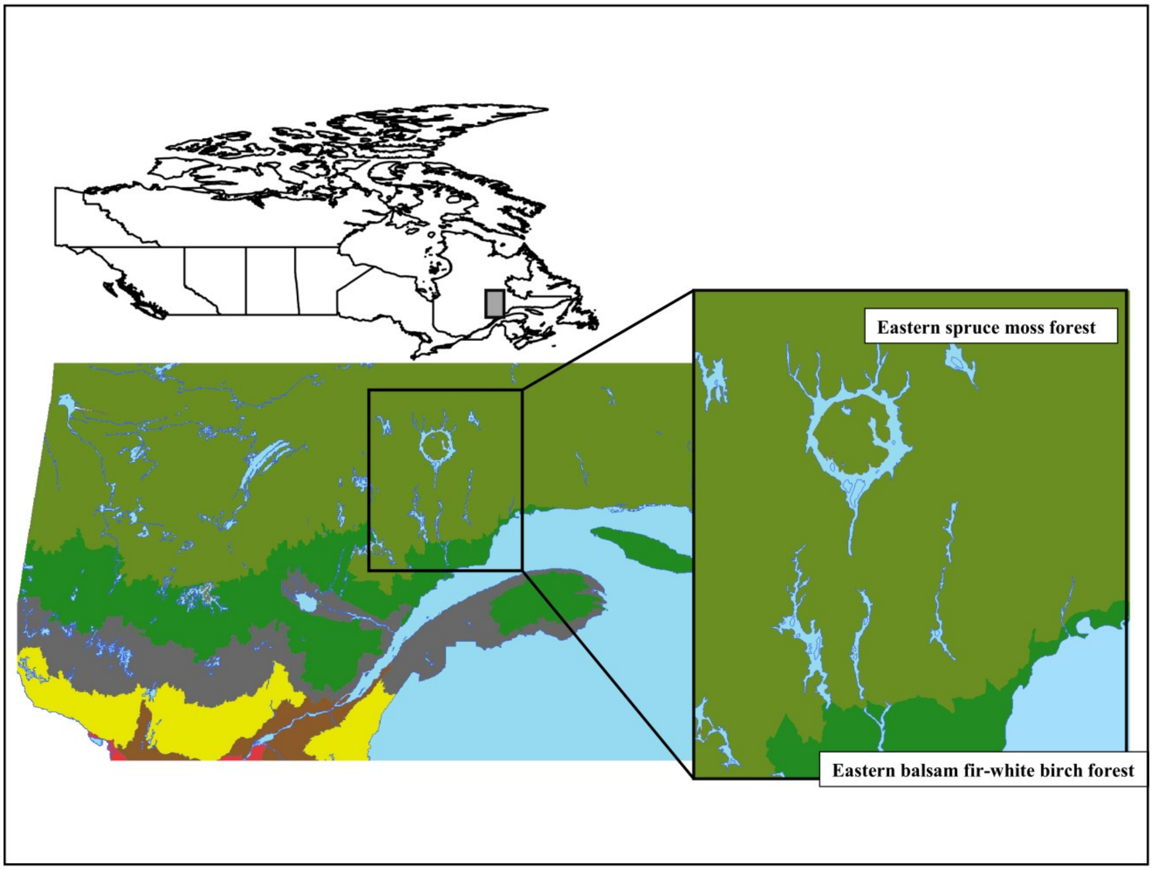

Figure 1: Study area. Colors represent bioclimatic subdomains.

Both the eastern fir and spruce subdomains are characterized by a generally undulating, heterogeneous relief. The mean altitude on the North Shore varies, ranging from 0 to 200 m along the St. Lawrence River to more than 500 m in the northern portion of the region, in the vicinity of the Manicouagan reservoir. Across the North Shore, surficial deposits consist primarily of undifferentiated glacial till of varying thickness but can also consist of fluvioglacial drift in the wider valleys. Rocky outcroppings frequently occur at the top of steep slopes. Below the 50th parallel, bedrock is omnipresent (Robitaille and Saucier 1998).

The SIFORT database

The system known as "SIFORT" ("Système d'Information FOREstière par Tesselle", or Tessera-based forestry information system) is a geobase that was established jointly by the Forest Protection Division of the Quebec Ministry of natural resources and wildlife (Ministère des Ressources naturelles et de la Faune MRNF-DEPF), the Quebec forest fire control agency (Société de protection des forêts contre le feu or SOPFEU) and the Quebec forest pest and disease control agency (Société de protection des forêts contre les insectes et maladies or SOPFIM) (Pelletier et al. 1998; Pelletier et al. 2007). SIFORT systematically samples the territory of Quebec, positioning a point at the center of a cell of 15 seconds by 15 seconds (i.e. mean area of 14 ha). The information contained in the database is derived from the ecoforestry maps of the Quebec Ministry of natural resources and wildlife (MRNF), which themselves have been based on three ten-year inventories. These inventories are based on aerial photograph interpretation complemented by field sampling. The aerial photograph interpretation can lead to a certain amount of errors which are hard to quantify. In spite of this error possibility, the SIFORT database has the advantage of affording a good-quality temporal analysis over extensive territories. The SIFORT system provides information about stand characteristics, soil characteristics and disturbances.

Windthrow

In the SIFORT database, the cells located in a windthrow area are divided into two categories – i.e., stand-replacing windthrows and partial windthrows. Windthrows are classified as stand-replacing or «total» whenever more than 75% of the basal area of trees in a polygon has been affected. A disturbance is said to be partial whenever 25 to 75% of the basal area has been affected. This classification was the same for the three inventories. In addition, since the SIFORT analysis was performed during three 10-year inventories, disturbances can be situated in time. Thus it is possible to determine whether a given disturbance occurred prior to the first inventory, between the first and second inventories, or between the second and third inventories.

Site and stand characteristics

The data used to describe the initial stand characteristics derived from the first 10-year inventory, conducted by the MRNF between 1970 and 1972 in the study area. Since the stand typology varied from one ten-year inventory to the next, integrating appellations from different inventories would have created problems. The edaphic data were taken from the third 10-year inventory because there was no such information in earlier inventories.

All the categories of stand density and height appearing in the forestry maps of the first 10-year inventory were kept. On the other hand, in order to simplify analysis, data from tree species groups were divided into 7 categories (Table 1). A detailed description of the various tree species groups is presented in Appendix A.

The slope classes appearing in the data of the first 10-year inventory were divided into 4 classes as presented in Table 1. Deposit and drainage classes were also grouped together. Drainage data were divided into 4 categories (Table 1). These categories were the same as those used by the MRNF in their "Field guides to ecological types" and were considered adequate for forest management purposes (Morneau and Landry 2007). Concerning surface deposit data, only thickness was retained for analytical purposes, since more than 96% of cells had a till-type deposit. Deposit thickness was thus divided up into classes in order to simplify analysis (Table 1).

Tableau 1: Classification of the variables examined and the methods used to inventory these variables.

Variables	Description	Methods
Windthrow	Partial windthrows (PW) and total windthrows (TW)	Determined via photo-interpretation.
Slope	Null: 0 à 3%, Gentle: 3 à 15%, Medium: 15 to 30% and Strong: 30% and over	Established on the basis of altitude and expressed to the nearest degree. Altitude is taken from the Government of Canada altimetric database every 3 sec and is expressed to the nearest metre.
Deposit thickness	Shallow: 0 to 50 cm, Medium: 50 cm to 1 m and Thick: over 1 m	Determined via photo-interpretation.
Drainage type	Xeric (X), Mesic (M), Subhydric (S) et Hydric (H)	Determined via photo-interpretation.
Tree species groups	Hardwoods (H), Mixed conifer-hardwood (MCH), Black spruce (BS), Mixed conifer-black spruce dominant (MCBS), balsam fir (BF), Mixed conifer-balsam fir dominant (MCBF) and Other (O)	Determined via photo-interpretation. Representation in terms of basal area of the species making up the stand.
Stand density	A: 81% and over, B: 61% to 81%, C: 41% to 60% and D: 25% to 40%	Determined via photo-interpretation. Per cent of cover formed by the ground projection of the crowns of trees over 7 m high.
Stand height	1: over 21 m; 2: 15 to 21 m; 3: 9 to 15 m; and 4: under 9 m with merchantable volume	Determined via photo-interpretation. Mean height of dominant and co-dominant trees.
Topex	Continuous numerical values	See topex section.
Wind at 10 m from ground	Continuous numerical values	See wind section.

Topex

The existence of a solid correlation between topography-based indices of wind exposure and real wind data has been demonstrated on several occasions previously (Ruel et al. 1997; Quine and White 1998). The wind exposure index used in this study is the topex-to-distance index (also referred to as distance-limited topex). This index is the sum of the angle to skyline for the main relief element in relation to the 8 cardinal directions around a given point and over a predetermined distance (referred to as the limiting distance). Horizontal is zero degrees, which means that a skyline higher than horizontal is positive topex values, and a skyline lower than horizontal is negative (Ruel et al. 1997; Quine and White 1998; Ruel et al. 2002). Thus a very negative topex value indicates that the point is highly exposed to wind – e.g., a mountaintop. Conversely, a very positive value indicates that the point is little exposed to wind – namely, at the base of several slopes, such as the bottom of a valley.

The Forest Inventory Unit of the MRNF has calculated the topex values for all of Quebec's forest territory. Topex data have been taken from a 100 m * 100 m grid with a limiting distance of 500 m (according to Quine and White 1998) using the routine of Ruel et al. (2002).

Wind

Wind data from the Canadian Wind Energy Atlas (http://www.windatlas.ca), hosted by Environment Canada, were used to characterize the regional climate. This atlas provides, across the entire territory of Canada, a description of the wind energy potential for any given location. It combines long-term climate data, field measurements and 3-D atmospheric modelling. Simulations were performed by Environment Canada at an average resolution of 5 km. The variable used in this study was the mean annual wind speed (m/s) estimated at 10 m above ground.

Statistical analyses

The study area was covered by slightly more than 500,000 cells. To begin with, cells representing non-forest land use were eliminated so as to keep only productive forest lands, which constituted approximately 80% of the total number of samples. Cells where man-made disturbances were observed were also removed from the analysis. Harvesting was more frequent in the southern part of the study area. In the North Shore region, harvesting has generally occurred in old-growth stands, which represents an important proportion of the stands. In spite of harvesting, a major proportion of the remaining stands were still over-mature. Approximately 10% of the total area has been cut. No documention indicating salvage logging after windthrow could be found. Finally, cells in which windthrow occurred prior to the first ten-year inventory were eliminated since no temporal dimension could be associated with them. Ultimately, the number of cells available for analysis was 216,312. Cells located in an area affected by windthrow were divided into five categories (Table 2) so as to monitor disturbance over two periods. In those categories, the letter “P” was used for partial windthrow and “T” for “total” stand-replacing windthrow. Position of the letters represents the inventory program. For example, OOP category represented a partial windthrow between the second and the third inventory program, OPT represented a partial windthrow between the first and the second inventory program and a stand-replacing windthrow between the second and the third inventory program, etc.

In the study area, the first inventory was conducted primarily in 1972, the second between 1987 and 1991, and the third primarily in 1999. The first period – namely, the one occurring between the first and second 10-year inventories – covered 15 to 19 years while the second – occurring between the second and third 10-year inventories – covered 8 to 12 years.

In order to minimize spatial autocorrelation, a stratified random subsample was subsequently produced, further lightening the data file. A third of cells in each windthrow category were conserved for the analysis. Ultimately, a third of the 216,312 cells covering the study area were kept.

Tableau 2: Description of windthrow categories.

Windthrow categories (symbols used)	Disturbance code in 1st 10-year inventory	Disturbance code in 2nd 10-year inventory	Disturbance code in 3rd 10-year inventory
OOO	-	-	-
OPP	-	PW*	PW
OPT	-	PW	TW**
OTT	-	TW	TW
OOP	-	-	PW
OOT	-	-	TW

*PW: Partial windthrow

**TW: Total windthrow

Statistical analyses were conducted using "R" software (R Development Core Team 2009). To begin with, a check was performed on colinearity between the different variables being examined. For both numerical variables – i.e., topex and wind speed – Pearson's correlation test was performed. For categorical variables, a visual analysis of the breakdown of variables was performed in order to check for the potential presence of correlation. In one single case, a clear link could be noted between two variables – namely, the type of drainage and the slope class. In order to choose between these two variables, an AIC (Akaike information criterion) was performed using three models – i.e., a null model, a model with drainage, and a model with slope class. The model with the slope variable proved to be the best of the three. The drainage variable was thus excluded from our analysis.

As one of the objectives of this study was to predict the probability of various combinations of windthrow (Table 2) according to site characteristics, multinomial logistic regression was used. In our case, 6 levels of Y were to be considered, thus making it possible to obtain 5 comparisons with the reference level, which was established as sites without windthrow (OOO). These comparisons were: OPP vs. OOO, OPT vs. OOO, OTT vs. OOO, OOP vs. OOO and OOT vs. OOO (Table 2).

Eleven models serving to predict the probability of various combinations of windthrow were pre-selected on the basis of our knowledge of factors influencing windthrow. Among these models, four were related to topographical and edaphic variables: 1) Slope, 2) Deposit, 3) Slope + Deposit, and 4) Slope + Deposit + Topex; three were related to stand variables: 1) Species + Density + Height + Density*Height, 2) Species + Density + Height + Density*Height + Topex, and 3) Species + Density + Height + Density*Height + Wind + Topex; and three were related to geographical variables: 1) Topex, 2) Wind, and 3) Wind + Topex. The eleventh model was a null model, thus the most restrictive model. The corrected Akaike information criterion (AIC_c), the delta AICc (Δ_i) and the Akaike weight (w_i) were calculated as a way of selecting the best model(s) among the set of 11(see Anderson et al. 2000 for details).

Results

Variations in descriptive statistics between the various categories of windthrow were relatively low. Indeed, the dominant deposit thickness was the same for each category of windthrow, this was also the case for the dominant slope class. The only exception was the OOT category, whose dominant slope class was medium. Concerning the topex and wind speed values, the means and standard deviations also showed a relatively low variability among the different categories of windthrow (Table 3).

Tableau 3: Descriptive statistics of numerical variables by category of windthrow.

Variables		**Categories of windthrow**					
		OOO	**OOP**	**OOT**	**OPP**	**OPT**	**OTT**
Topex	Mean	3	-33	7	0	7	23
Values	S.D.	24.06	44.19	17.85	56.47	18.84	22.93
Wind	Mean	4.0	3.5	4.1	3.0	4.2	3.1
Speed (m/s)	S.D.	1.34	1.34	0.07	0.28	1.41	0.21

A total of 72,104 cells were analyzed (Table 4). Cells located in a partial windthrow area were more numerous than those located in a severe windthrow area; this observation held for both of the periods under consideration. The proportion of cells affected by a windthrow was higher during the second period in comparison with the first period. Partial windthrows appearing during the third ten-year inventory (OOP) constituted the most frequently occurring category of windthrow in the study area (Figure 2). The slope and deposit conditions most frequently encountered on the North Shore territory were medium deposits and gentle slopes (Table 4).

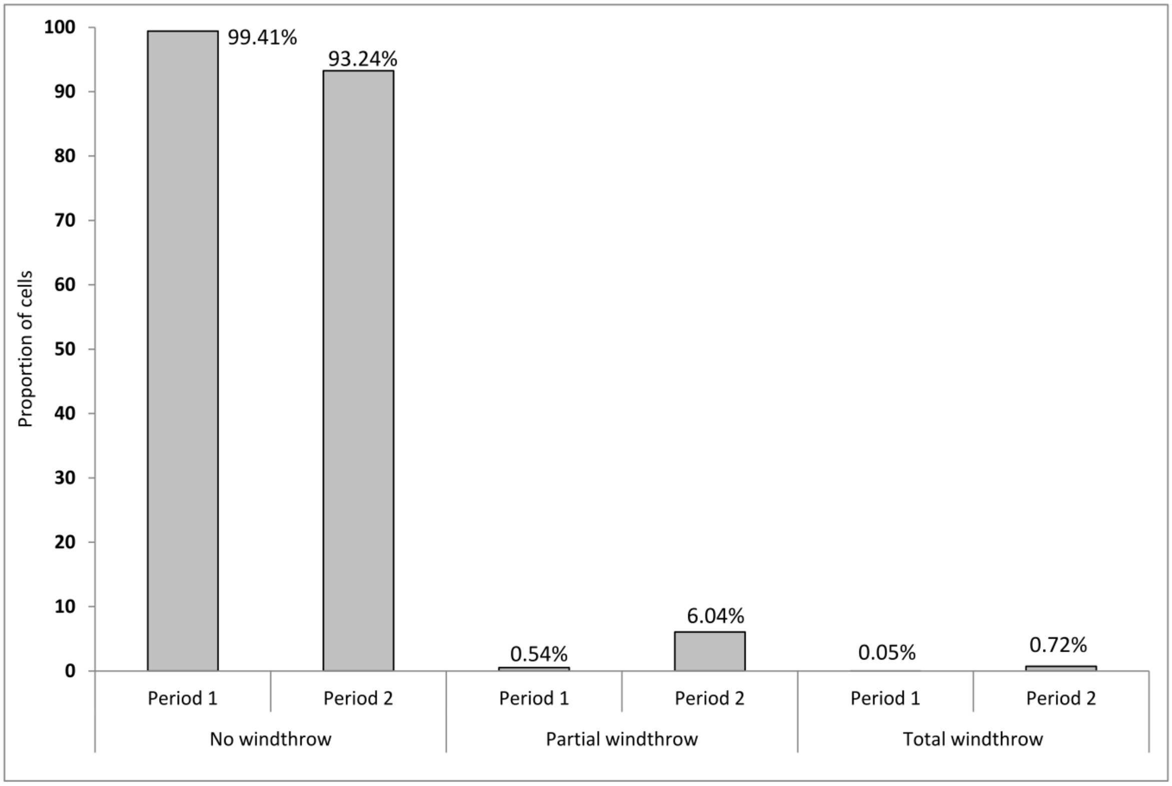

Figure 2: Evolution of areas affected by a partial windthrow or a total windthrow or that were unaffected by windthrow for the two periods under study. Period 1 occurred between the 1st and 2nd 10-year inventories and Period 2 between the 2nd and 3rd 10-year inventories.

Tableau 4: Distribution of observations across the classes of each variable. For the tree species groups, O: Others; H: Hardwood; MCH: Mixed conifer-hardwood; BS: Black spruce; MCBS: Mixed conifer-black spruce dominant; BF: Balsam fir; MCBF: Mixed conifer-Balsam fir dominant.

Variables		**Categories of windthrow**						**Total**
		OOO	**OOP**	**OOT**	**OPP**	**OPT**	**OTT**	
	O	3	0	0	0	0	0	3
	H	282	41	3	1	1	0	328
Tree species groups	MCH	2219	753	83	78	22	8	3163
	BS	61833	2455	237	197	32	23	64777
	MCBS	1259	328	43	23	3	3	1659
	BF	1604	385	44	24	8	0	2065
	MCBF	31	69	8	1	0	0	109
	A	2695	168	24	8	1	3	2899
Density	B	34173	2430	275	199	43	24	37144
	C	21096	1266	107	110	19	6	22604
	D	9267	167	12	7	3	1	9457
	1	2	1	0	0	0	0	3
Height	2	19368	1701	138	201	30	12	21450
	3	42493	2285	276	121	36	20	45231
	4	5368	44	4	2	0	2	5420
	Null	1256	17	1	0	1	0	1275
Slope	Gentle	57376	2047	174	195	32	14	59838
	Medium	5266	1559	189	109	29	13	7165
	Strong	3333	408	54	20	4	7	3826
Deposit thickness	Shallow	18780	807	92	58	15	6	19758
	Medium	39726	1782	201	142	29	19	41899
	Thick	8725	1442	125	124	22	9	10447

	X	2621	42	4	3	1	2	2673
Drainage	M	56361	3710	405	299	63	30	60868
	S	7271	275	9	22	2	2	7581
	H	978	4	0	0	0	0	982
Total		**67231**	**4031**	**418**	**324**	**66**	**34**	**72104**

A comparison of the 11 models made using the AICc showed the Slope+Deposit+Topex model to be the best (Table 5). This model had a delta AICc of 0 – that is, the lowest delta AICc among all the models. In addition, it had an Akaike weight of 1, meaning that there was a 100% probability that this model was the best one. The use of topex, slope or deposit thickness alone produced low-quality models. Grouping these 3 variables together within the same model improved their predictive power. The Slope+Deposit model came in second, with a delta AICc of 110.61. However, the Akaike weight was nil, indicating that there was no probability that this model would be the best of the 11 models. Thus, adding the topex variable to the Slope+Deposit model considerably enhanced its quality.

Estimates of slope were calculated in reference to gentle slope while those in relation to deposit were calculated in reference to thick deposit. For the categories of windthrow, the reference level was the OOO category. Negative estimates of slope and deposit indicated that windthrow probabilities were lower than those of the reference level. As showed by the negative sign of their coefficient, estimates of the intercept and topex values indicated that the probability of obtaining each of the categories of windthrow diminished as the topex value increased (Table 6).

Tableau 5: Hierarchy of models obtained using the AIC.

Models	K	LL*	AIC_c	Δ_i AIC_c	w_i
Slope+Deposit+Topex	35	-17726.61	35523.26	0	1
Slope+Deposit	30	-17786.92	35633.87	110.61	0
Species+Density+Height+Density*Height+Wind+Topex	105	-18538.36	37387.02	1863.76	0
Species+Density+Height+Density*Height+Topex	100	-18800.75	37801.79	2278.52	0
Species+Density+Height+Density*Height	95	-18818.02	37826.30	2303.03	0
Slope	20	-19081.54	38203.09	2679.83	0
Deposit	15	-20232.44	40494.88	4971.62	0
Topex+Wind	15	-20653.31	41336.63	5813.37	0
Wind	10	-20673.84	41367.68	5844.42	0
Topex	10	-20933.93	41887.86	6364.60	0
Null model	5	-20956.57	41923.15	6399.89	0

*LL: log-likelihood

Tableau 6: Estimates of parameters of the best model. Estimates of slope classes are established with gentle slope as reference level and estimates of deposit thickness with thick deposit as reference. The reference category for the windthrow type is OOO.

Parameters		Categories of windthrow				
		OOP	**OOT**	**OPP**	**OPT**	**OTT**
Intercept		-1.9176	-4.4365	-4.2938	-6.0831	-6.9857
Topex values		-0.0064	-0.0062	-0.0069	-0.0239	-0.0146
Slope	Null	-1.4716	-1.8160	-82.6384	-0.0154	-69.0698
	Medium	2.5999	2.9109	2.2656	2.7270	2.6705
	Steep	1.8883	2.2888	1.1974	1.1495	2.9083
Deposit	Shallow	-2.2122	-2.1179	-2.1683	-2.2216	-2.6279
	Medium	-2.0041	-1.8808	-1.9392	-2.0485	-1.6303

Topex value and windthrow probabilities

Among the different categories of windthrow, the OOP type of windthrow had the highest intercept value (Table 6). Accordingly, the probability associated with this category was the highest, regardless of slope class or deposit thickness. The probabilities of OOP decreased as topex increased. In two situations of slope class and deposit thickness, the probabilities of a partial windthrow between the second and third ten-year inventories (OOP) were greater than the probabilities of an absence of windthrow (OOO). Indeed, when deposit was thick and slope was medium (Figure 3b) or steep, the probabilities of OOP were higher than those of OOO for negative topex values. The probabilities of OOO again became higher than those of OOP when topex was positive. When slope was null, gentle or medium (Figure 3b), the OPT category had a relatively high probability in relation to very negative topex values. These probabilities again became quite low when topex was close to 0. On the other hand, when slope was steep, the probabilities of obtaining OPT were no higher than 1% – notwithstanding a very negative topex value. Concerning the other categories of windthrow – i.e., OOT, OPP and OTT – the probabilities remained below 5%, regardless of the conditions present.

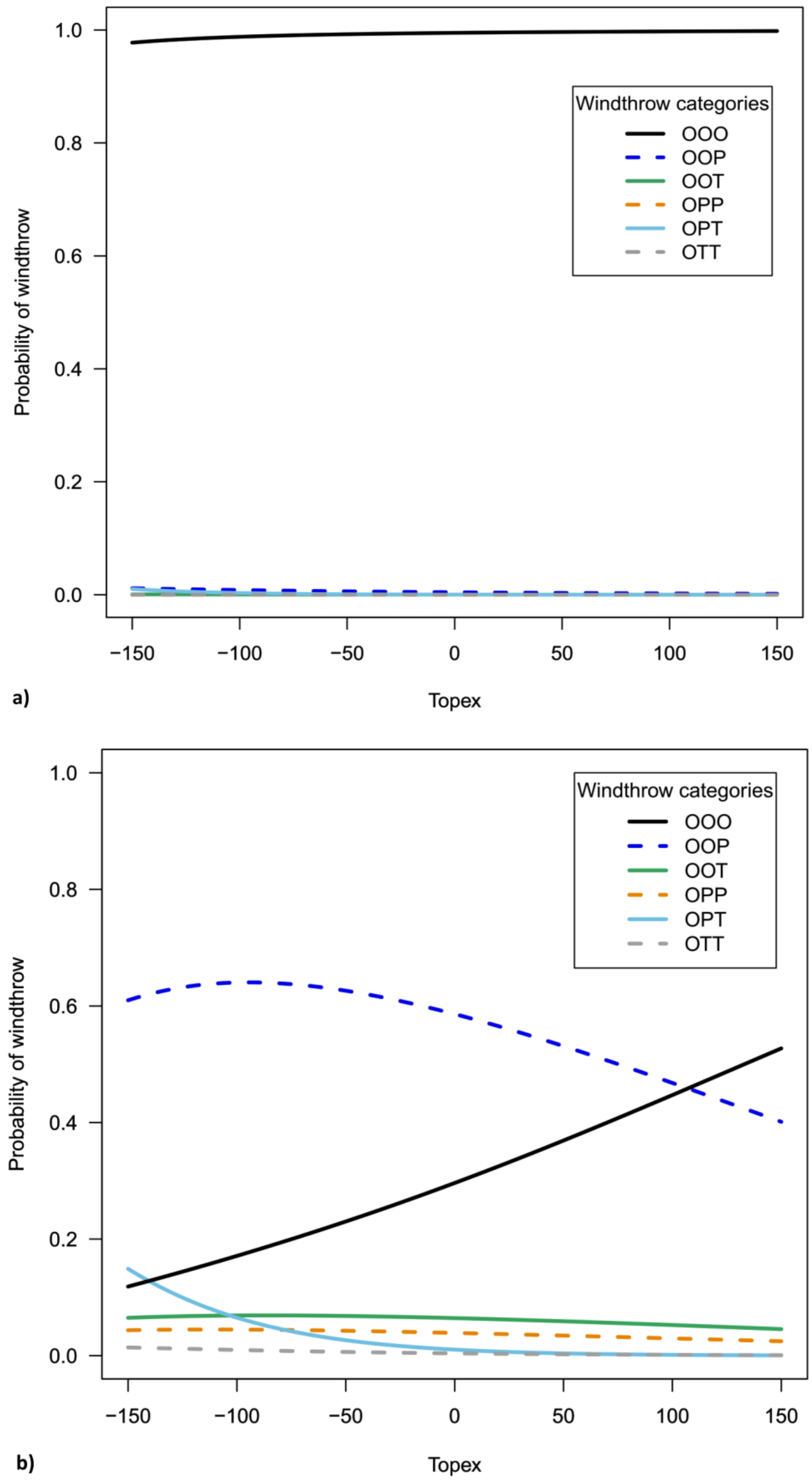

Figure 3: Probability of windthrow according to topex when: a) slope is null and deposit is medium (n=824); and b) slope is medium and deposit is thick (n=464).

Regardless of the category of windthrow, there was a negative relation between windthrow probability and topex value (Table 6). This effect of topex can be seen for all slope and deposit thickness classes (Tables 7 and 8). On the other hand, the effect of topex varied according to the categories of windthrow. The coefficient of the OPT and OTT categories was closer to 0 than was the coefficient of the other three categories (Table 6), indicating that the OPT and OTT categories were less influenced by the topex than the OOP, OOT and OPP categories were. For the site conditions occurring most frequently in the study area – i.e., a gentle slope and medium deposit thickness – the probability that there would be no windthrow (OOO) increased 4.5% in the case of a topex ranging from -150 to 0, and increased 1.4% in the case of a topex ranging from 0 to 150. For the same site conditions, the probability of obtaining the OOP category decreased 2.9% in the case of a topex ranging from -150 to 0, and decreased 1.2% in the case of a topex ranging from 0 to 150. Again, for the most common site conditions, windthrow probabilities for all categories combined decreased approximately 6% in the case of a topex ranging from -150 to 150.

Tableau 7: Probability (in %) of windthrow, all categories combined, in a given cell.

Slope class	**Deposit thickness**					
	Shallow deposit		Medium deposit		Thick deposit	
	Min topex	Max topex	Min topex	Max topex	Min topex	Max topex
Null	2	0	2	0	15	1
Low	6	1	7	1	35	6
Medium	45	9	50	11	88	47
Steep	27	5	32	6	77	30

Tableau 8: Number of cells (*n*) according to deposit thickness, slope classes and topex values.

Slope class	Deposit thickness					
	Shallow deposit		Medium deposit		Thick deposit	
	Min topex	Max topex	Min topex	Max topex	Min topex	Max topex
Null	2	16	251	573	69	364
Low	8265	7169	12748	22171	2562	6923
Medium	981	712	2065	2943	127	337
Steep	1414	1199	486	662	21	44

While following the same general pattern, the effect of the topex value on the probability of different categories of windthrow varied in relation to deposit thickness and slope class. When the deposit was medium and slope was null (Figure 3a) or gentle and when deposit was shallow and slope was null or gentle, the effect of the topex was minimal, across all 6 categories of windthrow. Windthrow probabilities were always lower than 7% (Tables 7 and 8). The cases where the influence of topex was most apparent occurred when the deposit was shallow and the slope medium, the deposit was medium and the slope medium, or the deposit was thick and the slope medium or steep (Figure 3b). The effect of topex was intermediate where the other conditions of slope and deposit were concerned (Tables 7 and 8).

The effect of slope on windthrow probabilities

For a given slope class, the coefficient remained the same, regardless of the category of windthrow (Table 6). The negative sign for the coefficients obtained for null slopes indicated a reduced windthrow probability in comparison with the reference category – i.e., gentle slopes. The OPP and OTT categories had a coefficient for null slopes that was lower than that obtained for the other categories of windthrow, indicating that in comparison with gentle slopes, the probabilities for these two categories were even lower than for the other windthrow categories. The positive sign for the coefficients of medium and steep slopes indicated that windthrow hazards were higher for these classes of slope than for gentle slopes. The higher values of coefficients for medium slopes in comparison with those for steep slopes indicated that windthrow probabilities were higher on medium slopes, with the exception of the OTT category, where the probabilities were higher on steep slopes (Table 6). Regardless of deposit thickness, a similar pattern could be seen among the various slope classes and the overall windthrow probability (that is, for all windthrow categories combined) (Tables 7 and 8). The lowest windthrow probabilities occurred among the samples belonging to a null or gentle slope class. For both these slope classes, the probability of encountering the OOO category was thus highest (Figures 4a and b). Steep slopes had an intermediate probability of windthrow. Medium slopes consistently produced the highest windthrow hazards; it was there also that the probabilities of encountering OOO were lowest. However, these hazards varied according to deposit thickness and topex value, as the model included all three variables (Figures 4a and b).

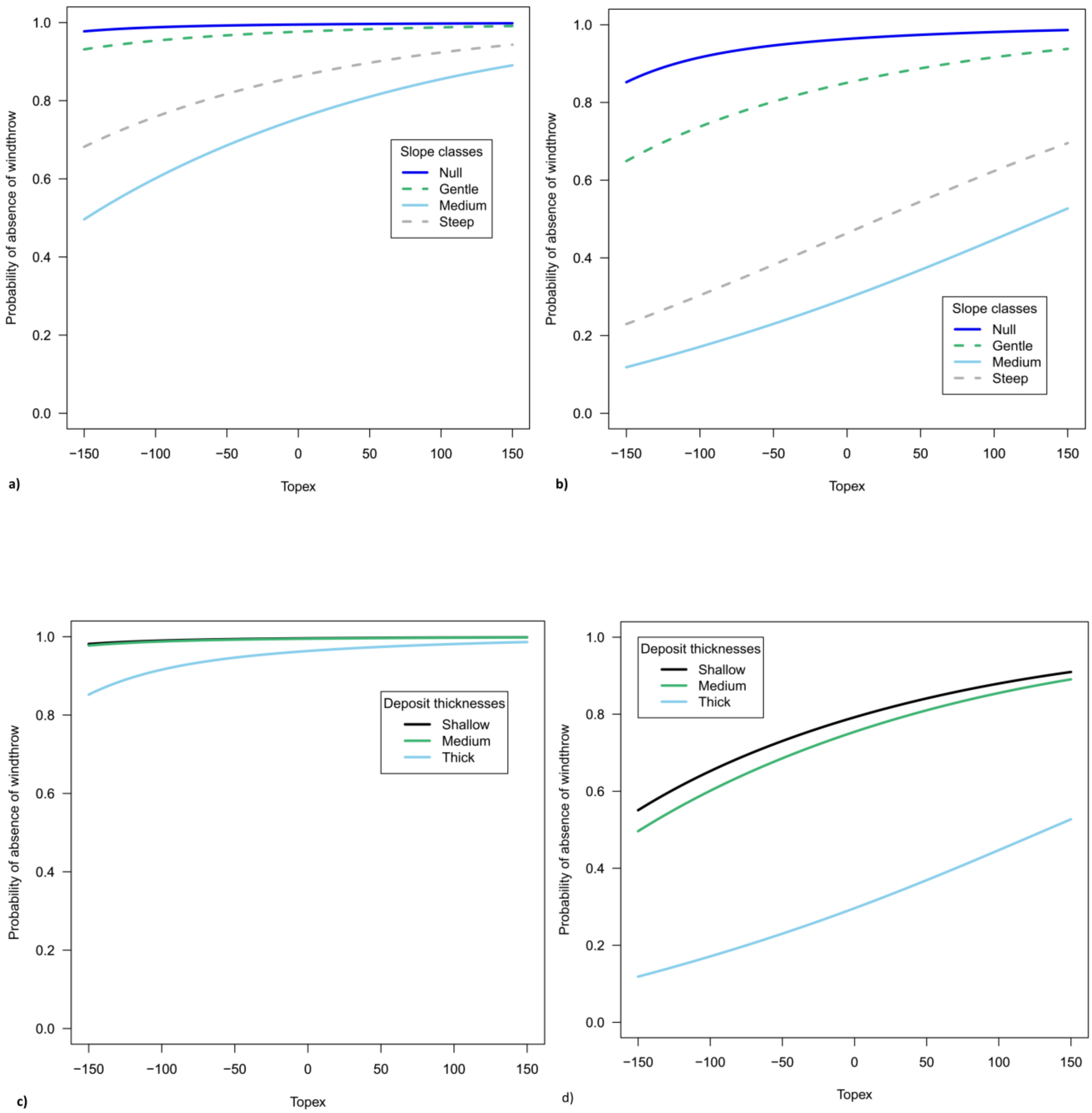

Figure 4: Probability of absence of windthrow (OOO) according to topex for different slope classes when deposit is a) medium and b) thick; and probability of absence of windthrow according to topex for different deposit thicknesses when slope is c) null and d) medium.

The effect of deposit thickness on windthrow probabilities

For a given deposit thickness, the sign for the coefficient remained the same, regardless of the windthrow category (Table 6). The negative sign for the coefficients for shallow and medium deposits indicated a lower probability of windthrow on these in comparison with thick deposits. The highest values for coefficients for deposits of medium thickness, as compared with those for shallow deposits, indicated that windthrow probabilities were greater for medium deposits than for shallow deposits. On the other hand, the coefficients of the OOP and OPT categories for medium deposits were lower than those obtained for other categories of windthrow, indicating that the difference in probability between medium and shallow deposits (reference category) was lesser for these two categories of windthrow (Table 6). Regardless of the slope class and the topex value, the influence of deposit thickness on windthrow probabilities followed the same overall pattern (Tables 7 and 8). That being said, slope classes and topex values influenced the hazard level, as the model included all these variables (Figures 4c and d). Deposits of medium thickness presented the lowest overall windthrow probabilities (i.e., for all categories combined). Windthrow probabilities were at their highest when deposits were thick; thus the probability of OOO in relation to these locations was lowest. Finally, windthrow probabilities were intermediate when shallow deposits were concerned. Once again, these windthrow probabilities varied according to the topex value (Figures 4c and d).

Windthrow cycle

Over the 30-year timeframe covered by this study, 6.75% of the territory underwent a windthrow, all categories of windthrow combined. Partial windthrows or those partial windthrows that became total windthrows account for 6.1% of the study territory. Thus the annual mean windthrow rate would appear to be 0.23% for the study area. Assuming that the windthrow cycle was constant over time, one could reckon that the entire study area will be affected by a windfall over an approximately 450-year-long period. If only stand-replacing windthrow were considered, the windthrow cycle at the regional scale would be around 4,600 years.

The slope and deposit conditions most frequently encountered on the North Shore territory were medium deposits thickness and gentle slopes (Table 4). Cells possessing these characteristics accounted for 48% of the total number of cells. Considering only these slope and deposit conditions, the annual windthrow rate would be 0.08% and the windthrow cycle would last 1,250 years. Finally, if only those cells having the strongest windthrow hazards were considered – i.e., those with a thick deposit and a medium slope – the annual windthrow rate would be 2.49%. Under these conditions, the windthrow cycle would last 40 years. However, it is important to mention that these highly windthrow-prone sites were rather rare, forming only 0.64% of the study area.

Discussion

The natural disturbance regime is often used as a model for designing ecosystem management strategies. This regime can be described according to the frequency, intensity and size of natural disturbances (Vaillancourt et al. 2009). In the region under study, the fire cycle has been calculated to last from 250 to 600 years (Bouchard et al. 2008) whereas that of severe spruce budworm epidemics is thought to be 2,860 years (Boucher et al. 2011). Gap dynamics were previously described by Pham et al. (2004) and Périgon (2006) while those of stand-replacing windthrows were described by Bouchard et al. (2009). On the other hand, partial windthrow dynamics have not been analyzed. The present study thus serves to supplement the available information concerning the frequency and intensity of windthrow for a region characterized by the low reoccurrence of stand-replacing disturbances.

The present results provide a basis for estimating the length of the windthrow cycle in the North Shore region. This approximately 450-year-long cycle would thus appear to be comparable to the fire cycle in the study area. The results of the present study demonstrate that windthrow is a non-negligible natural disturbance on the North Shore territory when partial windthrows, and not just stand-replacing windthrows, are considered. Windthrow dynamics in the study region are characterized by disturbances of intermediate intensity.

This is not only true for the Quebec North Shore region. Many studies have showed that partial windthrows are more important than stand-replacing windthrows for a given territory (Frelich and Lorimer 1991; Kuuluvainen 2009; Stueve et al. 2011). Our findings confirm those of Bouchard et al. (2009) according to whom stand-replacing windthrows constitute a relatively infrequent event on this territory. If only stand-replacing windthrows were considered in our study, the cycle would be approximately 4,600 years, which is similar or a little higher than severe windthrow cycle in the Great Lakes region (Canham and Loucks 1984; Lorimer and White 2003). At the same time, however, these results show the need to consider partial windthrows in the analysis of this kind of disturbance.

Windthrow dynamics do not occur over the territory with uniformity; thus the cycle was not constant throughout the study area and varied according to site characteristics. Topex value, slope and deposit thickness caused variations in windthrow probabilities and, by the same token, in the disturbance cycle. When only the most widespread site conditions of the study area were considered – i.e., gentle slope and medium-thick deposit (Table 4) – then the probabilities of a windthrow, over the approximately 30-year period covered by the analysis, ranged from 0.9% to 6.87%, all depending on the topex value. The OOP category alone accounted for 0.75% to 4.79% of these probabilities.

The relatively high incidence of partial windthrow that occurred during the second period (OOP) suggest that a particular meteorological event occurred during this period, especially considering that the time covered under this period was shorter than that of the first study period. Data from a weather station of Environment Canada located about 150 km west of the study area shows that, in the middle of the 1990's, some wind speed records were registered. Although it is impossible to know the specific moment of windthrow episodes, we know that something happened between the second and the third inventory. The second period followed a spruce budworm outbreak that occurred in 1980. This epidemic was particularly severe and primarily affected the southern portion of the North Shore, characterized in large part by balsam fir forests. Spruce budworm outbreak can cause direct death of trees but also increases windthrow in the stand. Trees previously protected by other trees become more susceptible to windthrow when there is an opening in the stand

(Morin 1994; Spence and MacLean 2011). Conversely, the impact of this epidemic on the black spruce forest (dominant in the northern portion) was weak (Bouchard and Pothier 2010). To verify whether the 1980 epidemic might have influenced or confounded partial windthrow occurring between the second and third ten-year inventories, the same statistical analyses were performed, but using only the cells covered by black spruce forests. Following these analyses, the Slope+Deposit+Topex model remained the best and the significance of OOP in comparison to other categories again stood out. Thus, the predominance of partial windthrows in this study did not appear to be either a consequence or a confounded effect of the spruce budworm epidemic.

Topex value and mean wind speed

The results of this study brought out an increase in windthrow probabilities in conjunction with a decrease in topex values for several slope and deposit situations. Topex is recognized as having good predictive power in relation to wind regimes (Ruel et al. 1997; Quine and White 1998). Trees growing at the top of a mountain are, as a rule, more exposed to winds than those growing in the middle of a slope or at the foot of a mountain (Ruel et al. 1998).

In this study, local variations in wind exposure, when estimated by the topex value, had a greater effect than the regional variations in weed speed described on the basis of the Canadian Wind Energy Atlas. On the other hand, Meng et al. (2008) noted an improvement of their windthrow prediction model (based on the tree height/diameter relationship) after incorporating wind data from this atlas. It should be noted, however, that Meng et al.'s study was conducted in Alberta (Canada), a province having a contrasting topography along with major regional wind speed variations. In our study, mean wind speeds at 10 m from the ground varied to a lesser degree, ranging from 3 m/s to 4.2 m/s (Table 3b). Although our study cannot be compared directly with that of Meng et al. (2008), it is nevertheless apparent that the regional variations considered in both studies are not on the same scale. Furthermore, it is conceivable that the weak resolution (5 km) of wind speed data did not make it possible to account for the topography present in the North Shore region. Topex value was estimated at a finer scale and thus better represents the effect of the topography.

Slope classes

The windthrow probabilities were greatest when the slope was medium and were lowest when the slope was null or gentle (Tables 7 and 8, Figures 4a and b). It is generally accepted in the literature that windthrow hazards are higher for a sloping site than for a flat area (Schaetzl et al. 1989a; Ulanova 2000). However, the higher windthrow probabilities shown for medium slopes in comparison to steep slopes are counterintuitive. Indeed, an increase in slope classes is often associated with an increase in windthrow probabilities (Ulanova, 2000). Our results could be due to the fact that other variables, not integrated in the model, could still play a role. Indeed, the proportion of balsam fir and mixed conifer-balsam fir dominant forest was nearly 4 times higher than the overall proportion of these species groups in medium slopes. As has been repeatedly demonstrated, balsam fir is more prone to windthrow than spruce, owing to its vulnerability to decay (Ruel and Benoit 1999; Ruel 2000). Thus the higher proportion of balsam fir on medium slopes could explain the higher incidence of windthrow on medium slopes.

Deposit thickness

Windthrow probabilities were lowest in relation to medium deposits. They were intermediate in relation to shallow deposits and highest in relation to thick deposits (Tables 7 and 8, Figures 4c and d). These results are counterintuitive, since, in theory, thicker soils should be more conducive to deep rooting and thus be less prone to windthrow (Everham and Brokaw 1996). Other authors have, nonetheless, obtained similar results. The study by Bouchard et al. (2009), conducted in the same region, arrives at a similar conclusion concerning the role of deposit thickness in relation to windthrow hazard. In that study, relatively deep tills (more than 25 cm) were affected more by windthrow than was the case with shallower deposits (Bouchard et al. 2009). Stueve et al. (2011) also noted, in another forest ecosystem, a higher proportion of windthrow on thick deposits – i.e., those having a thickness of more than 1.5 m. In our study area, a marked increase in windthrow probability in conjunction with shallow deposits would be surprising. In effect, both of the two dominant species – i.e., the black spruce and the balsam fir – possess a superficial root system, regardless of soil thickness (Burns and Honkala 1990). From this perspective, a winching study conducted by Elie and Ruel (2005) showed that rooting constraints such as soil thickness do not influence the mechanical resistance of black spruce to uprooting in relation to a broad range of conditions.

The effect of deposit could be partially linked to soil drainage. Although there was no correlation between the drainage variable and the deposit thickness, the proportion of cells having a thick deposit with hydric drainage was 3 times higher than for the overall proportion for this type of drainage. Several studies have demonstrated the links between soil drainage and the vulnerability of trees to windthrow (Schaetzl et al. 1989a; Mitchell 1995; Ruel 1995). In fact, wet soils restrict rooting in a way similar to shallow soils (Schaetzl et al. 1989a). Thus the fact that cells having a thick deposit are poorly drained offers a possible avenue for explaining the maximal windthrow probabilities for this type of deposit.

Conclusion

The present study has served to develop a fuller portrait of natural disturbances in Quebec's North Shore region. In particular, it stands out on account of its focus on an as yet little examined natural disturbance – namely, windthrow – and for having extended its scope beyond severe disturbances, which, all in all, play a minor role in the disturbance regime of this region in comparison with other boreal forest regions. Indeed, our analysis took into account windthrows of intermediate intensity – i.e., those between canopy gaps and total windthrows – an approach that had not been done in the study area until now. The results of this study have shown the relevance of going beyond stand-replacing windthrows when accounting for characterizing the windthrow regime. Various site characteristics also affected the windthrow regime, namely topex value, slope and deposit thickness. However, it is important to note that considering the scale on which this study was conducted, some effects may be confounded. More refined studies would make it possible to better understand the fundamental role of each variable.

From the perspective of ecosystem management, partial windthrow should be taken into consideration when devising forest management plans for the territory of the North Shore region. If the objective is to look at windthrow dynamics as a model for forest management, then it will be necessary to find alternatives to the careful logging around advance growth cut (CLAAG, also referred to in Quebec as the “coupe avec protection de la régénération et des sols” (CPRS)) and the harvesting with protection of small merchantable stems (also referred to in Quebec as “coupe avec protection des petites tiges marchandes” (CPPTM), an equivalent of HARP, or “harvest with regeneration protection”). A greater use of partial cuts would be required to better emulate the natural disturbance dynamics. The spatial organization of windthrow should also be studied, using both finer data and spatial data. Finally, standing and downed deadwood, regeneration and pit-and-mound topography are further examples of key attributes of post-windthrow forest ecosystems (Schaetzl et al. 1989b; Ulanova 2000) that should be accounted for when establishing silvicultural recommendations. Field surveys will thus be required in order to characterize various post-windthrow elements of the North Shore boreal forest.

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References

Anderson, D.R., Burnham, K.P., and Thompson, W.L. 2000 Null hypothesis testing: problems, prevalence and an alternative. J. Wildl. Manage. 64(4): 912-923.

Bauhus, J., Puettmann, K., and Messier, C. 2009 Silviculture for old-growth attributes. For. Ecol. Manage. 258: 525-537.

Bergeron, C., Ruel, J.-C., Élie, J.-G., and Mitchell, S.J. 2009. Root anchorage and stem strength of black spruce (*Picea mariana*) trees in regular and irregular stands. Forestry 82: 29-41.

Bergeron, Y., Engelmark, O., Harvey, B., Morin, H., and Sirois, L. 1998. Key issues in disturbance dynamics in boreal forests: Introduction. J. Veg. Sci. Special Feature: 464-468.

Bouchard, M., Pothier, D., and Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Can. J. For. Res. 38: 1621-1633.

Bouchard, M., Pothier, D., and Ruel, J.-C. 2009. Stand-replacing windthrow in the boreal forests of eastern Quebec. Can. J. For. Res. 39: 1-7.

Bouchard, M., and Pothier, D. 2010. Spatiotemporal variability in tree and stand mortality caused by spruce budworm outbreaks in eastern Quebec. Can. J. For. Res. 40: 86-94.

Boucher, Y., Bouchard, M., Grondin, P., and Tardif, P. 2011. Le registre des états de référence: intégration des connaissances sur la structure, la composition et la dynamique des paysages forestiers naturels du Québec méridional. Mémoire de recherche forestière no. 161, Direction de la recherche forestière, Ministère des Ressources naturelles et de la Faune, 21 p.

Burns, R.M., and Honkala, B.H. 1990. Silvics of North America. Volume 1, conifers. Forest Service, United States Department of Agriculture, Washington DC.

Burton, P.J., Messier, C., Weetman, G.F., Messier, C., and Tittler, R. 2003. The current state of boreal forestry and the drive for change. *In:* Towards sustainable management of the boreal forest. Burton, P.J., Messier, C., Smith, D.W., and Adamowicz, W.L. (eds). NRC Research Press, Ottawa, Ontario, Canada, pp. 1-40.

Canham, C.D., and Loucks, O.L. 1984. Catastrophic windthrow in the presettlement forests of Wisconsin. Ecology 65(3): 803-809.

Elie, J.-G., and Ruel, J.-C. 2005. Windthrow hazard modelling in boreal forests of black spruce and jack pine. Can. J. For. Res. 35: 2655-2663.

Everham, E.M., and Brokaw, N.V.L. 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. 62(2): 113-185.

Fischer, J., Lindenmayer, D.B. and Manning, A.D. 2006. Biodiversity, ecosystem function, and resilience: ten guiding principles for commodity production landscapes. Front. Ecol. Environ. 4(2): 80-86.

Food and Agriculture Organization of the United Nations (FAO). 2009. State of the world's forests 2009, Rome, 164 p.

Frelich, L.E., and Lorimer, C.G. 1991. Natural disturbance regimes in hemlock-hardwood forests of the upper Great Lakes region. Ecol. Monogr. 61(2): 145-164.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D., Drapeau, P., De Grandpré, L., Claveau, Y., and Paré, D. 2009. Forest ecosystem management, origins and foundations. *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., and Bergeron, Y. (eds). Presses de l'Université du Québec, Montreal, Canada, pp. 13-37.

Jetté, J.-P., Vaillancourt, M.-A., Leduc, A., and Gauthier, S. 2009. Ecological issues related to forest management. *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. and Bergeron, Y. (eds). Presses de l'Université du Québec, Montreal, Canada, pp. 1-10.

Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. Ambio 38(6): 309-315.

Lorimer, C.G., and White, A.S. 2003. Scale and frequency of natural disturbances in the northeastern US: implications for early successional forest habitats and regional age distributions. For. Ecol. Manage. 185: 41-64.

McCarthy, J. 2001. Gap dynamics of forest trees: A review with particular attention to boreal forests. Environ. Rev. 9: 1-59.

McCarthy, J.W., and Weetman, G. 2007. Stand structure and development of an insect-mediated boreal forest landscape. For. Ecol. Manage. 241: 101-114.

Meng, S.X., Huang, S., Lieffers, V.J., Nunifu, T., and Yang, Y. 2008. Wind speed and crown class influence the height-diameter relationship of lodgepole pine: Nonlinear mixed effects modeling. For. Ecol. Manage. 256: 570-577.

Mitchell, S.J. 1995. The windthrow triangle: A relative windthrow hazard assessment procedure for forest managers. For. Chron. 71(4): 446-450.

Mitchell, S.J., and Beese, W.J. 2002. The retention system: reconciling variable retention with principles of silvicultural systems. For. Chron. 78(3): 397-403.

Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal Zone of Quebec. Can. J. For. Res. 24: 730-741.

Morneau, C., and Landry, Y. 2007. Guide de reconnaissance des types écologiques des régions écologiques 6h - Collines du lac Péribonka et 6i - Hautes collines du réservoir aux Outardes. Ministère des Ressources naturelles et de la Faune, Forêt Québec, Direction des inventaires forestiers, Division de l'analyse et de la diffusion des informations forestières et écologiques.

Niemelä, J. 1999. Management in relation to disturbance in the boreal forest. For. Ecol. Manage. 115: 127-134.

Pelletier, G., Dumont, Y., Bédard, M., and Bergeron, J. 1998. SIFORT, un système hybride des modes vectoriels et matriciels pour une nouvelle approche de l'analyse forestière. Arpenteur-Géomètre 23(3): 8-9.

Pelletier, G., Dumont, Y., and Bédard, M. 2007. SIFORT, Système d'Information FORestière par Tesselle. Manuel de l'usager. Ministère des Ressources naturelles et de la Faune, Québec, 125 p.

Périgon, S. 2006. Dynamique de trouées dans de vieux peuplements résineux de la Côte-Nord, Québec. M.Sc. thesis, Université du Québec à Montréal, Montréal, Canada, 107 p.

Pham, A.T., De Grandpré, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. 34: 353-364.

Quine, C.P., and White, I.M.S. 1998. The potential of distance-limited topex in the prediction of site windiness. Forestry 71(4): 325-332.

R Development Core Team. 2009. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Ministère des Ressources Naturelles, Direction de la gestion des stocks forestiers and Direction des relations publiques, Québec, 213 p.

Ruel, J.-C. 1995. Understanding windthrow: Silvicultural implications. For. Chron. 71(4): 434-444.

Ruel, J.-C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. For. Ecol. Manage. 135: 169-178.

Ruel, J.-C., and Benoit, R. 1999. Analyse du chablis du 7 novembre 1994 dans les régions de Charlevoix et de la Gaspésie, Québec, Canada. For. Chron. 75(2): 293-301.

Ruel, J.-C., Mitchell, S.J., and Dornier, M. 2002. A GIS based approach to map wind exposure for windthrow hazard rating. North. J. Appl. For. 19(4): 183-187.

Ruel, J.-C., Pin, D., and Cooper, K. 1998. Effect of topography on wind behavior in a complex terrain. Forestry 71(3): 261-265.

Ruel, J.-C., Pin, D., Spacek, L., Cooper, K., and Benoit, R. 1997. The estimation of wind exposure for windthrow hazard rating: comparison between strongblow, MC2, topex and a wind tunnel study. Forestry 70(3): 253-266.

Schaetzl, R.J., Johnson, D.L., Burns, S.F., and Small, T.W. 1989a. Tree uprooting: review of terminology, process and environmental implications. Can. J. For. Res. 19: 1-11.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., and Small, T.W. 1989b. Tree uprooting: a review of impacts on forest ecology. Vegetatio 79: 165-176.

Spence, C.E., and MacLean, D.A. 2011. Comparing growth and mortality of a spruce budworm (*Choristoneura fumiferana*) inspired harvest versus a spruce budworm outbreak. Can. J. For. Res. 41: 2176-2192.

Stueve, K.M., Perry, C.H., Nelson, M.D., Healey, S.P., Hill, A.D., Moisen, G.G., Cohen, W.B., Gormanson, D.G., and Huang, C. 2011. Ecological importance of intermediate windstorms rivals large, infrequent disturbances in the northern Great Lakes. Ecosphere 2(1), article 2: 1-21.

Ulanova, N.G. 2000. The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manage. 135: 155-167.

Vaillancourt, M.-A. 2008. Effets des régimes de perturbation par le chablis sur la biodiversité et les implications pour la récupération. Ministère des Ressources naturelles et de la Faune, Direction du développement socio-économique, des partenariats et de l'éducation et Service de la mise en valeur de la ressource et des territoires fauniques, Québec, 58 p.

Vaillancourt, M.-A., De Grandpré, L., Gauthier, S., Leduc, A., Kneeshaw, D., Claveau, Y., and Bergeron, Y. 2009. How can natural disturbances be a guide for forest ecosystem management? *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., and Bergeron, Y. (eds). Presses de l'Université du Québec, Montreal, Canada, pp. 39-55.

Chapitre II

WINDTHROW CHARACTERISTICS IN THE EASTERN BOREAL FOREST OF CANADA AT TWO SPATIAL SCALES

Abstract

Windthrow is a dominant natural disturbance in the boreal forest of eastern Canada. To provide a complete picture of the range of variability of a natural disturbance, its spatial distribution at stand (polygon) and landscape levels has to be considered. Our study characterized both partial (PW) and total windthrow (TW) spatial distributions at landscape level and patchiness within affected stands. Also, windthrow spatial characteristics were compared with spatial characteristics of harvested areas. At the landscape level, our results showed that TW polygons were more isolated than PW and that mean shape complexity of disturbed polygons was relatively low, regardless if the disturbance was a windthrow or a harvested area. At the polygon level, residual trees covered a significantly higher proportion of PW polygons than TW polygons and cutblocks. Cutblocks and TW did not share many spatial characteristics at the polygon level. Cutblocks had a significantly higher proportion of complete canopy openness than TW and they did not share the same within-polygon shape and isolation characteristics. Our results showed a high variability in PW size and density in the area. Thus, when emulating natural disturbances, managers should create a range of cutblock sizes and densities. Partial cutting and variable retention cuttings are two examples of harvesting methods more similar to PW.

Keywords: partial windthrows, total windthrows, clear-cuts, landscape, polygon, shape, size, mean-nearest neighbor distance, density, canopy openness.

Résumé

Afin de fournir un portrait global de la plage de variabilité naturelle d'une perturbation naturelle, ses caractéristiques spatiales à l'échelle du peuplement et du paysage doivent être connues. Notre étude a caractérisé la distribution spatiale du chablis partiel (CHP) et du chablis total (CHT) à l'échelle du paysage ainsi qu'à l'intérieur des peuplements affectés. De plus, les caractéristiques spatiales du chablis ont été comparées à celles des coupes totales. À l'échelle du paysage, nos résultats ont démontré que les CHT étaient plus isolés que les CHP et que la complexité moyenne de la forme des polygones était relativement faible, autant pour les CHP, les CHT et les coupes. À l'échelle du polygone, les îlots d'arbres sur pied résiduels couvraient une proportion significativement plus élevée des polygones de CHP que des CHT et des coupes. Toujours à l'échelle du polygone, la plupart des caractéristiques spatiales des CHT et des coupes étaient différentes. La proportion du polygone avec une ouverture de la canopée de classe 4 (75 à 100% d'ouverture) était significativement plus élevée pour les coupes que pour les CHT. De plus, « les patchs » de différentes classes d'ouverture de la canopée ne possédaient pas les mêmes caractéristiques de forme et d'isolement entre les coupes et les CHT. Nos résultats ont démontré que, dans notre zone d'étude, les CHP possédaient une grande variabilité quant à leur taille et leur densité. Ainsi, les gestionnaires devraient maintenir cette variabilité en ce qui a trait aux coupes, en assurant une variabilité en termes de taille et de densité. La coupe partielle et la coupe à rétention variable sont deux traitements qui seraient plus appropriés pour émuler les CHP que ne l'est la coupe totale.

Mots clés: chablis partiels, chablis totaux, coupes totales, paysage, polygone, forme, taille, distance moyenne du plus proche voisin, densité, ouverture de la canopée.

Introduction

As ecosystem management becomes a standard practice in forestry in Canada (Mitchell and Beese 2002; Gauthier et al. 2009) and also across the world (Kuuluvainen 2009), knowledge of the effects of natural disturbances on ecosystems is essential. Moreover, understanding natural disturbances can help us choose silvicultural treatments that reduce the differences between natural and managed forests (Gauthier et al. 2009). In the eastern part of the boreal forest of Quebec (Canada), the fire cycle is longer than in the western part (Bouchard et al. 2008). In western Quebec, the fire cycle ranges between 100 and 200 years (Bergeron et al. 2006) while in the east, it could be as long as 500 years (Bouchard et al. 2008). Consequently, other natural disturbances such as windthrow and outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) play a preeminent role in regulating forest ecosystems composition and function in this latter region (Ruel 2000; Pham et al. 2004; Waldron et al. 2013a). Windthrow episodes are known to contribute many biological legacies to the ecosystem, such as pit-and-mound microtopography, seedbed heterogeneity, downed woody debris, snags, and residual living trees (Ulanova 2000; Franklin et al. 2007; Waldron et al. 2013b).

Knowledge of windthrow in the eastern boreal forest of Quebec is relatively scarce, but the phenomenon has received greater attention in recent years. At a landscape level, partial windthrow i.e., windthrow that affected less than 75% of the canopy, dominates the eastern Quebec boreal forest. Stand-replacing windthrows (i.e. > 75% of the canopy is lost) are also present but to a lesser extent (Bouchard et al. 2009; Waldron et al. 2013a). To provide a complete picture of the range of variability exhibited by a natural disturbance, its ecological consequences must be understood, together with the characterization of its severity and occurrence (Vaillancourt et al. 2009). At a landscape level, the stand and soil factors that influence windthrow probabilities have been previously examined in the study area (Waldron et al. 2013a). Likewise, Bouchard et al. (2009) examined the occurrence of stand-replacing windthrows over areas greater than 5 ha. At the stand level, the consequences of windthrow on the forest structural attributes, plant diversity and regeneration have been described (Waldron et al., submitted). However, the description of a natural disturbance is incomplete if its spatial distribution is not considered at both stand and landscape levels (Landres et al. 1999; Vaillancourt et al. 2009).

The only spatial information that is readily available in Quebec regarding windthrow has been provided by forest inventory maps that were created by the Quebec Ministry of Natural Resources (MNR), and which were derived from photographic interpretations. On these maps, windthrow polygons are characterized as partial when 25% to 75% of the canopy is damaged, and as stand-replacing (or total) when more than 75% of the canopy is affected. However, the minimum size of a mapped polygon ranges between 2 and 8 ha (Létourneau et al. 2009). Consequently, it is impossible at this scale to capture the spatial characteristics of windthrow within the polygons. In a windthrow episode, smaller patches within the affected stand remain intact. In other words, tree uprooting or breakage may be complete in some parts of a stand affected by windthrow, while other parts are partially affected or not affected at all (Lindemann and Baker 2001, Mitchell 2013). Thus, intra-polygon windthrow descriptions would likely provide more information than simply characterizing the event as a partial windthrow, a total windthrow, or as undisturbed (Peterson and Pickett 2003). Describing this finer spatial distribution could serve as a tool for 1) selecting appropriate harvesting methods and 2) defining the size and density of retention patches that are to be left standing in the cutblock when using usual harvesting techniques or when salvage logging is undertaken. At the landscape level, wind storms can create patches of different sizes and shapes (Everham and Brokaw 1996). The spatial distribution of windthrows and their characteristic sizes and shapes are essential for natural disturbance-based management. With this information, forest managers are more likely to know the appropriate size and distribution of the cutblocks in the landscape for better emulating natural processes.

In the eastern Quebec boreal forest, careful logging with protection of regeneration and soils (or *coupe avec protection de la régénération et des sols* (CPRS)) is currently the principal method of timber harvesting (Groot et al. 2005). Thus, it is relevant to determine if the spatial dispersion of windthrow at the landscape-level, as well as the internal structure of affected polygons, differs from CPRS. The aims of our study were: (1) to characterize the spatial repartition of windthrow at the landscape-level, (2) to characterize patchiness within polygons that are affected by partial windthrow and stand-replacing windthrow, and (3) to compare windthrow spatial characteristics at both polygon- and stand-levels with the spatial characteristics of cutblocks.

Materials and methods

Study area

The study was conducted in the boreal forest of Quebec, Canada, in the black spruce-feather moss bioclimatic subdomain (Fig. 5). The dominant tree species are black spruce (*Picea mariana* (Mill.) B. S. P.) and balsam fir (*Abies balsamea* (L.) Mill.), but white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) also occur in the canopy. Topography in this region is complex, including both high elevation sites and deep valleys. The mean slope is 14% and the mean altitude is 442 m (Robitaille and Saucier 1998). The area is further characterized by high annual precipitation (1300 mm) and low annual mean temperatures (between -2.5°C and 0°C) (Robitaille and Saucier 1998). These particular conditions explain why the eastern boreal forest of Quebec has a longer fire cycle than its western counterpart (Bouchard et al. 2008). Because of the long fire cycle, there is a high proportion of old-growth forest and of balsam fir. These conditions make the stands more susceptible to windthrow and gap dynamic processes (Boucher et al. 2003; Pham et al. 2004; De Grandpré et al. 2009).

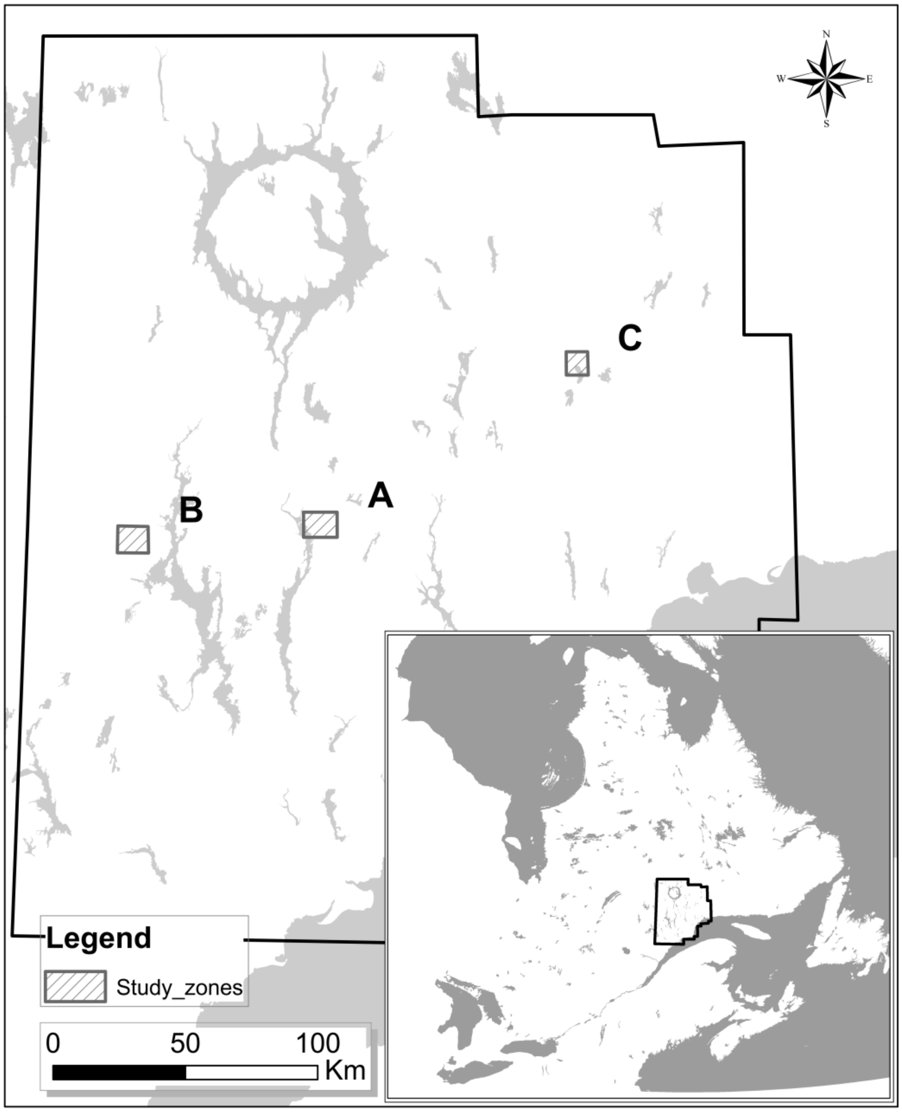

Figure 5: Study area. A, B and C represent the three zones where spatial analysis were conducted.

Windthrow selection and photo-interpretation

The study was performed at two spatial scales, i.e., the polygon-level and the landscape-level. To describe the spatial characteristics of windthrows and cutblocks at these two levels, three zones (A, B and C) of 5 800 ha, 4 400 ha and 5 000 ha, respectively, were selected in the eastern black spruce- feather moss bioclimatic subdomain (Fig. 5). A proportion of the stands in the three zones had been affected by windthrows of differing sizes and severities. The zones were selected to cover a large area of the subdomain and to capture the diversity of stand and windthrow disturbance characteristics within the landscape (Table 9). Thus, the three study zones were not intended to portray the true windthrow rates at a regional level. As three zones were used for the analysis, we expected that all of the partial and total windthrows would not originate from a single windstorm episode, thereby avoiding a potential « snap shot effect ». This is why most of our analyses were not executed to compare the three zones but to integrate the natural variability of both partial and total windthrows in the study area.

At the landscape-level, analyses were executed on polygons as they were identified by the Quebec MNR on maps from the third-decade inventory. Partial windthrows (PW), stand-replacing windthrows or total windthrows (TW), and cuts (CUT) polygons were used. At the polygon-level, we characterized within-polygon structure from a set of 1:15 000 aerial photographs that were taken for each zone between July and September 1999. Percentages of canopy openness within cells measuring 50 m by 50 m on a side were visually estimated with a stereoscope. We chose this cell dimension after trying grids of finer and coarser resolution. It would have been difficult to evaluate precisely the windthrow proportion within smaller cells and also would have been too time consuming considering the large area that our study covered. The severity of windthrow or cutting was determined for each cell and associated with one of four classes of canopy openness: 1) 0-25%; 2) 25-50%; 3) 50-75%; and 4) 75-100%. For the cutblocks, the same method was used. A grid was produced for each zone that represented the spatial distribution of the canopy openness (Fig. 6).

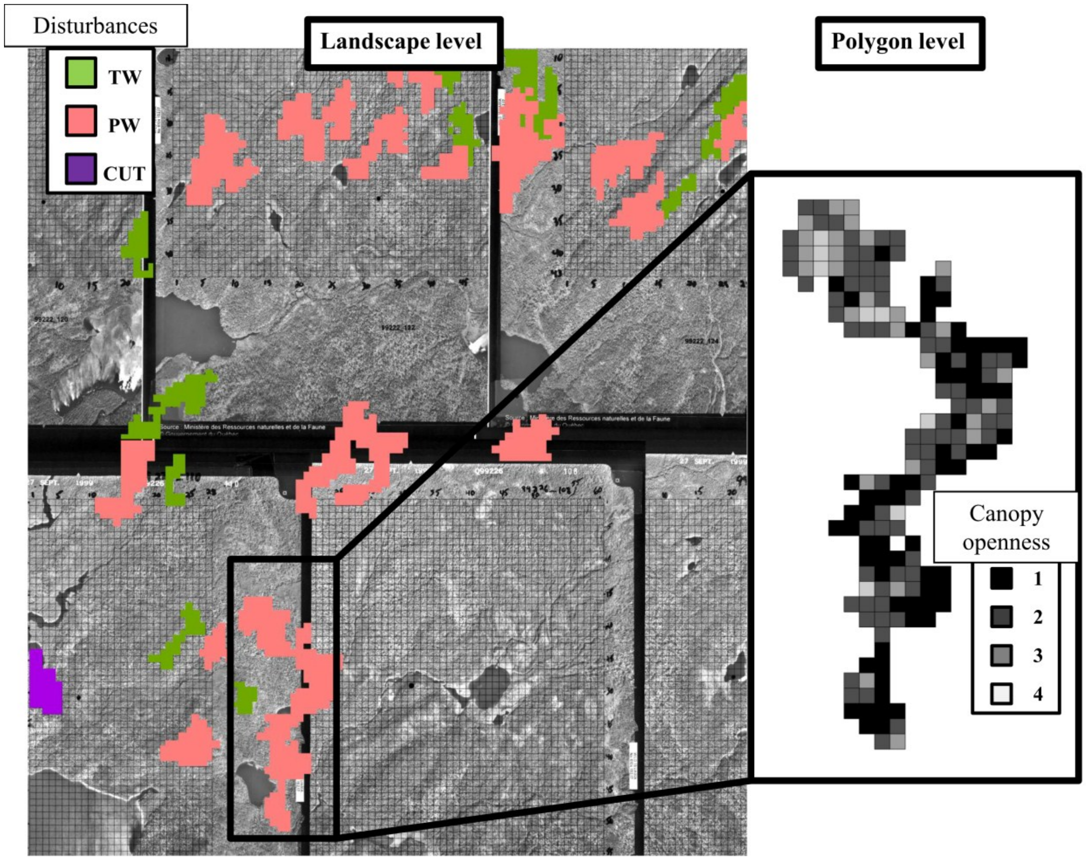

Figure 6: Two scales of analyses. At the landscape-level, disturbed polygons appearing on the Quebec MNR maps from the third-decade inventory were used for the analysis. At the intra-polygon level, canopy openness classes were used for the analysis, as visually estimated in 50 m by 50 m grid with a stereoscope.

Analysis

Analyses were performed at two spatial scales, i.e., landscape- and intra-polygon levels (Fig. 6). Roads, water and non-forested zones were excluded from analysis and a 50 meter-wide buffer zone around each of these features was also excluded.

Landscape level

In total, zone A contained 10 polygons in which there was total windthrow, 15 partial windthrows, and one cutblock; zone B had 11 total windthrows, 26 partial windthrows, and four cutblocks; and zone C contained six total windthrows, 19 partial windthrows, and six cutblocks. Partial and total windthrows, as well as cutblocks, were used to execute a series of spatial analyses using the FRAGSTATS outputs (McGarial and Marks 1995) of the Patch analysis interface of ArcMap 10.1.

FRAGSTATS metrics were chosen as to avoid correlations and redundancy (Madoui et al. 2010). Consideration was also given to metrics used in previous studies to facilitate comparison. The classes TW, PW and CUT were considered in the analysis. Seven metrics were chosen. Two of these metrics were related to landscape composition: the total area (TA) and the total area of each polygon type in the landscape (CA). Two metrics were related to patch interspersion or diversity: the area-weighted mean polygon fractal dimension (AWMPFD) and mean nearest-neighbor (MNN) distance. Finally, three metrics were related to the fragmentation level: the number of polygons (NP), mean polygon size (MPS) and polygon density (PD). See Appendix B for a complete description of these metrics.

FRAGSTATS outputs for some of the landscape metrics are only descriptive. As only one value per landscape or zone is available, no subsequent statistical tests were possible. This is the case for the number of polygons (NP), class area (CA), the area-weighted mean polygons fractal dimension (AWMPFD), the mean nearest-neighbor (MNN) distance and polygon density (PD) (Table 9). Comparisons between the three zones were performed for metric MPS with non parametric one-way ANOVA (Kruskal-Wallis tests), at $P \leq 0.05$. Stats package of the R statistical environment was used (v. 2.15.2, R-Development Core Team 2011). When a significant difference was observed, pairwise comparisons were performed. In these cases, a Bonferroni correction was used so α value of 0.05 was divided by three, as three comparisons were executed.

Polygon-level

At the polygon-level, the four classes of canopy openness were used to perform a series of spatial analyses in the disturbed stand polygons (PW, TW and CUT) that appeared on the maps. Adjacent cells with the same percent openness class were merged to form patches (Figure 6). A 50 meter-wide buffer zone was established when a windthrow polygon and a harvested polygon touched one another. Again, these analyses at the polygon-level were performed with FRAGSTATS functions of the Patch analysis extension of ArcMap 10.1.

The same set of metrics was chosen for the analyses at the polygon-level. Two metrics were related to polygon composition: total area (TA) and total area of each severity class patch in the polygon (CA). Two metrics were related to patch interspersion or diversity: the area-weighted mean or patch fractal dimension (AWMPFD) and the mean nearest-neighbor (MNN) distance. Finally, three metrics were related to the fragmentation level: number of patches (NP), mean patch size (MPS) and patch density (PD).

Comparisons among PW, TW and CUT for each of the canopy openness classes were made using Kruskal-Wallis. These tests were performed for canopy classes 1 and 4, as they were the two categories in which we were particularly interested. When a significant difference was observed, pairwise comparisons were performed between disturbances. Again, a Bonferroni correction was used. Comparisons between patch sizes were done for metrics MNN, PD and CA, again with the Kruskal-Wallis test. Polygon sizes were separated into three categories, to have a sufficient sample size in each category. This is why polygon size categories were not exactly the same for PW, TW and CUT. When a significant difference was observed, pairwise comparisons were executed between size categories. Again, a Bonferroni correction was used. Finally, comparisons of MNN and AWMPFD between disturbance types were represented as cumulative frequencies. When, within a polygon, only one patch of a canopy openness category was present, the MNN value was equal to zero. Comparisons between disturbances were performed with Kolmogorov-Smirnov tests with the package Stats of R statistical environment (R-Development core team 2011). As

Kolmogorov-Smirnov test allowed the comparison between two distributions only, we performed pairwise comparisons between disturbances and used a Bonferroni correction. As three comparisons among disturbance types were possible, we used $P \leq 0.016$.

Results

Landscape level

NP and CA were related to the characteristics of the three zones, as represented in Table 9. The AWMPFD outputs showed that mean shape complexity of polygons was relatively low, as all values were close to 1. The measurement of polygon isolation, i.e., the MNN, showed that for zones B and C, TW were more isolated than PW. In zone C, which was the zone with the largest area covered by cutblocks, cutblocks were closer to each other than in zone B. Polygon density (PD) was directly related to the number of polygons (NP), and also to total landscape area (TA). Our results showed that proportions and densities of partial windthrows in the landscapes were highly variable. This was not the case for total windthrow polygons, which were present in similar proportions and densities in the three zones. Regardless of zone, the density, the number of polygons and the percentage of total windthrows within the landscape also were lower than for partial windthrows (Table 9). Mean patch size (MPS) was significantly higher in zones A and B than for zone C for partial windthrow, but the three zones did not differ in terms of total windthrows and harvested polygons (Table 10).

Tableau 9: FRAGSTATS output for five landscape metrics in each of the tree zones, i.e., polygon number (NP), class area (CA), area-weighted mean polygon fractal dimension (AWMPFD), mean nearest neighbor (MNN) and polygon density (PD).

	Zone A (TA=5800 ha)			**Zone B (TA=4400 ha)**			**Zone C (TA=5000 ha)**		
	PW	**TW**	**CUT**	**PW**	**TW**	**CUT**	**PW**	**TW**	**CUT**
NP	15	11	1	26	11	4	19	6	6
CA (ha)	230.09	73.91	9.24	721.93	49.21	362.09	179.00	96.25	1981.2
% of the zone	3.97	1.27	0.16	16.41	1.11	8.23	3.58	1.93	39.63
AWMPFD	1.11	1.11	1.04	1.14	1.12	1.13	1.11	1.13	1.19
MNN (m)	281.22	208.36	-	154.23	353.57	219.33	190.69	248.95	72.14
PD (no/ha)	0.0026	0.0019	0.0002	0.0059	0.0025	0.0009	0.0038	0.0012	0.0012

Tableau 10: Area effect on the landscape metric mean patch size (MPS). When the Kruskal-Wallis test was significant at $P \leq 0.05$, pairwise comparisons were performed between polygon sizes. Means with different letters significantly differ at $P \leq 0.016$ after Bonferroni correction.

	Zone	N	Min	Max	Mean	S.D.	Kruskal-Wallis test
Partial windthrow							
Mean polygon size (ha)	A	15	5	45	15.33[a]	10.62	10.1, *df* = 2, *P* = 0.006
	B	26	6	138	28.31[a]	37.14	
	C	19	1	51	9.47[b]	12.36	
Total windthrow							
Mean polygon size (ha)	A	10	3	15	7.10	3.96	2.66, *df* = 2, *P* = 0.26
	B	11	2	9	4.82	2.09	
	C	6	2	53	16.17	19.24	
Cut							
Mean polygon size (ha)	A	1	9	9	9.00	-	2.60, *df* = 2, *P* = 0.27
	B	4	13	266	90.75	118.27	
	C	6	13	1539	329.17	598.30	

Patch size repartition followed an inverse asymmetric bell-shaped distribution for partial windthrow (Fig. 7). However, even if most of the partial windthrow polygons are smaller than 25 ha, the polygons of 26-100 ha and 101 to 500 ha covered a large proportion of the partial windthrow total cover (Fig. 8). Total windthrow patch size followed an inverse J-shaped distribution. About 45% of the total windthrow polygons were smaller than 5 ha, and no total windthrow polygons were larger than 100 ha. For the cutblock polygons, the proportion of 11-25 ha, 26-100 ha and 101-500 ha polygons were similar and no cutblocks were smaller than 6 ha (Fig. 7).

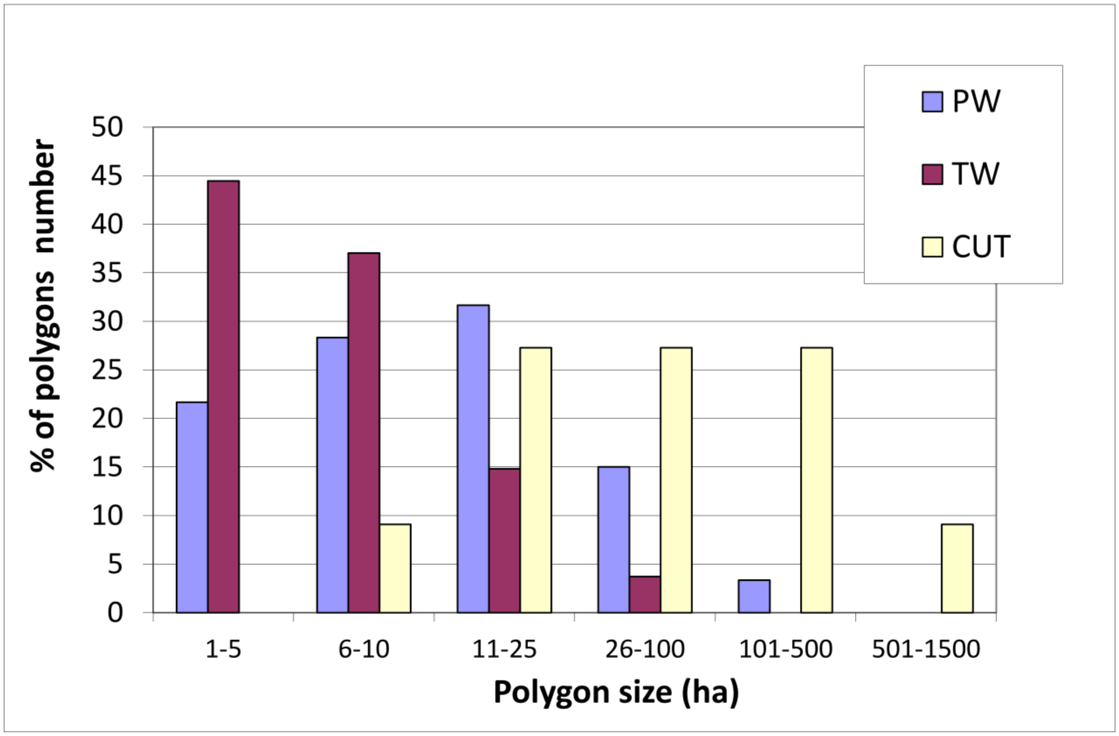

Figure 7: Partial windthrow (PW), total windthrow (TW) and cutblock (CUT) size repartition in proportion of the total polygons number.

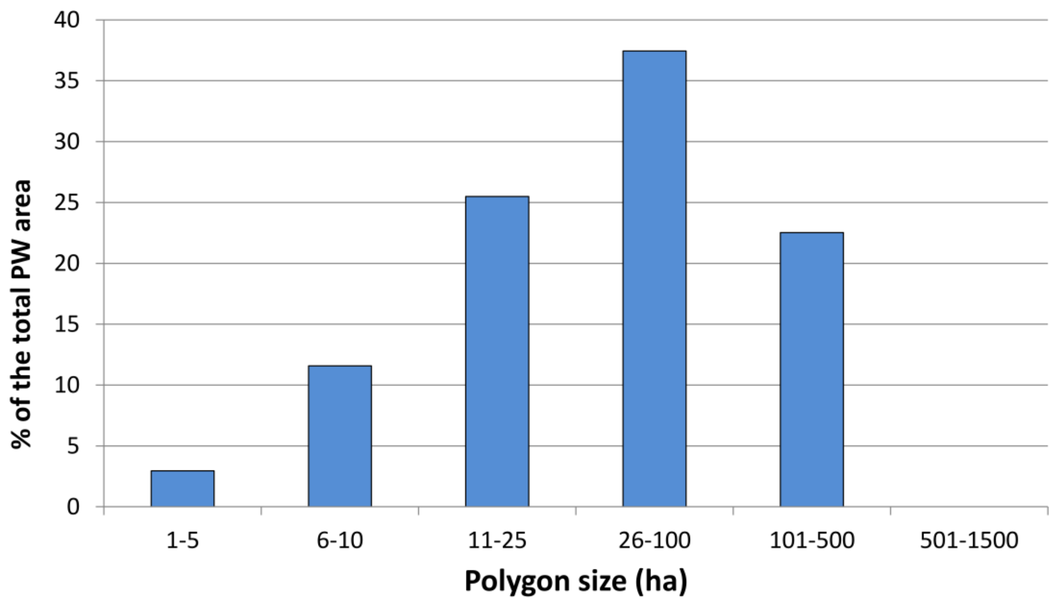

Figure 8: Partial windthrow (PW) polygon size, in relation to the proportion of the total area covered by PW in the landscape.

Polygon-level

With the exception of mean polygon size, no significant differences were found in polygon characteristics among the three zones. To provide the best description of spatial structure within a polygon across the whole region, results from the three zones were merged together. The mean proportions of polygons covered by different canopy openness classes were different between disturbance types. The residual trees (canopy openness class 1) covered a significantly higher proportion of the partial windthrow polygons. More than 60% of partial windthrow polygons were covered by standing tree patches. Total windthrow polygons and cutblocks were not different from one another, with about 10% of their areas remaining in standing trees (Fig. 9). The canopy openness class 4, which represented either a total blow down or a clear cut, covered a different proportion of the polygons, depending on disturbances. Cutblock polygons had more than 60% of their areas in openings. Around 15% of total windthrow and < 5% of partial windthrow polygons were blown down completely (Fig. 9). It is worth noting that, even in total windthrow polygons, significant structure remains as partially damaged patches.

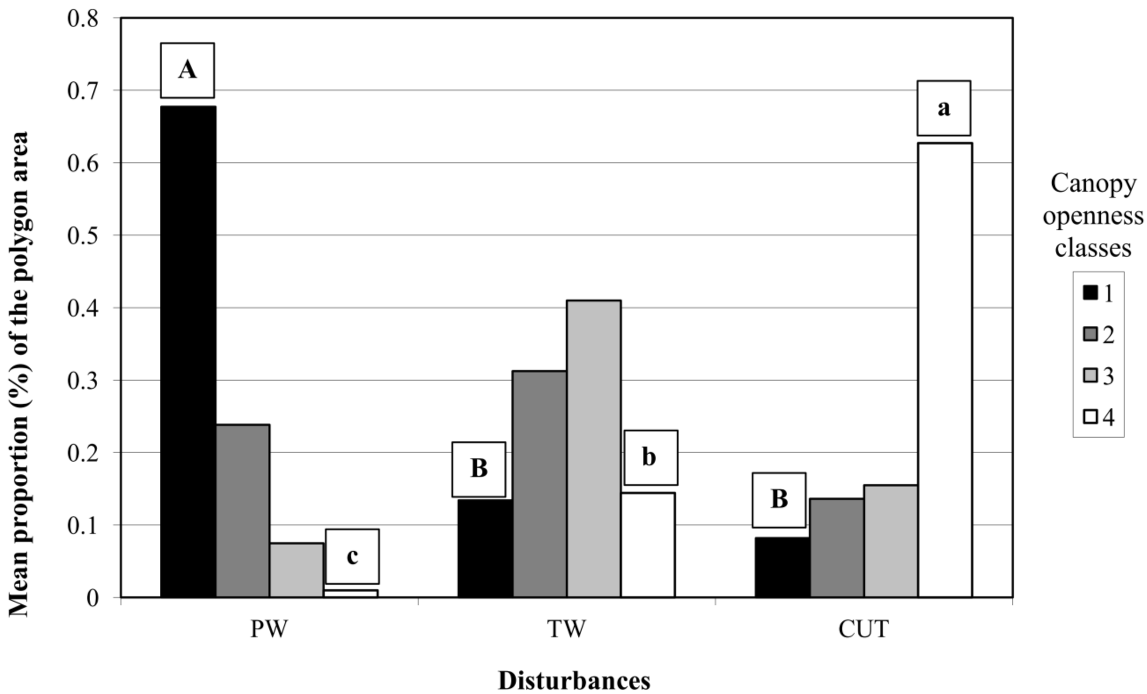

Figure 9: Mean proportion of the PW, TW and CUT polygons that were covered by the different canopy openness classes. Mean proportion with the same letter do not differ between disturbances at $P \leq 0.016$ after Kruskal-Wallis tests. Uppercase letters were used for canopy openness class 1 and lowercase letters were used for canopy openness class 4.

Polygon size influenced some of metrics, with respect to residual tree cover (canopy openness class 1). Residual tree patches within disturbance polygons were not affected by polygon size, except for partial windthrows. Even if the density of patches of residual trees patches (canopy openness of class 1) was higher in smaller polygons, the percentage of the polygons covered by residual trees was not influenced by polygon size. In other words, the number of residual tree areas was high in smallest partial windthrows, but these areas were also small. The opposite phenomenon was observed in the largest polygons. The intermediate size polygons had the highest total canopy openness (Table 11).

Tableau 11 : Polygon size effect on residual forest (canopy openness of class 1). When the Kruskal-Wallis ANOVA was significant at $P \leq 0.05$, pairwise comparisons were made among size classes. Means with different letters significantly differ from one another at $P \leq 0.016$, after Bonferroni correction.

	Polygon Size	**N**	**Min**	**Max**	**Mean**	**S.D.**	**Kruskal-Wallis test**
Partial windthrow							
Density of class 1	a) 0-10 ha	30	0.11	1.00	0.47^a	0.41	33.13, *df* = 2,
	b) 11-25 ha	19	0.05	0.35	0.14^b	0.09	$P < 0.001$
	c) > 25 ha	11	0.02	0.20	0.07^c	0.08	
% of polygon covered by class 1	a) 0-10 ha	30	0	100	65.01	27.12	3.73, *df* = 2,
	b) 11-25 ha	19	9	93	62.99	24.77	$P = 0.15$
	c) > 25 ha	11	38	90	73.61	17.81	
Total windthrow							
Density of class 1	a) 0-5 ha	12	0	0.67	0.30	0.30	1.76, *df* = 2,
	b) 6-10 ha	10	0	0.44	0.21	0.13	$P = 0.41$
	c) > 10 ha	5	0	0.30	0.14	0.11	
% of polygon covered by class 1	a) 0-5 ha	12	0	50	15.69	20.18	0.26, *df* = 2,
	b) 6-10 ha	10	0	67	16.67	22.83	$P = 0.88$
	c) > 10 ha	5	0	13	6.42	7.26	

Cut							
Density of class 1	a) 0-15 ha	4	0.00	0.27	0.18	0.12	1.98, *df* = 2,
	b) 16-200 ha	4	0.12	0.22	0.18	0.05	*P* = 0.37
	c) > 200 ha	3	0.08	0.17	0.14	0.05	
% of polygon covered by class 1	a) 0-15 ha	4	0	10	6.35	4.38	3.39, *df* = 2,
	b) 16-200 ha	4	4	13	7.67	3.77	*P* = 0.18
	c) > 200 ha	3	8	14	11.24	2.63	

Polygon size influenced more variables when canopy openness class 4 was considered. The density of class 4 was related to polygon size only for the cutblocks. However, the number of samples for cutblocks was low compared to partial and total windthrow patches. The mean percentage of the polygons covered by the class 4 was significantly different between polygon sizes only for partial windthrows. The largest partial windthrow polygons had the highest proportion of total canopy openness. However, proportions are below 2%, no matter the polygon size (Table 12).

Tableau 12: Polygon size effect on canopy openness of class 4 (75 to 100% of the canopy affected by wind or logging). When the Kruskal-Wallis ANOVA was significant at $P \leq 0.05$, pairwise comparisons were made among size classes. Means with different letters significantly differ from one another at $p \leq 0.016$, after Bonferroni correction.

	Polygon Size	**N**	**Min**	**Max**	**Mean**	**S.D.**	**Kruskal-Wallis test**
Partial windthrow							
Density of class 4	a) 0-10 ha	30	0	0.25	0.04	0.07	4.74, *df* = 2,
	b) 11-25 ha	19	0	0.19	0.03	0.05	*P* = 0.09
	c) > 25 ha	11	0	0.11	0.03	0.04	
% of polygon covered by class 4	a) 0-10 ha	30	0	4	0.88^{b}	1.74	6.34, *df* = 2,
	b) 11-25 ha	19	0	6	0.78^{ab}	1.64	*P* = 0.04
	c) > 25 ha	11	0	6	1.61^{a}	2.18	
Total windthrow							
Density of class 4	a) 0-5 ha	12	0.00	0.33	0.26	0.18	0.83, *df* = 2,
	b) 6-10 ha	10	0.00	0.33	0.21	0.15	*P* = 0.66
	c) > 10 ha	5	0.09	0.36	0.21	0.13	
% of polygon covered by class 4	a) 0-5 ha	12	0	19	9.29	6.99	4.39, *df* = 2,
	b) 6-10 ha	10	0	29	15.58	13.71	*P* = 0.11
	c) > 10 ha	5	2	44	25.64	17.62	

Cut							
Density of class 4	a) 0-15 ha	4	0.07	0.11	0.08[a]	0.02	6.40, $df = 2$,
	b) 16-200 ha	4	0.02	0.07	0.04[ab]	0.03	$P = 0.04$
	c) > 200 ha	3	0.02	0.03	0.02[b]	0.01	
% of polygon covered by class 4	a) 0-15 ha	4	58	83	69.30	10.56	2.14, $df = 2$,
	b) 16-200 ha	4	65	78	70.61	5.61	$P = 0.34$
	c) > 200 ha	3	62	67	65.22	2.52	

The cumulative frequency distributions of mean nearest-neighbor (MNN) distances for each disturbance type were calculated for the four canopy openness classes. Classes 2 and 3 were grouped together as they behaved in the same way. For canopy openness class 1, there were significant differences between distributions of the partial windthrows and cutblocks (Kolmogorov-Smirnov tests: $D = 0.9$, $P \leq 0.001$) as well as for total windthrows and cutblocks ($D = 0.81$, $P = 0.0003$). Partial windthrows and total windthrows did not significantly differ ($D = 0.26$, $P = 0.2$). Distance between patches of residual trees was significantly larger for cutblocks, with a minimal value of 100 m. In contrast, windthrow polygons had 50% of the patches in class 1 that had no neighbors (Figure 10a).

For openness classes 2 and 3, there were significant differences in distributions of mean nearest-neighbor distances for partial windthrows and cutblocks (Kolmogorov-Smirnov tests: $D = 0.42$, $P = 0.003$) and for total windthrows and cutblocks ($D = 0.5$, $P \leq 0.001$). Partial and total windthrow distributions did not differ from one another ($D = 0.2$, $P = 0.12$) (Figure 10b). Mean nearest-distances between patches with intermediate canopy openness classes were relatively short as more than 80% of the values are less than 200 m, regardless of disturbance type.

The distribution of mean nearest-neighbor distances between two patches of canopy openness 4 was not significantly different between disturbance types (PW-TW: $D = 0.2$, $P = 0.8$; PW-CUT: $D = 0.2$, $P = 0.9$; TW-CUT: $D = 0.23$, $P = 0.84$). However, some trends can be observed. Partial windthrows had more than 60% of the canopy openness of class 4 patches without any neighbor. Also, the maximal mean nearest-neighbor distance value for partial windthrows is 600 m, but it is 100 m for cutblocks and 200 m for total windthrows (Figure 10c).

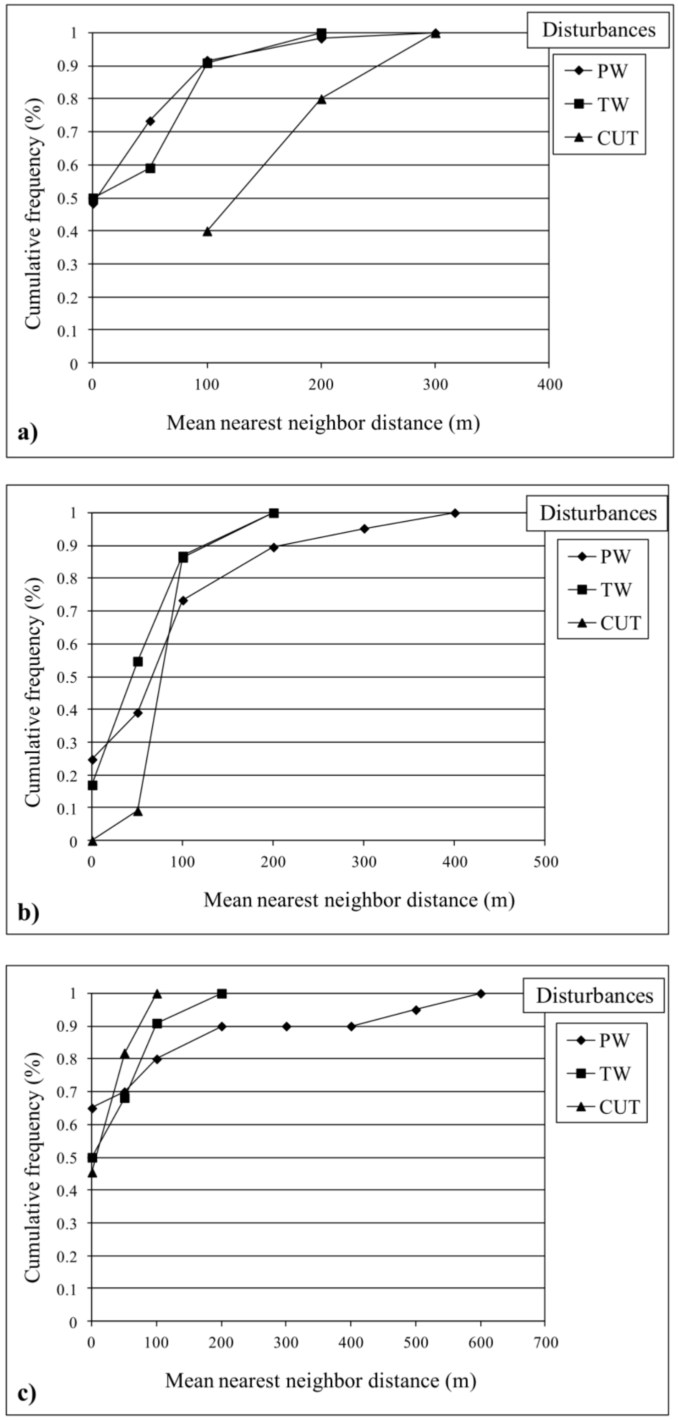

Figure 10: Cumulative frequency distribution of mean nearest-neighbour (MNN) distances for each disturbance type for a) canopy openness of class 1; b) canopy openness of classes 2 and 3; and c) canopy openness of class 4.

Area-weighted mean patch fractal dimensions (AWMPFD) were also calculated for the three polygon types, for each canopy openness class (Fig. 9). For the patches of standing residual trees (canopy openness class 1), there were no significant differences in distribution of total windthrows and cutblocks (Kolmogorov-Smirnov test: D = 0.48, P = 0.09). Partial windthrows and total windthrows (D = 0.69, $P \leq 0.001$), together with partial windthrows and cutblocks (D = 0.7, $P \leq 0.001$) had significantly different distributions. Even if complexity index values were relatively low (i.e. close to 1), partial windthrow polygons were the type of disturbance with the highest shape complexity for areas covered by residual trees. Cutblock polygons were more uniform in terms of shape complexity, since all values were between 1 and 1.1 (Fig. 11a). As previously noted, cutblocks had < 10% of their area covered by residual trees, which may help explain the low degree of shape complexity.

For canopy openness classes 2 and 3, shape complexity value distributions were similar among disturbance types, with no significant differences between any of the distributions at $P \leq 0.016$ (PW-TW: D = 0.23, P = 0.04; PW-CUT: D = 0.31, P = 0.06; TW-CUT: D = 0.27, P = 0.21) (Fig. 11b).

Lastly, for shape complexity of patches with class 4 canopy openness, partial windthrow and total windthrow distributions had significantly different distributions (D = 0.4, P = 0.06), as well as total windthrows and cutblocks (D = 0.59, P = 0.01) and partial windthrows and cutblocks (D= 0.9, $P \leq 0.001$). The situation for canopy openness of class 4 was opposite to that of class 1. Partial windthrows had the most uniform shape complexity and cutblocks had the highest variety of shapes. However, about 2% of the partial windthrow polygons were covered by a canopy openness of class 4, versus > 60% for cutblocks. This may have contributed to higher degree of heterogeneity in shape complexity for cutblocks (Fig. 11c).

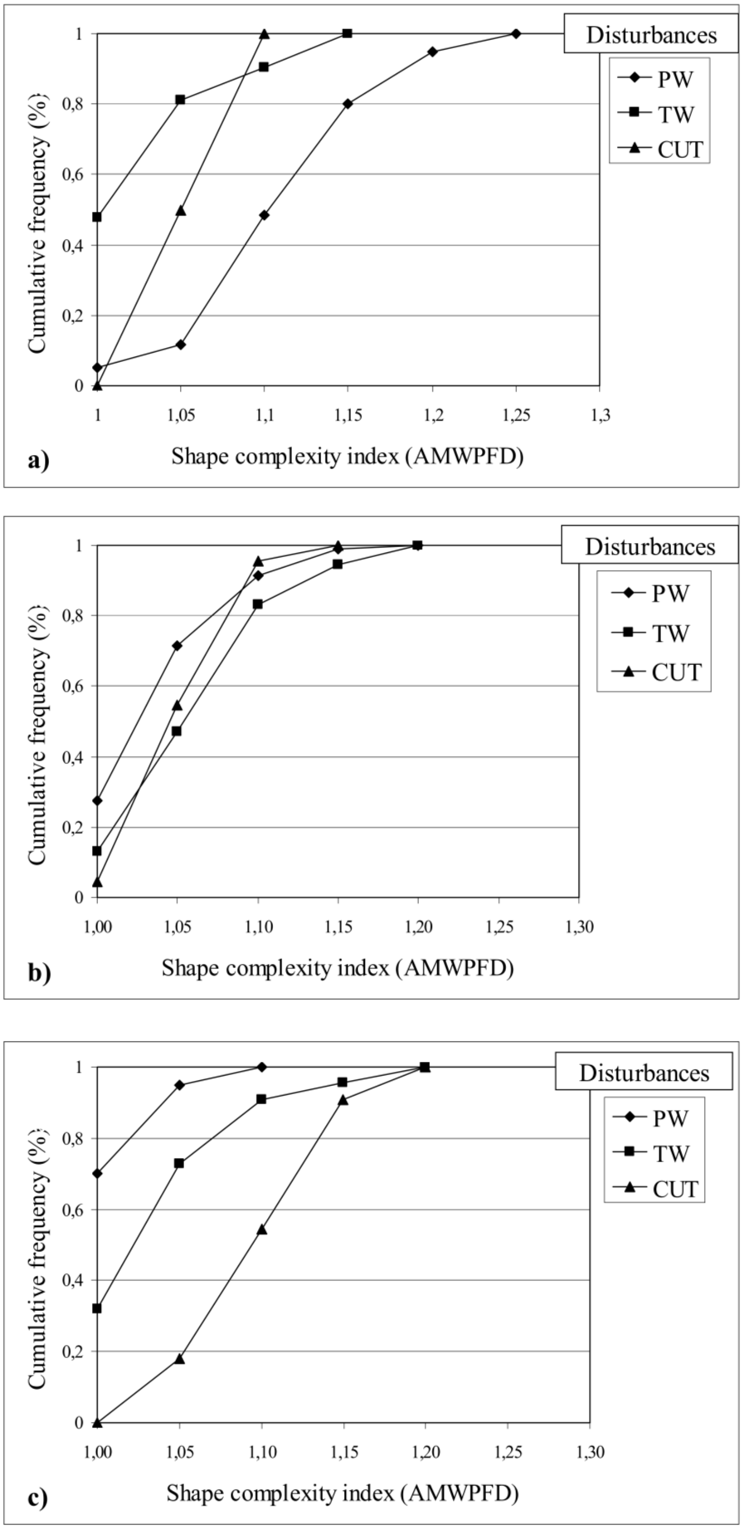

Figure 11: Cumulative frequency distribution of shape complexity index (area-weighted mean patch fractal dimension: AWMPFD) of each disturbance type for a) canopy openness class 1; b) canopy openness of classes 2 and 3; c) canopy openness class 4.

Discussion

Landscape level

When we looked at the maximal sizes of the cutblocks, we noted that their range was different from that of the total windthrow polygons. If we examine zone C, even if cutblocks and TW had the same number of polygons in the same densities, cutblocks covered an area more than 20 times larger than TW. Thus, our results showed that CPRS did not reproduce total windthrow polygons in term of size. It is important to mention that most cutblocks had a size smaller than 200 ha and were separated by buffer strips 60 to 100 m in width. As the grids that we used had a dimension of 50 m, two cutblocks were often touching one another and were subsequently merged. This may explain why some of the cutblocks were as large as 1500 ha.

The study was conducted with aerial photographs from the third forest inventory conducted by the Quebec Ministry of Natural Resources taken in 1999, given the ones from the latest inventory were not available for our study area. At this time, logging operations were executed following RSFM (Regulation respecting standards of forest management for forests in the domain of the State). In RSFM, rules were established for size and dispersion of cutblocks, as well as for the buffer strips (Government of Quebec 2013). However, since 2004-2005, increasing concern regarding forest caribou populations (*Rangifer tarandus caribou)* has conducted to derogations from the RSFM in our study areas. Some of the cutblocks are now aggregated and buffer strips are replaced by residual forest areas that were distributed within the cutblock aggregation (J. Duval, MRN, personal communication 2013). Also, in recent years, massive salvage logging plans have been implemented in the area because of major windthrow episodes (Ruel et al. 2010). It would have been interesting to compare the spatial characteristics of cutblocks that had been recently logged (both traditional logging and salvage) to partial and total windthrow polygons.

Our study area is characterised by relatively infrequent forest fires, but when fire occurs, burned patches are large (De Grandpré et al. 2009). Total windthrow in the landscape added to a certain number of stands that originated from stand-replacing disturbances (cohort 1 sensu Bergeron et al. 2002). However, most of these first cohort stands were created by large openings caused by fires and harvest operations (CPRS and salvage logging). In other words, total windthrows increased the heterogeneity of the canopy cover at the landscape level, by creating areas of young stands that were smaller compared to what are commonly generated by fire. However, total windthrows remain a relatively uncommon natural disturbance in the eastern boreal forest of Quebec in comparison with partial windthrows (Bouchard et al. 2009; Waldron et al. 2013a). Consequently, from an ecosystem management perspective, it is not total windthrows that should be reproduced at landscape level but rather partial windthrows. Our results showed a high degree of variability in partial windthrow size and density in the area. Thus, ecosystem-based management planning should aim to create a range of cutblock sizes and densities with the characteristics of partial windthrow within them. Waldron et al. (2013a) found that, at regional scale, more than 6% of the area had been affected by partial windthrows within a 30 year period. At the landscape level, this percentage could be used in the implementation of ecosystem management strategies.

Partial windthrow polygons exhibited a wide range of sizes and densities in the landscape. This size repartition depends upon stand and site characteristics, together with wind regimes or storm intensities (Mitchell 2013). The dominance of small size partial windthrow at landscape-level has been observed before (Nowacki and Kramer 1998; Lindemann and Baker 2001). However, the shapes of partial windthrow polygons were similar among the three zones, as were the shapes of total windthrows. The high degree of variability in windthrow polygon size and the low degree of variation in their shapes has been previously observed in the Southern Rocky Mountains (Lindemann and Baker 2001). Partial windthrows were more heterogeneous in terms of size, density, and intervening distances compared to total windthrow polygons.

Polygon level

Overall, cutblocks and total windthrows did not share many spatial characteristics at polygon level. Cutblocks had a significantly higher proportion of canopy openness of class 4 than did total windthrows and they did not have the same within-polygon shape and isolation characteristics. Also, the abundance of canopy openness classes of 25 to 50% and 50 to 75% was different between total windthrows and cutblocks. This confirms that CPRS did not emulate total windthrows, as they were different, both at the landscape and polygon level. The shape measurement of a patch gives information about the proportion of edges, which could influence the presence of some plant and wildlife species (Hunter and Schmiegelow 2011). However, edges impact after a partial disturbance such as partial windthrow is harder to evaluate because of the relatively low-contrast or soft edges between the disturbed and undisturbed forest. Considering that the maximal value for the area-weighted mean patch fractal dimension is 2, all canopy openness areas, regardless the disturbance type, had a relatively simple shape as no value exceeded 1.25. It means that the edge proportion is relatively low and is not affected neither by the severity of canopy openness or the type of disturbance. This result could possibly be related to the methods that we employed, using agglomeration of square cells, so that shape may be far more complex at a finer scale.

The importance of residual tree cover after a partial windthrow was confirmed by our results. Also, canopy openness classes 2 and 3 were present in partial windthrows at different levels. These results confirm that after partial windthrows, residual forest cover was still present over most of the area, with less than 2% of the polygon area represented by canopy openness class 4. Total windthrows, in contrast, had a higher mean percentage of area covered by canopy openness class 4, or about 15%. Furthermore, intermediate canopy openness classes were present in higher proportions in total windthrows than in partial windthrows. These results indicate that, even if residual tree cover was not as important in total versus partial windthrows, total windthrows maintained a certain structural heterogeneity. In contrast to total windthrows, partial windthrow polygons did not increase the number of first cohort stands in the forest landscape. However, if partial windthrows are salvaged, they could lose much of their structural heterogeneity (Waldron et al. 2013b) and result in a first cohort stand (sensu Bergeron et al. 2002), which happens in the case of CPRS or total windthrows.

Management implications

To avoid over-representation of first cohort stands in the landscape, where partial windthrows are an important component (Waldron et al. 2013a), some silvicultural systems could be implemented. In our study area, different cutting treatments have been previously tested. These harvest methods have included traditional CPRS, partial cutting that involves the removal of stems with DBH larger than 14 cm (CPPTM in Quebec, HARP in Ontario), and selection cutting (Ruel et al. 2007). Selection cutting, which typically leads to the harvesting of 30 to 40% of stand basal area, maintained the irregular size distribution of stems (Ruel et al. 2007). Also, this method maintained several structural key attributes in the stand, such as large DBH trees (Cimon-Morin et al. 2010). From an ecosystem point-of-view, selection cutting would be an interesting option. Yet this option leads to an increase in harvesting costs (Moore et al. 2012), which could be hard to justify in the context of black spruce forest, except where some special values call for this treatment.

Variable retention cutting is an example of a harvesting method that leaves a certain proportion of trees standing within cutblocks, which is not the case with traditional CPRS (Price et al. 1998, Lindemann and Baker 2001). Mean size of partial windthrow polygons was between 45 and 140 ha. It means that cutblocks could cover a variety of sizes, while remaining within the natural range of the partial windthrow regime. Our results showed that larger partial windthrows had a higher density of areas of residual trees; thus, tree retention within cutblocks could follow the same rules. Shape complexity indices within partial windthrows are more heterogeneous for canopy openness class 1, which could allow managers to maintain a variety of forms and sizes of retention areas within the cutblocks. As more than 60% of partial windthrow polygons are represented by canopy openness class 1, a minimum retention rate should be imposed on cutblocks in some of the harvested area to allow representation of partial windthrows at the polygon level. In Quebec, retention patch sizes are currently between 150 to 300 m^2, with a minimal cover of 5% of the cutblocks (Leblanc and Pouliot 2011). This minimum value of residual trees cover, probably inspired by fire regimes, is very low in comparison with what we had for windthrow polygons. Thus, 5% of cutblock coverage by residual trees does not allow the maintenance of structural attribute heterogeneity that we encountered in post-windthrow stands.

Some harvesting rules should be implemented for salvage logging operations as well. A certain number of green trees and dead wood should be left in cutblocks. In doing so, a reduction of key attributes and biological legacies following salvage logging operations could be minimized (Jönsson et al. 2007; Waldron et al. 2013b).

Conclusion

We have described for the first time spatial characteristics of windthrow in a portion of the boreal forest where forest fires are relatively infrequent. The importance of partial windthrow compared to total windthrow has previously been demonstrated for this region (Bouchard et al. 2009; Waldron et al. 2013a). Our results showed that partial windthrows are spatially heterogeneous at both landscape and polygon levels, which could allow forest managers to practice a variety of harvesting methods that would maintain the ecosystem within its natural range of variability. In doing so, cutblocks would have different sizes and keep a high cover of residual trees. These methods should consider other characteristics of partial windthrow, i.e., biological legacies, together with the frequency of disturbance. Total windthrows remain rare events in our study area. Thus, clear-cutting operations should not be executed with the objective of emulating total windthrows. Fire cycles are relatively long in the eastern boreal forest of Canada (Bouchard et al. 2008). When fires occur, they often burn large areas (De Grandpré et al. 2009); so total cutting is more similar to fire than to total windthrows. However, as partial windthrow cycles are similar to fire cycles in our study area (Waldron et al. 2013a), a range of cutblock sizes and densities should be implemented to reproduce partial windthrow spatial heterogeneity.

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References

Bergeron, Y., Cyr, D., Drever, R.D., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, È., Leduc, A., Le Goff, H., Lesieur, D., and Logan, K. 2006. Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Can. J. For. Res. 36: 2737-2744.

Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the boreal forest. Silva Fenn. 36(1): 81-95.

Bouchard, M., and Pothier, D. 2008. Simulations of the effects of changes in mean fire return intervals on balsam fir abundance, and implications for spruce budworm outbreaks. Ecol. Model. 218: 207-218.

Bouchard, M., Pothier, D., and Ruel, J.-C. 2009. Stand-replacing windthrow in the boreal forests of eastern Quebec. Can. J. For. Res. 39: 481-487.

Boucher, D., De Grandpré, L., and Gauthier, S. 2003. Développement d’un outil de classification de la structure des peuplements et comparaison de deux territoires de la pessière à mousses du Québec. Forest. Chron. 79(2): 318-328.

De Grandpré, L., Gauthier, S., Allain, C., Cyr, D., Périgon, S., Pham, A.T., Boucher, D., Morissette, J., Reyes, G., Aakala, T., and Kuuluvainen, T. 2009. Towards an ecosystem approach to managing the boreal forest in the north shore region: disturbance regime and natural forest dynamics. *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpre, L., Kneeshaw, D.D., Morin, H., Drapeau, P., Bergeron, Y. (eds), Presses de l'Université du Québec, Montreal, Canada, pp. 229-255.

Everham, E.M., and Brokaw, N.V.L. 1996. Forest damage and recovery from catastrophic wind. Bot. Rev. 62(2): 113-185.

Franklin, J. F., Mitchell, R. J., and Palik, B. J. 2007. Natural disturbance and stand development principles for ecological forestry. Gen. Tech. Rep. NRS-19. Newtown Square, PA: U.S. Department of Agriculture, Forest Service, Northern Research Station, 44 p.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D., Drapeau, P., De Grandpré, L., Claveau, Y., and Paré, D. 2009. Forest ecosystem management, origins and foundations. *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., and Bergeron, Y. (eds). Presses de l'Université du Québec, Montreal, Canada, pp. 13-37.

Gouvernement du Québec, 2013. Règlement sur les normes d'intervention dans les forêts du domaine de l'État (RNI). Loi sur les forêts. Lien URL : http://www2.publicationsduquebec.gouv.qc.ca/dynamicSearch/telecharge.php?type=3&file=/F_4_1/F4_1R7.HTM

Greenberg, C. H. et Lanham, J. D. 2001. Breeding bird assemblages of hurricane-created gaps and adjacent closed canopy forest in the southern Appalachians. For. Ecol. Manage. 154: 251-260.

Groot, A., Lussier, J.-M., Mitchell, A.K. and MacIsaac, D.A. 2005. A silvicultural systems perspective on changing Canadian forestry practices. For. Chron. 81(1): 50-55.

Hirao, T., Murakami, M., Iwamoto, J., Takafumi, H., and Oguma, H. 2008. Scale-dependent effects of windthrow disturbance on forest arthropod communities. Ecol. Res. 23: 189-196.

Jönsson, M.T., Fraver, S., Jonsson, B.G., Dynesius, M., Rydgård, M., and Esseen, P.-A. 2007. Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. For. Ecol. Manage. 242: 306-313.

Kuuluvainen, T. 2009. Forest management and biodiversity conservation based on natural ecosystem dynamics in Northern Europe: the complexity challenge. Ambio 38(6): 309-315.

Landres, P.B., Morgan, P., and Swanson, F.J. 1999. Overview of the use of natural variability concepts in managing ecological systems. Ecol. Appl. 9(4): 1179-1188.

Leblanc, M., and Pouliot, B. 2011. La coupe avec protection de la régénération et des sols avec rétention de bouquets. Fondements et exécution opérationnelle. Ministère des Ressources naturelles et de la Faunes, Québec, Canada, 9 p.

Létourneau, J.-P., Bard, A., Lambert, J., Lord, G., and Faucher, A. 2009. Normes de cartographie écoforestière. Troisième inventaire écoforestier. Ministère des Ressources naturelles et de la Faune, Direction des inventaires forestiers et Service aux citoyens, Québec, Canada, 95 p.

Lindemann, J.D., and Baker, W.L. 2001. Attributes of blowdown patches from a severe wind event in the Southern Rocky Mountains, USA. Lands. Ecol. 16: 313-325.

Madoui, A., Leduc, A., Gauthier, S., and Bergeron, Y. 2010. Spatial pattern analyses of post-fire residual stands in the black spruce boreal forest of western Quebec. Int. J. Wildland Fire 19: 1110-1126.

McGarial, K. and Marks, B.J. 1995. FRAGSTAT: Spatial pattern analysis program for quantifying landscape structure. United States Department of Agriculture, Pacific Northwest Research Station, Portland, Oregon, 120 p.

Mitchell, S. J. 2013. Wind as a natural disturbance agent in forests: a synthesis. Forestry 86(2): 147-157.

Mitchell, S.J., and Beese, W.J. 2002. The retention system: reconciling variable retention with principles of silvicultural systems. For. Chron. 78(3): 397-403.

Moore, T.Y., Ruel, J.-C., Lapointe, M.-A., and Lussier, J.-M. 2012. Evaluating the profitability of selection cuts in irregular boreal forests: an approach based on Monte Carlo simulations. Forestry 85(1): 63-77.

Peterson, C.J., and Pickett, S.T.A. 2003. Patch type influences on regeneration in a western Pennsylvania, USA, catastrophic windthrow. Oikos 90(3): 489-500.

Pham, A.T., De Grandpré, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. 34: 353-364.

Price, K., Pojar, J., Roburn, A., Brewer, L., and Poirier, N. 1998. Windthrown or clearcut What's the difference? Northwest Sci. 72(Special Issue 2): 30-33.

R-Development Core Team. 2011. R: a language and environment for statistical computing. R Project for Statistical Computing, Vienna, Austria.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Ministère des ressources naturelles du Québec, Direction de la gestion des stocks forestiers et Direction des relations publiques, 213 p.

Ruel, J.-C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. For. Ecol. Manage. 135: 169-178.

Ruel, J.-C., Achim, A., Raul, E.H., Cloutier, A., Brossier, B. 2010. Wood degradation after windthrow in a northern environment. Forest Prod. J. 60: 200-206.

Ulanova, N.G. 2000. The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manage. 135: 155-167.

Vaillancourt, M.-A., De Grandpré, L., Gauthier, S., Leduc, A., Kneeshaw, D., Claveau, Y., and Bergeron, Y. 2009. How can natural disturbances be a guide for forest ecosystem management? *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., and Bergeron, Y. (eds). Presses de l'Université du Québec, Montreal, Canada, pp. 39-55.

Waldron, K., Ruel, J.-C., and Gauthier, S. 2013a. The effects of site characteristics on the landscape-level windthrow regime in the North Shore region of Quebec, Canada. Forestry 86(2): 159-171.

Waldron, K., Ruel, J.-C., and Gauthier, S. 2013b. Forest structural attributes after windthrow and consequences of salvage logging. For. Ecol. Manage. 289: 28-37.

Waldron, K. Ruel, J.-C., Gauthier, S., De Grandpré, L., and Peterson, C.J. Effects of windthrow and salvage logging on microsites, plant composition and regeneration. Accepted in Appl. Veg. Sc.

Chapitre III

FOREST STRUCTURAL ATTRIBUTES AFTER WINDTHROW AND CONSEQUENCES OF SALVAGE LOGGING[2]

[2] Version intégrale d’un article publié / Intergral version of a published paper:
Waldron, K., Ruel, J.-C., and Gauthier, S. 2013. Forest structural attributes after windthrow and consequences of salvage logging. Forest Ecology and Management 289: 28-37.

Abstract

In the eastern boreal forest of Quebec (Canada) windthrow is a major natural disturbance, given the long fire cycle interval. Understanding windthrow is essential for ecosystem-based forest management. Dead wood, live trees, and pit-and-mound microtopography are major post-windthrow attributes with known ecological importance. So far, these structural post-windthrow attributes have not been described for this ecosystem. In addition, ecological consequences of salvage logging after windthrow remain unknown, with no specific salvage standard being applied to maintain such attributes and biological legacies. In this study, comparisons were made between salvaged and unsalvaged windthrow to identify which post-windthrow attributes were more greatly affected by harvest operations and to clarify management options. Downed coarse woody debris (downed CWD), snags, live trees, and pits and mounds were characterized. We showed that downed CWD and snags diminished after salvage operations, with a more uniform distribution among decay classes. Pit and mound density was reduced after salvage logging compared to unsalvaged windthrow, with pits being smaller in the salvaged plots. From an ecosystem management perspective, retention patches with dead wood and standing live trees should be kept in salvaged cut-blocks. To minimise salvage operation effects on microtopography, machinery trails should be reduced to a minimum. Also, a certain proportion of windthrow should be exempted from logging operations.

Keywords: windthrow, salvage logging, structural attributes, ecosystem management, boreal forest.

Résumé

Le chablis est une perturbation naturelle dominante dans la forêt boréale de l'est du Québec (Canada) vu le long cycle de feu. La compréhension du chablis est donc essentielle dans une optique d'aménagement écosystémique. Le bois mort, les arbres sur pied résiduels et la microtopographie en monticules et en cuvettes sont des attributs post-chablis avec une importance écologique bien connue. À ce jour, ces attributs structuraux post-chablis n'ont pas été décrits dans cet écosystème. De plus, les conséquences écologiques des coupes de récupération effectuées après chablis demeurent inconnues et aucune norme spécifique n'est appliquée pour le maintien des attributs clés et des legs biologiques. Cette étude comparait donc les chablis récoltés et non récoltés afin d'identifier quels attributs post-chablis étaient le plus affectés par les opérations de récolte et ainsi, de mettre en lumière les options sylvicoles à prioriser. Le bois mort au sol, les chicots, les arbres vivants et la microtopographie en monticules et en cuvettes ont été caractérisés. Nous avons démontré que les coupes de récupération affectaient négativement la quantité de débris ligneux au sol et les chicots, qui avaient aussi une répartition plus uniforme entre les classes de dégradation. La densité des monticules et des cuvettes était réduite après coupe de récupération comparativement au chablis laissé intact, et les cuvettes étaient de plus petites dimensions dans les chablis récoltés. Dans une perspective d'aménagement écosystémique, des îlots de rétention d'arbres affectés par le chablis, avec du bois mort et des arbres vivants, devraient être maintenus à l'intérieur des assiettes de coupe de récupération. Afin de réduire les impacts négatifs des coupes de récupération sur la microtopographie, les sentiers de machinerie devraient être réduits à un niveau minimum. De plus, une certaine proportion de chablis devrait être exempte d'opérations de récolte.

Mots clés: chablis, coupe de récupération, attributs structuraux, aménagement écosystémique, forêt boréale.

Introduction

Ecosystem management, also known as natural disturbance-based management, has become the standard for forest management, not only in many regions of Canada, and throughout the world (Mitchell and Beese 2002; Fischer et al. 2006). Understanding natural disturbance is essential for establishing silvicultural treatments that reduce the disparity between natural and managed ecosystems (Gauthier et al. 2009). In the eastern boreal forest of Quebec (Canada), ecosystems can be affected by several episodes of windthrow, both partial and stand-replacing, which make windthrow one of the most important types of natural disturbance in the region (Ruel et al. 2010; Waldron et al. 2013). The higher occurrence of windthrow in the eastern compared to the western part of the boreal forest can be explained by the longer fire cycle in the former (Bouchard et al. 2008). While most studies of natural disturbance in the boreal forest of Quebec have focused on wildfire or insect outbreaks, an increased understanding of windthrow is essential for improving our understanding of forest dynamics, particularly in forests with long forest fire intervals, such the northeastern boreal forest of Canada (Bouchard et al. 2009; Waldron et al. 2013).

Windthrow creates attributes and biological legacies within ecosystems, including dead wood, pit-and-mound microtopography, and seedbed diversity (Beatty and Stone 1986; Schaetzl et al. 1989; Ulanova 2000). The ecological importance of snags and woody debris on the ground has been demonstrated repeatedly (Siitonen 2001; Jonsson et al. 2005) . Moreover, organisms that use dead wood are associated with either one or with many specific categories of dead wood and, thus, decay class and size both play a role from an ecological standpoint (Caza 1993; Siitonen 2001; Jonsson et al. 2005). Pit-and-mound microtopography refers to the slight surface elevations and depressions that are formed by tree uprooting. Uprooting mixes the soil, increasing nutrient element availability (Beatty and Stone 1986; Ulanova 2000). In certain forest ecosystems, these features can cover a relatively high proportion of the forest floor (Ulanova 2000). This particular form of microtopographic disturbance also exposes or creates a variety of seedbeds, thereby promoting the germination and the growth of different plant species (Peterson and

Campbell 1993; McCarthy 2001). From the perspective of natural-based management, these post-windthrow attributes should be described.

In many parts of the world, salvage operations are undertaken following episodes of natural disturbance. Effects of salvage logging following fire have recently received considerable attention from the scientific community (Nappi et al. 2004; Greene et al. 2006; Nappi et al. 2011). Yet, the ecological consequences of salvage logging after windthrow largely remain unknown in Quebec and there is no specific standard by which this technique can be implemented to maintain post-windthrow attributes. This lack of information should induce caution in our current management practices. Indeed, by looking at studies conducted elsewhere in the world on post-windthrow salvage logging (Loeb 1999; Greenberg 2001; Lain et al. 2008), we can suppose that key structural attributes as dead wood, pit-and-mound microtopography and live trees would be reduced by salvage logging operations. The comparison between salvaged and unsalvaged windthrow could help highlight those post-windthrow attributes that are more affected by harvest operations (Gauthier et al. 2009) and improve management choices. Therefore, the aims of our study were 1) to characterize post-windthrow structural attributes and 2) to compare those attributes with a post-windthrow salvage-logged area.

Materials and methods

Study area

The study was conducted in the eastern black spruce-feather moss subdomain of the boreal forest, which lies within the North Shore administrative region of Quebec, Canada (Figure 10). Black spruce (*Picea mariana* (Mill.) B.S.P.) and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant tree species, but white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) can also be found. The area is characterized by low occurrence of fire because of its humid and cold climate. Fire cycles on the North Shore range from 270 to over 500 years (Cyr et al. 2007; Bouchard et al. 2008). Mean annual precipitation is about 1300 mm and mean annual temperature ranges between -2.5°C and

0°C. The main surface deposit is glacial till, with rock outcrops frequently occurring at the tops of steep slopes (Robitaille and Saucier 1998).

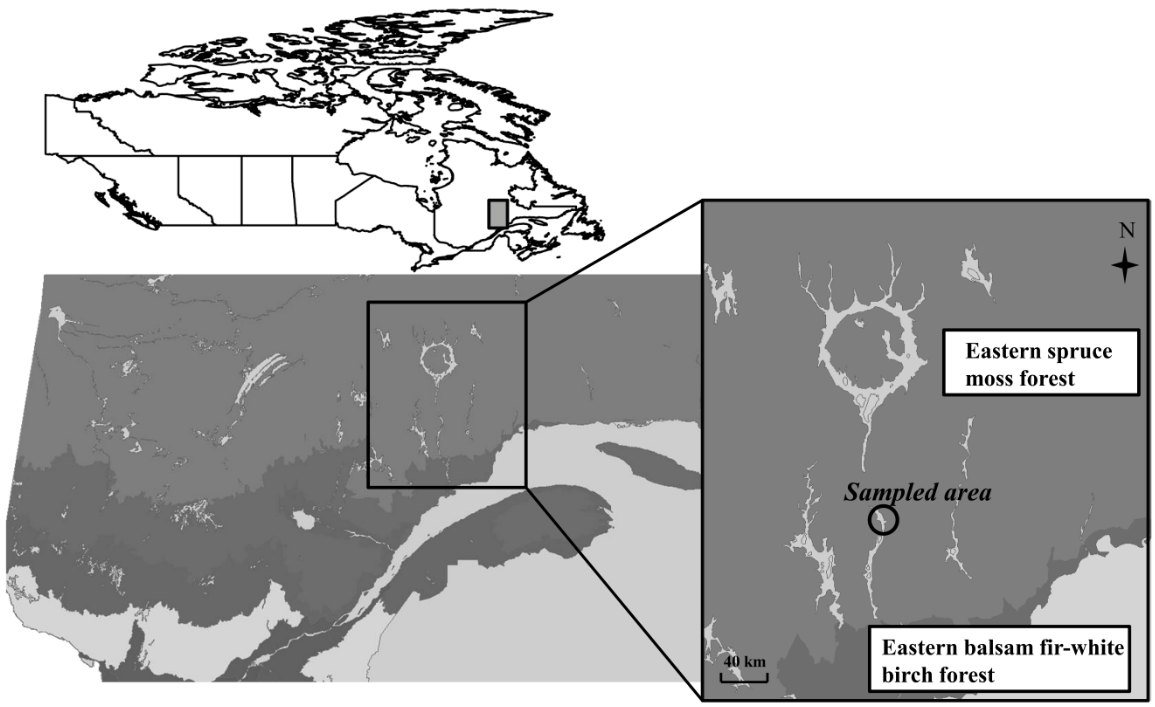

Figure 12: Study area.

Given the long fire cycles in the region (Bouchard et al. 2008), windthrow and outbreaks of spruce budworm (*Choristoneura fumiferana* (Clemens)) are the main natural disturbances in this ecosystem, with associated gap dynamics (Pham et al. 2004; De Grandpré et al. 2009; Bouchard and Pothier 2010). Stands with irregular age structure represent a large proportion of black spruce forests of the area (Boucher et al. 2003). In recent years, the region has been severely affected by several windthrow episodes. In 2003, a partial windthrow occurred followed by a major windthrow event in 2006. In total, over 88 000 ha were affected by windthrow (both partial and severe) during this period. A major salvage planning process followed the 2006 windthrow. The ensuing salvage operations affected more than 20,000 ha (Ruel et al. 2010).

Data collection

Salvage logging plans of the main forest products company, Resolute Forest Products, were used to select salvaged sites. Salvaged sites had been harvested in the summer of 2007 or 2008. Not only are downed trees harvested during logging but standing trees are also removed, which helps to compensate for higher logging costs (Roy 2008) and the reduced wood quality of dead trees (Ruel et al. 2010). Harvesting was conducted with a single-grip harvester and a forwarder. These harvest machines had inflatable tires with chains to increase traction (Jean-François Gauthier, personal communication). Cut-blocks having similar stand characteristics and a wide range of windthrow severities were chosen. High resolution aerial photographs that were provided by the Quebec Ministry of Natural Resources and Wildlife (MRNFQ), together with field estimation, were used to determine windthrow severity of each plot. These severities were distributed over four classes, which were: (1) 0-24%, (2) 25-49%, (3) 50-74%, and (4) 75% or greater stand mortality. Six cut-blocks of approximately 25 ha were sampled. In each cut-block, sampling followed a systematic approach, with a plot (0.04 ha) established every 100 m. Unsalvaged plots were grouped in 12 blocks, based on initial stand and soil characteristics, determined with the forest inventory maps provided by MRNFQ. The number of blocks was higher in the unsalvaged treatment as it was not possible to use a systematic approach because of safety and accessibility issues. A relatively wide range of windthrow severities were represented in sampled plots, but, because of safety issues, most of the plots were restricted to severity classes 1 to 3 (Table 14).

Data were collected during the summers of 2008 and 2010. A total of 137 plots of 11.28 m radius (0.04 ha) were sampled. Ninety-four of these plots were located in salvage logging and 43 were located in unlogged windthrown areas (Table 14). After salvage logging, downed coarse woody debris (downed CWD) and standing dead and living trees were measured on all 94 plots during summer, 2008. Microtopographic features were measured only on 49 plots in 2010, because the other 45 plots had been scarified between 2008 and 2010. All measurements in the unlogged plots were taken during the summer of 2010.

Tableau 13: Number of salvaged and unsalvaged plots in each windthrow severity class.

Severity class	Unsalvaged plots	Salvaged plots
1	15	5
2	12	48
3	14	25
4	2	16
Total:	43	94

Downed CWD were quantified and described in the main plot of 400 m^2. We measured all downed material in plots with diameters greater than 9 cm and lengths greater than 30 cm. Downed material volume was estimated with the Smalian's formula by taking both end diameters plus the length. Even if some authors have suggested other formula for wood estimation (Fraver et al. 2007), we chose Smalian's because it is the one used by MRNFQ and forest industries of Quebec (Lemieux 2011). When debris on the ground was a whole tree, butt (large end) diameter was taken and length measured until the diameter had decreased to 9 cm. When the log crossed a plot boundary, only the portion within the plot was measured. Downed CWD was classified according to Hunter's decay stages (Hunter 1990; Hunter and Schmiegelow 2011). This deadwood classification system or similar systems are widely used in Quebec and elsewhere (Jenkins et al., 2004; Webster and Jenkins, 2005; Cimon-Morin et al., 2010; Barrette et al., 2012). It can be directly used in the field to characterize degradation of trees in the forest. There are two Hunter classifications, one for standing trees and one for trees on the ground. There are five classes for downed wood material. Class 1 is characterized by an intact bark and wood texture with the presence of twigs. Class 2 also as an intact bark but there is no more twigs on the log. Classes 3 and 4 have lost almost all the bark and are sagging near the ground or totally on the ground. Finally, class 5 refers to a soft and powdery wood texture partially covered by bryophytes (Hunter and Schmiegelow 2011).

Standing dead trees (snags) and standing live trees were also quantified and described in the main plot of 400 m^2. Living trees and snags with a diameter at breast height (DBH) that was > 9 cm, were measured. Snags were trees with no green foliage. DBH of both living and dead standing trees were measured and regrouped into classes. Sixteen initial DBH classes have been collapsed to five for subsequent analyses. Snags and living trees were also classified according to Hunter's decay stages (Hunter 1990). There are seven classes for standing trees. Classes 1 and 2 represent standing living trees and classes 3 to 7 are for dead trees. Class 3 represents a dead but intact tree, class 4 is trees which are losing bark, class 5 is clean of bark, class 6 is broken and decomposed and class 7 is highly decomposed (Hunter and Schmiegelow 2011).

Three transects of 19.54 m were placed to form a triangle within each 400 m^2 plot; one of the corners was oriented northward from the plot centre. Further, dimensions were measured for treefall pits and mounds that were crossed by each transect. Maximal lengths and widths were measured for pits and mounds, as well as pit depth and mound height. Positions of pits, mounds, and forest floor along each transect were measured to obtain the area occupied by microtopography.

Statistical analysis

Downed CWD volume, snag density, live tree density and pit-and-mound microtopography dimensions and cover proportion were analyzed. ANOVAs ($p = 0.05$) using type III sums of squares were conducted for each of these response variables. Because of a significant Levene's test, we also included a different variance term for each treatment with the varIdent function of R to meet assumptions of homogeneity of variance (Pinheiro and Bates 2000). Responses variables were $\log_{10}$ or square-root transformed when necessary. In all the analysis, we used mixed-models to account for the nested structure of the data. For the unsalvaged windthrow treatment, plots with similar stand and site characteristics were regrouped into blocks, as were plots within the same cut-block for the salvage logging treatment. Blocks and plots were used as random factors. The analyses were conducted using the packages nlme, car and multicomp in the R statistical environment (R-Development Core Team 2011). For downed CWD volume and snag density, the influence of treatments, windthrow severity, decay classes and their interactions were tested. For live tree density, the influence of treatments, windthrow severity, and DBH classes and their interactions were tested. With contingency-tables and χ^2tests, we compared CWD volume, snags density and live trees density distributions between treatments. The effect of treatments on pit-and-mound microtopography area, sizes and proportions were tested. Microtopography characterization did not include windthrow severity classes because only one value of forest floor, pits and mounds was present for severity class 4; thus, it was not possible to calculate a standard error for this treatment.

Results

Coarse woody debris

When comparing the mean volumes and lengths of downed CWD, significant interactions were noted between treatments and severity, and between treatments and decay classes (Table 15). Distribution of downed CWD among decay classes was different between treatments ($\chi^2 = 1118.9$, $df = 4$, $p < 0.001$). The total mean volumes of downed CWD were 80.3 m^3/ha and 43.8 m^3/ha for unsalvaged and salvaged windthrow respectively. Partial χ^2 tests done between treatments showed a significant difference for all the decay classes ($p < 0.001$). Mean downed CWD volume is greater in the unsalvaged treatment than in the salvaged plots for decay classes 2 to 5. In the unsalvaged plots, decay classes 2 and 5 had the greatest volume of downed CWD (26.47 ± 5.52 m^3/ha and 20.08 ± 3.34 m^3/ha) and in the salvaged plots, decay classes 2 and 3 had the greatest volume of downed CWD (14.63 ± 1.52 m^3/ha and 16.33 ± 1.36 m^3/ha) (Figure 11).

Tableau 14: ANOVA summary of linear mixed-effect models for the effects of treatments, decay classes, and windthrow severity on CWD volume and length and snag density. Significant effects ($p < 0.05$) are indicated in bold.

Source	Num. *df*	CWD volume		CWD length		Snag density	
		F	*p*	*F*	*p*	*F*	*p*
Treatments	1	13.03	**0.0026**	50.09	**<0.0001**	85.68	**<0.0001**
Decay classes	4	58.03	**<0.0001**	8.06	**<0.0001**	12.27	**<0.0001**
Severity	3	8.63	**<0.0001**	4.99	**0.0027**	0.12	0.9494
Treat* Decay	4	7.11	**<0.0001**	18.74	**<0.0001**	11.95	**<0.0001**
Treat*Severity	3	5.36	**0.0017**	5.16	**0.0022**	0.49	0.6910

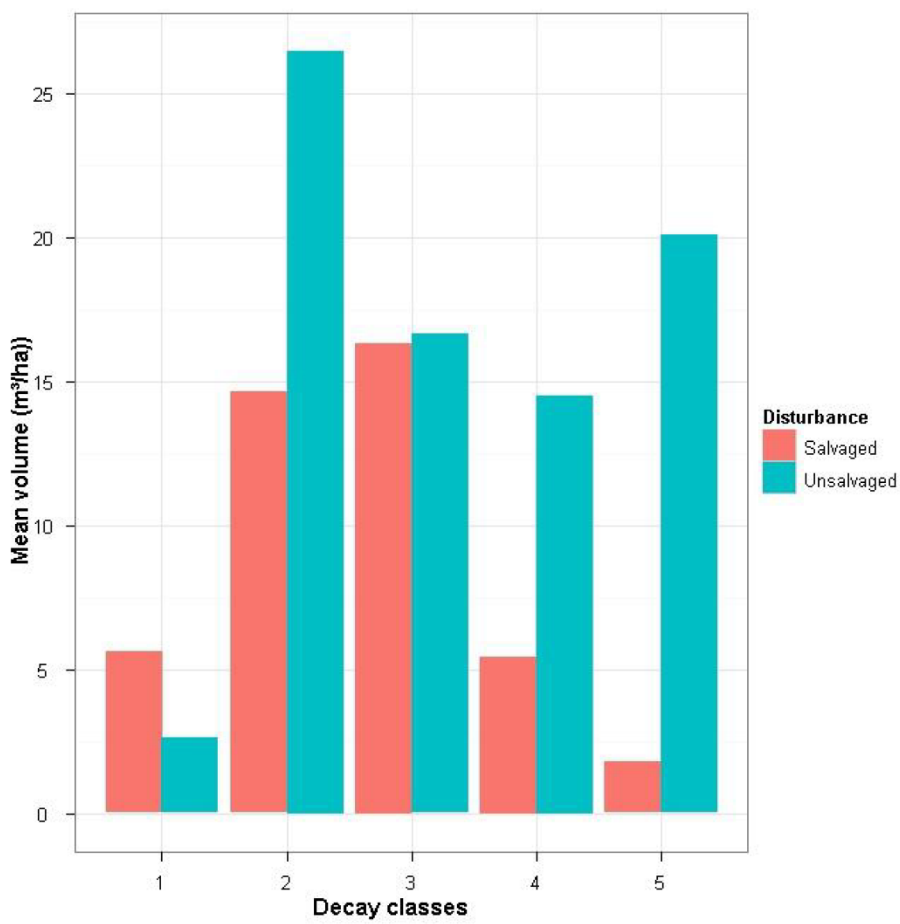

Figure 13: Mean volume of downed CWD (m3/ha) after windthrow were salvaged or left unsalvaged, as a function of decay class.

Distribution of downed CWD among windthrow severity classes was different between treatments (χ^2 = 471.1, df = 3, p < 0.001). Partial χ^2 tests conducted between treatments showed a significant difference for windthrow severity classes 2 to 4 (p < 0.001). There was no difference between treatments for severity class 1 (χ^2 = 1.7, df = 1, p = 0.18). Volume of downed CWD for severity classes 2, 3 and 4 in the windthrow treatment was higher than in the salvage logging treatment. The increase of downed CWD volume with the severity is more pronounced for the unsalvaged treatment than for the salvaged one (Figure 12).

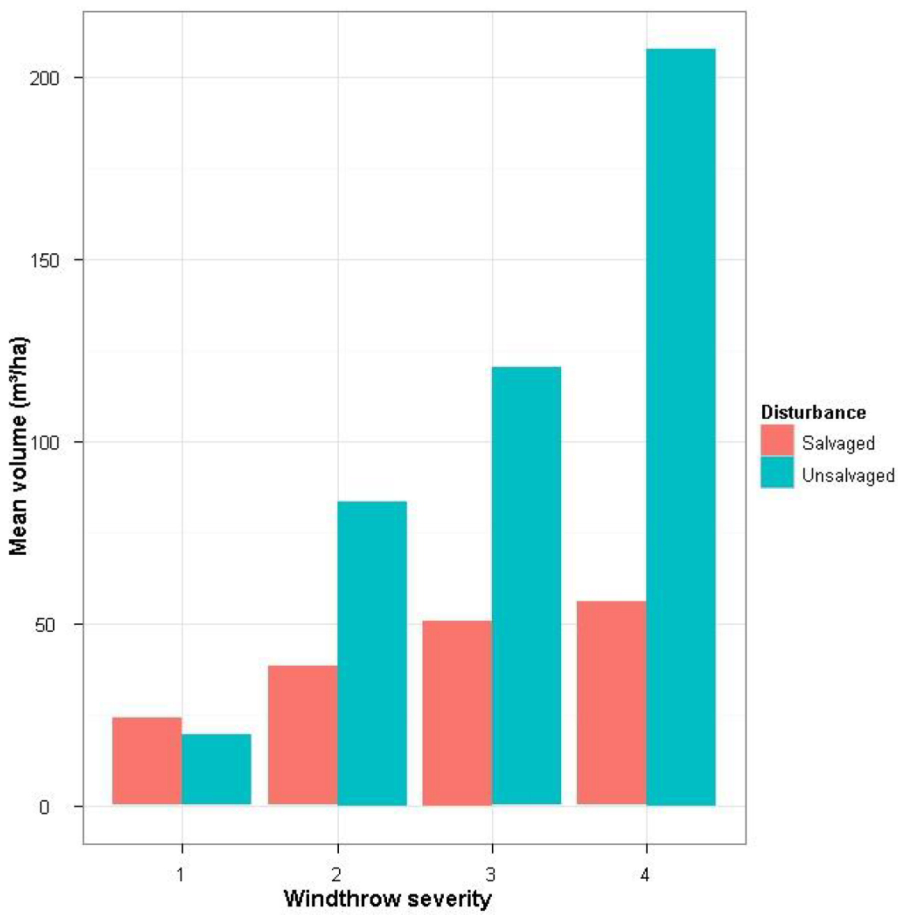

Figure 14: Mean volume of downed CWD (m3/ha) after windthrows were salvaged or left unsalvaged, as a function of windthrow severity.

Snags

Mean snag density differed between treatments, but this difference depended on decay classes (treatments*decay classes interaction). Windthrow severity had no significant effect (Table 15). Distribution of snag density among decay classes was different between treatments (χ^2 = 62.4, *df* = 4, p < 0.001). The total mean densities of snags were 312.5 stems/ha and 41 stems/ha for unsalvaged and salvaged windthrow respectively. Partial χ^2 tests done between treatments showed a significant difference for decay classes 3, 5 and 6 (p < 0.001). There was no difference between treatments for decay class 4 (χ^2 = 3.8, *df* = 1, p = 0.052) and for decay class 7 (χ^2 = 0.18, *df* = 1, p = 0.67). Unsalvaged windthrow showed a higher density of snags than salvaged windthrow, regardless of decay class, except for classes 4 and 7, which did not differ from salvaged windthrow. For unsalvaged windthrow, decay class 5 had the highest mean density of snags (121.02 ± 23.09 stems/ha; Figure 13) and after salvage logging, decay class 6 had the highest mean density of snags (13.95 ± 2.20 stems/ha).

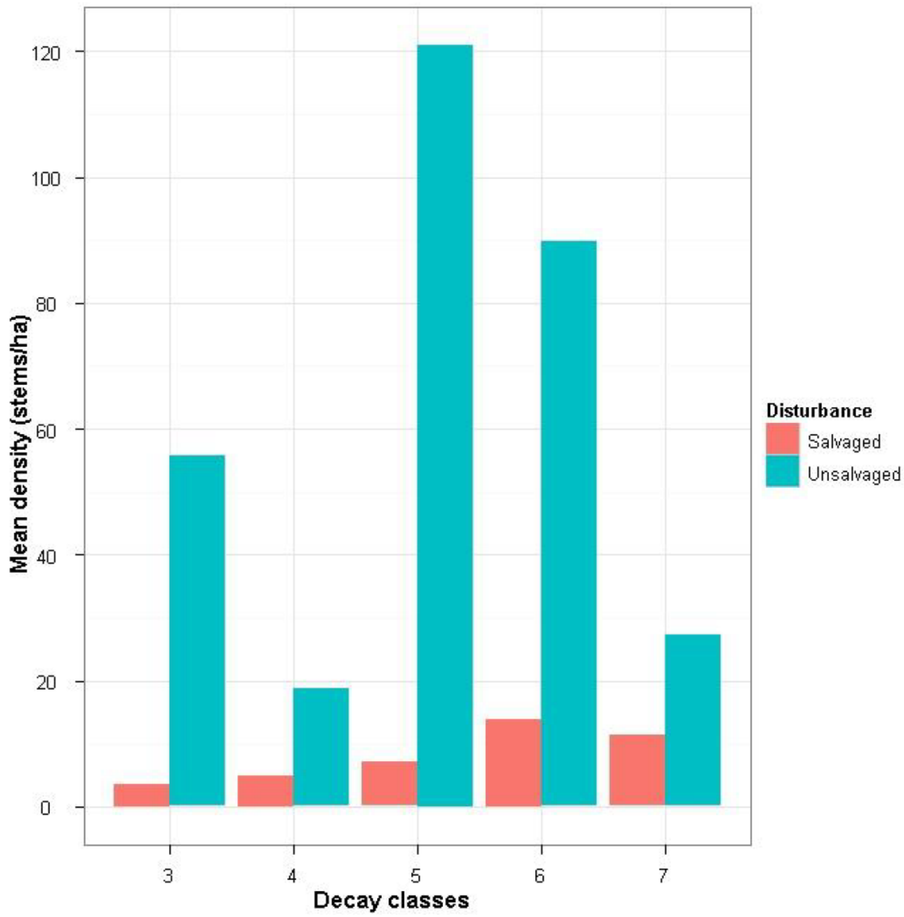

Figure 15: Snags mean density (stems/ha) after windthrows were salvaged or left unsalvaged, as a function of decay class.

Standing living trees

Densities of live trees varied among the plots, given significant interactions between treatments and DBH classes, and between treatments and windthrow severity (Table 16). Unsalvaged and salvaged windthrows have been presented in separate figures because of the scale difference. The mean density of living trees was lower in the salvaged treatment than after unsalvaged windthrow, regardless of DHB categories. Distribution of live trees density among DBH categories was different between treatments (χ^2 = 33.5, *df* = 4, $p <$ 0.001). Partial χ^2 tests conducted between treatments showed a significant difference for all the DBH classes ($p < 0.001$). For salvaged windthrows, DBH class 10 had the highest tree density (Figure 14a), with a mean density of 9.31 ± 1.51 stems/ha. In the unsalvaged windthrow treatment, DBH class 12 had the highest tree density with a mean of 375.58 ± 41.16 stems/ha. DBH classes 20 and 24 and more had the lowest mean density (Figure 14c).

The mean density of living trees was lower in the salvaged treatment than in unsalvaged windthrow, regardless of severity classes. Distribution of live trees density among windthrow severity classes was different between treatments ($\chi^2 = 108.5$, $df = 3$, $p < 0.001$). Partial χ^2 tests done between treatments showed a significant difference for all the severity classes ($p < 0.001$). In salvaged windthrow, live tree density was about the same for all severity class and was always under 4 stems/ha (Figure 14b). In unsalvaged windthrow, severity class 1 had the highest tree density, with 296.67 ± 31.44 stems/ha (Figure 14d).

Tableau 15: ANOVA summary of the linear mixed-effect model of standing live tree density. Significant factors ($p < 0.05$) are indicated in bold.

Effect	**Num. *df***	***F***	***p***
DBH	4	26.40	**<0.0001**
Windthrow severity	3	3.52	0.0173
Treatments	1	872.31	**<0.0001**
Treat*Windthrow severity	3	10.74	**<0.0001**
Treat*DBH	4	27.42	**<0.0001**

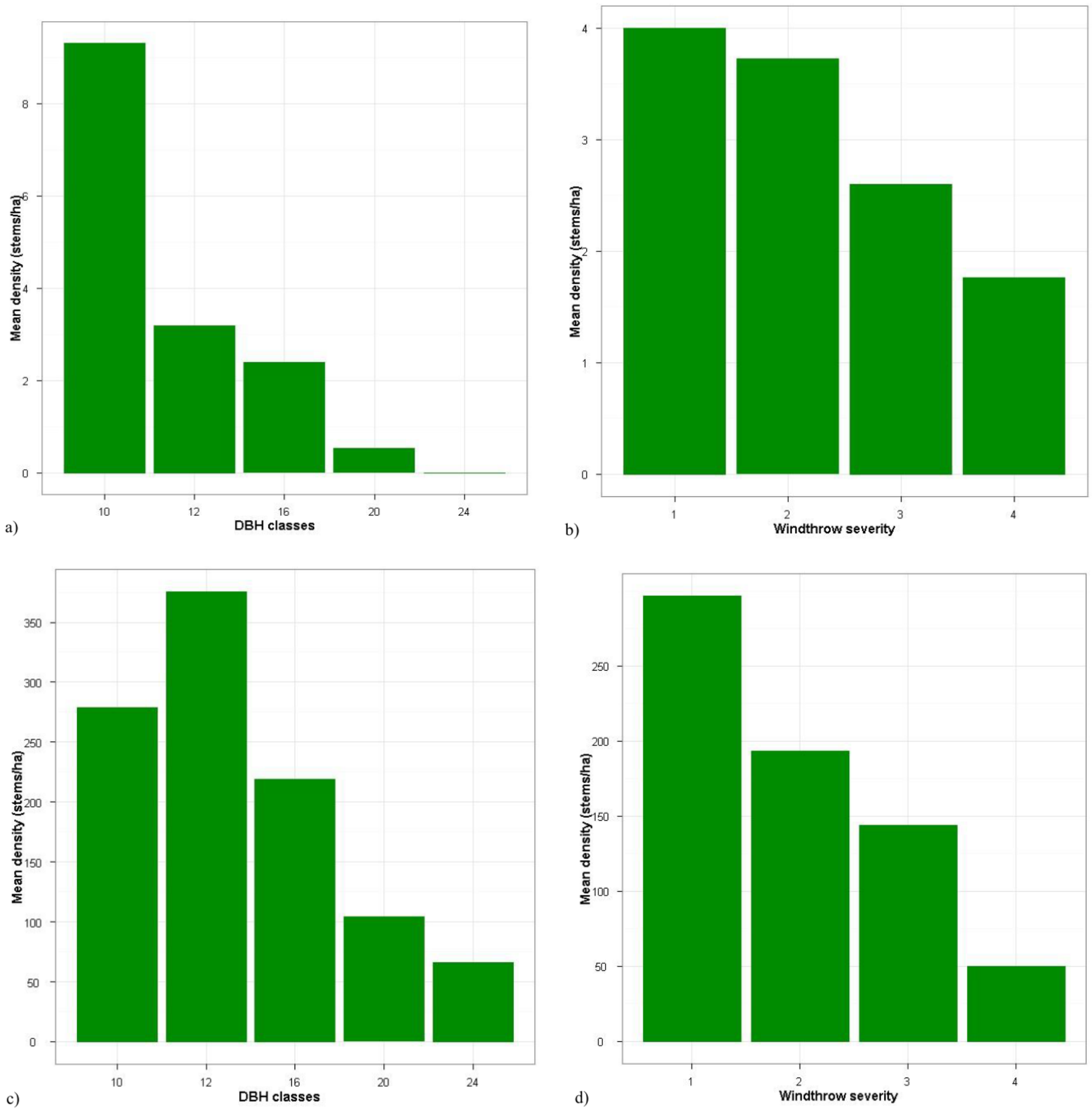

Figure 16: Mean density of live trees (stems/ha) after windthrows were salvaged (a, b) or left unsalvaged (c, d), as a function of DBH class and windthrow severity.

Microtopography

Pit and mound area was influenced by the type of microtopography and the interaction between the type of microtopography and the treatment. Treatments alone had no significant effects on pit and mound sizes. Considering the treatments and type of microtopography interaction, only pits in the unsalvaged treatment were significantly larger than the other microtopographic types (Table 17). Pit depth and mound height were not influenced by the treatment (Table 17).

Along the transects, nine mounds and eight pits have been encountered in the salvaged plots, and 37 mounds and 31 pits in the unsalvaged ones. In other words, 40% of the plots after unsalvaged windthrow had at least one pit and/or mound compared to 16% of the plots after salvage logging. Mean density of microtopographic features (pits and mounds) by plot were significantly different between treatments, but the type of microtopography (pits or mounds) had no influence on the mean number per plot (Table 17).

Microtopography types (pits, mounds and forest floor), treatments, and their interaction influenced significantly the proportion of transects that were covered by pits, mounds and forest floor. Severity of windthrow did not significantly affect cover proportions of microtopography and forest floor. Cover was similar for pits and mounds, regardless of treatments. The proportion of forest floor (i.e., undisturbed ground surface) was significantly greater than that of pits and mounds in both treatments. The forest floor proportion in unsalvaged windthrows was significantly greater than after salvage logging (Table 17).

Tableau 16: Mean values (± SE) for size of microtopographic features, number of microtopographic features, and mean proportion (%) of transects covered by pits, mounds and forest floor by plot. Within row, values superscripted by the same letter do not differ significantly at p = 0.05.

	Salvaged			Unsalvaged		
	Mounds	**Pits**	**Forest floor**	**Mounds**	**Pits**	**Forest floor**
Area (m^2)	1.04^b (0.21)	1.31^b (0.48)	-	1.61^b (0.18)	2.70^a (0.48)	-
Height or depth (m)	0.79^a (0.13)	0.23^b (0.04)	-	0.97^a (0.08)	0.24^b (0.03)	-
Number	0.15^b (0.04)		-	0.58^a (0.12)		-
Proportion of transects	0.27^c (0.11)	0.18^c (0.09)	99.55^a (0.19)	1.13^c (0.32)	0.98^c (0.36)	97.93^b (0.57)

Discussion

Characterization of post-disturbance attributes and biological legacies is important for measuring the effects of silvicultural practices on ecosystems and for implementing ecosystem forest management (Gauthier et al. 2009). Our study has described, for the first time, the post-windthrow structural attributes of an eastern Canadian boreal forest. It also qualified the alterations to post-windthrow structural attributes that are imposed by salvage logging.

Dead wood

Our results have shown that mean volumes of downed CWD of all decay classes are affected by salvage logging and that decay class 5 was the most affected. Highly decomposed downed CWD is used by many deadwood-dependent organisms (Siitonen

2001; Vaillancourt et al. 2008; Jacobs and Work 2012) and, thus, the substantial amounts of wood occupying advanced decay classes after windthrow could have a major ecological role. Scandinavian studies have shown that many deadwood-dependent organisms are on the red list (Berg et al. 1994; Jonsell et al. 1998; Jonsson et al. 2005). It leads us to think that many wood-dependent organisms may be affected by the dead wood volume reduction after salvage logging operations. Also, field observations have demonstrated a clear trend towards shorter downed CWD lengths after salvage logging compared to unsalvaged windthrow. Differences in lengths or diameters of downed CWD after salvage logging operations have been previously demonstrated in other forest ecosystems (Loeb 1999; Greenberg 2001). The absence of large dimension downed CWD after salvage logging can decrease structural heterogeneity of the ecosystem and could affect biodiversity. When salvage operations were preceded by a severe windthrow, about the same quantity of CWD was left in the cut-block relative to that found in salvage logging following partial windthrow. This result showed that a substantial quantity of downed CWD is harvested in salvage operations, in spite of the difficulty of harvesting when a high proportion of trees are on the ground.

The distribution of downed CWD volume among decay classes in unsalvaged windthrow could be explained by the imposition of two recent windthrow episodes, one in 2003 followed by one in 2006. Within the same area, Ruel et al. (2010) found that downed trees, which had been dead for four years, were already highly degraded. Our sampling was done seven years after the first windthrow event and four years after the second. Thus, trees that had been affected by these events were already degraded, which could explain the low proportion of downed CWD in decay class 1 and the large quantity of degraded downed CWD. The large volume of downed CWD in decay class 2 may be explained by high individual tree mortality following the 2006 windthrow event. In our plots, mean total downed CWD volume was about 80 m^3/ha, which is similar to estimates made for old-growth boreal forest found in eastern Canada (Sturtevant et al. 1997; Cimon-Morin et al. 2010). When considering only windthrows where >50% of the basal area had been affected, mean volume was between 120 and 200 m^3/ha. Our results showed that downed CWD volume in unsalvaged windthrow increases with disturbance severity, which was not surprising.

In terms of decay stages, snags after salvage logging were not as abundant and diversified as in unsalvaged windthrow. In fact, all decay classes after salvaged operations had about the same density of snags, which was not the case for the unsalvaged treatment. In other words, salvage logging results not only in a density reduction of standing deadwood but also a decline in its structural complexity. This reduction could have adverse ecosystem-level effects, since dead wood of different decay classes is an important resource for many different fauna and fungi. The low occurrence of old snags after salvage logging and the lack of recruitment of dead trees can negatively affect bird populations, for example, as snags of later decay stages can support large secondary cavity-nesting species (Vaillancourt et al. 2008).

In unsalvaged windthrows, the distribution of snags among the different decay classes was heterogeneous, which reflects not only the two windthrow episodes but also the continued effects of individual tree mortality. Aakala et al. (2008) showed that, in the eastern boreal forest of Quebec, the transition of snags between the earliest and the intermediate decay classes occurred rapidly; further, the residence time for snags in intermediate classes was longer than the initial stage. In five years, a substantial proportion of snags in the initial decay classes, therefore, would become and remain intermediate (Aakala et al. 2008). In our study, the high density of snags in intermediate decay class could be the consequence of the 2003 windthrow episode, while the high density of decay class 3 individuals could be the result of the 2006 windthrow. These results agree with those of Aakala et al. (2008), since our data were collected in 2010, i.e., 7 and 4 years after the recent windthrow episodes. Disturbance severity had no effect on snag density. This result could be explained by a higher mortality rate via uprooting than by stem breakage in black spruce stands (Fleming and Crossfield 1983; Cimon-Morin et al. 2010). The mean density of snags after windthrow was 62.5 stems/ha in our study site, with a maximum density in the intermediate decay class. The preponderance of snags in intermediate decay classes has been observed in natural forests in the region (Desponts et al. 2004; Vaillancourt et al. 2008). To our knowledge, no studies regarding post-windthrow snag density have been published for old-growth boreal forest. In our study area, Pham et al. (2004) reported a mean snag density of 155 (±54.2) stems/ha in old-growth black spruce forest, while Aakala et al. (2008) found a similar snag density of 131.9 (±45.4) stems/ha. Neither of these studies, though, was conducted on a site that had recently been affected by windthrow. Our results showed that snag density after windthrow is lower than the densities encountered by other authors in the same area when the forest remained unaffected by recent windthrow (Pham et al. 2004; Aakala et al. 2008). This difference could be attributed to the breakage or knockdown of snags by falling trees in windthrow-affected areas.

Living trees

Our results have shown that live tree density was strongly reduced by salvage logging and that large trees were largely absent after salvage operations. Trees that were left on cut-blocks were smaller, probably because they are less profitable for industry. Even if most living trees that remain in the ecosystems following windthrow are in the smallest DBH categories, there are still a certain number of large individuals. The definition of "large tree" can differ among ecosystems, but in our study area, trees greater than 20 cm DBH were generally considered as such (Vaillancourt et al. 2008). Large living trees in an ecosystem are essential to the fauna (Nilsson et al. 2002) and, if they fall, they would provide considerable downed CWD input. Live trees also contribute to the variation in light and humidity conditions experienced by understory vegetation and seedbeds. The density of living trees is a post-windthrow structural characteristic, but their spatial distribution must also be considered from the viewpoint of ecosystem management. Our study did not evaluate the spatial distribution of trees but an ongoing study in the same area will provide some information regarding this aspect (see chapter II of this thesis).

Microtopography

Pit-and-mound microtopography is characteristic of post-windthrow environments (Ulanova 2000; McCarthy 2001) and its ecological importance is well-known. Pit-and-mound microtopography increases seedbed heterogeneity (Jonsson and Esseen 1990; Ulanova 2000) and thus, can increase plant species richness in comparison to unaffected forest floor (Peterson and Campbell 1993). This microtopography also promotes tree seedling establishment (Kuuluvainen and Juntunen 1998; Šebková et al. 2012). Thus, in forest ecosystem management, knowledge about post-windthrow pit-and-mound microtopography is essential and conservation of microtopographic complexity is important.

Pit and mound sizes are associated with tree and root system dimensions (Peterson et al. 1990; Clinton and Baker 2000). In our study, most trees were black spruces and balsam firs that originated from old stands (>70 years old). The size similarity among the uprooted trees in the salvaged and unsalvaged treatments can explain the absence of differences in mound area and height and pits depth. The smaller area covered by pits after salvage logging compared to after unsalvaged windthrow may be explained by the fact that, after tree harvesting, stumps are partially or completely returned to their pre-windthrow position (Doyon and Bouffard 2008). The number of pits and mounds, together with the proportion of transects that were covered by pits and mounds, was higher after windthrow than after salvage logging, probably for the same reason. Also, logging trails were frequent and penetrated deeply into the soil of harvested sites, which can contribute to reducing the number and cover of pits and mounds after salvage operations. In contrast, pit and mound cover in unsalvaged plots was lower than results that have been obtained in other studies. For example, Peterson et al. (1990) found that 11% of their study area in Pennsylvania was covered by pits and mounds, while Cooper-Ellis et al. (1999) obtained an 8.3% cover in Massachusetts. Harrington and Bluhm (2001) calculated 4.4% for pit and mound area in their study site in Georgia. Pit and mound cover appears to be quite variable among forest ecosystems, so comparisons between studies are difficult to make.

Management implications

Our study showed some differences in structural attributes between unsalvaged and salvaged windthrows. As ecosystem management should be adaptative (Gauthier et al.

2009), studies can and should be used to improve silvicultural and management practices. Even if substantial quantities of windthrow are not salvaged, salvage logging is often concentrated locally, which reduces post-disturbance attributes at a local and regional scale. However, salvaged logging can be performed with caution to minimise negative impacts on the ecosystem (Foster and Orwig 2006). To preserve a certain quantity of living trees, downed CWD and snags, retention practices should be established in salvage logging operations, with retention patches identified prior to harvest operations. To maintain post-windthrow structural condition, larger retention patches are better. These patches should maintain within the salvaged area not only downed CWD and snags of different decay classes, but also living trees with a wide variation in size (Jönsson et al. 2007). Some trees will likely fall in the years following variable retention, particularly larger trees (e.g. Jönsson et al. 2007; Lavoie et al. 2012). In black spruce stands with an irregular structure, this proportion remains relatively small (Lavoie et al. 2012) and windthrow that occurs in retention patches would allow deadwood recruitment in salvaged logging blocks.

Thresholds of downed CWD volume or snag density that need to be maintained on cut-blocks are difficult to establish because of the lack of studies regarding relationships between the fauna and dead wood quantity and characteristics in our study area. Variable retention standards that have been used in the area could be applied for now. However, monitoring studies of attributes and the use of retention patches by fauna should be done and thresholds subsequently changed, where required. In addition, to minimise the impact of salvage operations on microtopography, machinery trails should be reduced to their minimum. At the management unit scale, a certain amount of windthrow should be preserved. Thresholds that have been previously suggested in Quebec for salvage logging following fire could be used (Nappi et al. 2011), in a manner that respects the precautionary principle. For instance, 30% of the windthrow that occurred in the last five years could be kept intact, with a certain quantity located beside intact forest. Also, portions of forest that were unaffected by windthrow should be kept intact along the disturbance perimeter, because of their potential ecological roles. Again, silvicultural and management strategies must be implemented in an adaptative fashion, with a monitoring plan in place (Drapeau et al. 2009; Gauthier et al. 2009).

Conclusion

This study has described for the first time the post-windthrow structural attributes of irregular-structured boreal forest in eastern Quebec. To apply ecosystem management, an understanding of natural disturbances is essential, and this study has increased knowledge regarding the effects of windthrow. Our results have shown reduction and a more uniform distribution of post-windthrow structural attributes due to salvage logging. Downed CWD, snags, living trees and, to a lesser extent, pit-and-mound microtopography, were all affected by salvage logging operations. This study provides decision-support by identifying which post-windthrow attributes are more affected by salvage operations, and highlighting the improvements that can be made in post-windthrow forest management to reduce the gap between natural disturbances and managed forests. Other key post-windthrow attributes, such as tree regeneration, vegetation biodiversity and seedbed condition should also be considered in salvage logging operations. Spatial organization of windthrow should also be studied to choose the sites where salvage logging operation should occur.

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References

Aakala, T., Kuuluvainen, T., Gauthier, S., and De Grandpré, L. 2008. Standing trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. For. Ecol. Manage. 255: 410-420.

Barrette, J., Pothier, D., Auty, D., Achim, A., Duchesne, I., and Gélinas, N. 2012. Lumber recovery and value of dead and sound black spruce trees grown in the North Shore region of Québec. Ann. Forest Sci. 69: 603-615.

Beatty, S.W., and Stone, E.L. 1986. The variety of soil microsites created by tree falls. Can. J. For. Res. 16: 539-548.

Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., and Weslien, J. 1994. Threatened plant, animal, and fungus species in Swedish forests: distribution and habitat associations. Conserv. Biol. 8: 718-731.

Bouchard, M., and Pothier, D. 2010. Spatiotemporal variability in tree and stand mortality caused by spruce budworm outbreaks in eastern Quebec. Can. J. For. Res. 40: 86-94.

Bouchard, M., Pothier, D., and Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. Can. J. For. Res. 38: 1621-1633.

Bouchard, M., Pothier, D., and Ruel, J.-C. 2009. Stand-replacing windthrow in the boreal forests of eastern Quebec. Can. J. For. Res. 39: 481-487.

Boucher, D., De Grandpré, L., and Gauthier, S. 2003. Développement d'un outil de classification de la structure des peuplements et comparaison de deux territoires de la pessière à mousses du Québec. Forest. Chron. 79(2): 318-328.

Caza, C.L. 1993. Woody debris in the forests of British Columbia: a review of the Literature and current research. Research Program, Ministry of Forests, Province of British Columbia, 115 p.

Cimon-Morin, J., Ruel, J.-C., and Darveau, M. 2010. Short term effects of alternative silvicultural treatments on stand attributes in irregular balsam fir-black spruce stands. For. Ecol. Manage. 260: 907-914.

Clinton, B.D., and Baker, C.R. 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. For. Ecol. Manage. 126: 51–60.

Cooper-Ellis, S., Foster, D.R., Carlton, G., and Lezberg, A. 1999. Forest response to catastrophic wind: results from an experimental hurricane. Ecology 80: 2683-2696.

Cyr, D., Gauthier, S., and Bergeron, Y. 2007. Scale-dependent determinants of heterogeneity in fire frequency in a coniferous boreal forest of eastern Canada. Landscape Ecol. 22: 1325-1339.

De Grandpré, L., Gauthier, S., Allain, C., Cyr, D., Périgon, S., Pham, A.T., Boucher, D., Morissette, J., Reyes, G., Aakala, T., and Kuuluvainen, T. 2009. Towards an ecosystem approach to managing the boreal forest in the north shore region: disturbance regime and natural forest dynamics. *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpre, L., Kneeshaw, D.D., Morin, H., Drapeau, P., Bergeron, Y. (eds), Presses de l'Université du Québec, Montreal, Canada, pp. 229-255.

Desponts, M., Brunet, G., Bélanger, L., and Bouchard, M. 2004. The eastern boreal old-growth balsam fir forest: a distinct ecosystem. Can. J. Botany 82: 830-849.

Doyon, F., and Bouffard, D. 2008. Étude sur le bois mort, les microsites et la régénération après chablis catastrophiques dans les érablières du Témiscamingue. Institut Québécois d'Aménagement de la Foret Feuillue, Ripon, Québec Rapport technique, 37 p.

Drapeau, P., Leduc, A., Kneeshaw, D., and Gauthier, S., 2009. An adaptive framework for monitoring ecosystem management in the boreal black spruce forest. *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpre, L., Kneeshaw, D.D., Morin, H., Drapeau, P., and Bergeron, Y. (eds), Presses de l'Université du Québec, Montreal, Canada, pp. 343-372.

Fischer, J., Lindenmayer, D.B., and Manning, A.D. 2006. Biodiversity, ecosystem function, and resilience. Ten guiding principles for commodity production landscapes. Front. Ecol. Environ. 4: 80-86.

Fleming, R.L., and Crossfield, R.M. 1983. Strip cutting in shallow-soil upland black spruce near Nipigon, Ontario. III-Windfall and mortality in the leave strips, preliminary results, 27 p.

Foster, D.R., and Orwig, D.A. 2006. Preemptive and salvage harvesting of New England forests: when doing nothing is a viable alternative. Conserv. Biol. 20: 959-970.

Fraver, S., Ringvall, A., and Jonsson, B.G. 2007. Refining volume estimates of down woody debris. Can. J. For. Res. 37: 627-633.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D., Drapeau, P., De Grandpré, L., Claveau, Y., and Paré, D. 2009. Forest ecosystem management, origins and foundations. *In*: Ecosystem management in the boreal forest. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpre, L., Kneeshaw, D.D., Morin, H., Drapeau, P., and Bergeron, Y. (eds), Presses de l'Université du Québec, Montreal, Canada, pp. 13-38.

Greenberg, C.H. 2001. Response of reptile and amphibian communities to canopy gaps created by wind disturbance in the southern Appalachians. For. Ecol. Manage. 148: 135-144.

Greene, D.F., Gauthier, S., Noël, J., Rousseau, M., and Bergeron, Y. 2006. A field experiment to determine the effect of post-fire salvage on seedbeds and tree regeneration. Front. Ecol. Environ. 4: 69-74.

Harrington, T.B., Bluhm, A.A., 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia Piedmont USA. For. Ecol. Manage. 140: 265-275.

Hunter, M.L. 1990. Wildlife, forests, and forestry. Principles of managing forests for biological diversity. Prentice Hall (Ed.), Upper Saddle River, 370 p.

Hunter, M.L., and Schmiegelow, F.K.A. 2011. Wildlife, forests, and forestry. Principles of managing forests for biological diversity. Second ed., Prentice Hall (Ed.), Upper Saddle River, 259 p.

Jacobs, J.M., and Work, T.T. 2012. Linking deadwood-associated beetles and fungi with wood decomposition rates in managed black spruce forests. Can. J. For. Res. 42: 1477-1490.

Jenkins, M.A., Webster, C.R., Parker, G.R., and Spetich, M.A. 2004. Coarse woody debris in managed central hardwood forests of Indiana USA. Forest Sci. 50: 781-792.

Jonsell, M., Weslien, J., Ehnstrom, B., 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodivers. Conserv. 7: 749-764.

Jonsson, B.G., and Esseen, P.-A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. J. Ecol. 78: 924-936.

Jonsson, B.G., Kruys, N., and Ranius, T. 2005. Ecology of species living on dead wood – lessons for dead wood management. Silva Fenn. 39: 289-309.

Jönsson, M.T., Fraver, S., Jonsson, B.G., Dynesius, M., Rydgård, M., and Esseen, P.-A. 2007. Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. For. Ecol. Manage. 242: 306-313.

Kuuluvainen, T., and Juntunen, P. 1998. Seedling establishment in relation to microhabitat variation in a windthrow gap in a boreal *Pinus sylvestris* forest. J. Veg. Sci. 9: 551-562.

Lain, E.J., Haney, A., Burris, J.M., and Burton, J. 2008. Response of vegetation and birds to severe wind disturbance and salvage logging in a southern boreal forest. For. Ecol. Manage. 256: 863-873.

Lavoie, S., Ruel, J.-C., Bergeron, Y., and Harvey, B. 2012. Windthrow after group and dispersed tree retention in eastern Canada. For. Ecol. Manage. 269: 158–167.

Lemieux, R. 2011. Méthodes de mesurage des bois. Instructions techniques. Exercice 2011–2012. Ministère des Ressources naturelles et de la Faune, Forêt Québec, Direction de l'aménagement des forêts publiques et privées, Service des stratégies d'aménagement, Québec, 198 p.

Loeb, S.C. 1999. Responses of small mammals to coarse woody debris in a southern pine forest. J. Mammal. 80: 460-471.

McCarthy J., 2001. Gap dynamics of forest trees: a review with particular attention to boreal forests. Environ. Rev. 9: 1-59.

Mitchell, S.J., and Beese, W.J. 2002. The retention system: reconciling variable retention with principles of silvicultural systems. Forest. Chron. 78(3): 397-403.

Nappi, A., Drapeau, P., and Savard, J.-P.L. 2004. Salvage logging after wildfire in the boreal forest: is it becoming a hot issue for wildlife? Forest. Chron. 80(1): 67-74.

Nappi, A., Bujold, F., Chabot, M., Dumont, M.-C., Duval, J., Drapeau, P., Gauthier, S., Brais, S., Peltier, J., and Bergeron, I. 2011. La récolte dans les forêts brûlées – Enjeux et orientations pour un aménagement écosystémique. Ministère des Ressources naturelles et de la Faune, Direction de l'environnement et de la protection des forêts, Québec, 51 p.

Nilsson, S.G., Niklasson, M., Hedin, J., Aronsson, G., Gutowski, J.M., Linder, P., Ljungberg, H., Mikusinski, G., and Ranius, T. 2002. Densities of large living and dead trees in old-growth temperate and boreal forests. For. Ecol. Manage. 161: 189-204.

Peterson, C.J., and Campbell, J.E. 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. B. Torrey Bot. Club 120: 451-460.

Peterson, C.J., Carson, W.P., McCarthy, B.C., and Pickett, S.T.A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. Oikos 58: 39-46.

Pham, A.T., De Grandpré, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. 34: 353-364.

Pinheiro, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-plus. Springer ed, New York, USA, 528 p.

R-Development Core Team. 2011. R: a language and environment for statistical computing. R project for statistical computing, Vienna, Austria.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Ministère des ressources naturelles du Québec, Direction de la gestion des stocks forestiers et Direction des relations publiques, 213 p.

Roy, V. 2008. La récupération des arbres ‘‘secs et sains’’ et renversés: effet sur la productivité d’une abatteuse-façonneuse. Chaire de recherche industrielle CRNSG Université Laval en sylviculture et faune, Bulletin d’information No 11.

Ruel, J.-C., Achim, A., Raul, E.H., Cloutier, A., Brossier, B. 2010. Wood degradation after windthrow in a northern environment. Forest Prod. J. 60: 200-206.

Schaetzl, R.J., Burns, S.F., Johnson, D.L., and Small, T.W. 1989. Tree uprooting: a review of impacts on forest ecology. Vegetatio 79: 165-176.

Šebková, B., Šamonil, P., Valtera, M., Adam, D., and Janik, D. 2012. Interaction between tree species populations and windthrow dynamics in natural beech-dominated forest, Czech Republic. For. Ecol. Manage. 280: 9-19.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms: fennoscandian boreal forests as an example. Ecol. Bull. 49: 11-41.

Sturtevant, B.R., Bissonette, J.A., Long, J.N., and Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol. Appl. 7: 702-712.

Ulanova, N.G. 2000. The effects of windthrow on forests at different spatial scales: a review. For. Ecol. Manage. 135: 155-167.

Vaillancourt, M.-A., Drapeau, P., Gauthier, S., and Robert, M., 2008. Availability of standing trees for large cavity-nested birds in the eastern boreal forest of Québec Canada. For. Ecol. Manage. 255: 2272-2285.

Waldron, K., Ruel, J.-C., and Gauthier, S. 2013. The effects of site characteristics on the landscape-level windthrow regime in the North Shore region of Quebec Canada. Forestry 86(2): 159-171.

Webster, C.R., and Jenkins, M.A. 2005. Coarse woody debris dynamics in the southern Appalachians as affected by topographic position and anthropogenic disturbance history. For. Ecol. Manage. 217: 319-330.

Chapitre IV

EFFECTS OF POST-WINDTHROW SALVAGE LOGGING ON MICROSITES, PLANT COMPOSITION AND REGENERATION[3]

[3] Version intégrale d'un article sous presse / Intergral version of a paper in press:
Waldron, K., Ruel, J.-C., Gauthier, S., De Grandpré, L., and Peterson, C.J. Effect of post-windthrow salvage logging on microsites, plant composition and regeneration. Accepted in Applied Vegetation Science.

Abstract

Understanding windthrow dynamics is essential to ecosystem-based forest management, particularly in regions with long fire cycles, where windthrow is predominant in the ecosystem. Notably, key post-windthrow attributes such as understory plant composition, tree regeneration and forest floor characteristics have not yet been described in the eastern boreal forest of Canada. Moreover, ecological consequences of salvage logging after windthrow remain unknown, precluding the development of salvage guidelines that can help maintain such attributes. Here we describe the understory vegetation, tree regeneration and forest floor in salvaged and unsalvaged windthrow as a means of documenting salvage logging effects on some of the key attributes of post-windthrow ecosystems. We showed that salvage logging affected advance regeneration and reduced forest floor heterogeneity. Also, some understory species present in the unsalvaged ecosystem were absent in the salvaged windthrow. From an ecosystem-based forest management perspective, natural post-windthrow understory conditions and microsite heterogeneity can be in part maintained in salvaged cutblocks by incorporating retention patches that include downed and standing dead wood and living trees of diverse sizes. As preliminary general standards for salvage logging after wind disturbance, these steps will favour plant regeneration and augment diversity.

Keywords: post-disturbance key attributes black spruce-feather moss forest, ecosystem management, Shannon's diversity index, understory plants diversity, forest floor heterogeneity, pit-and-mounds microtopography, windthrow severity.

Résumé

Une meilleure connaissance de la dynamique du chablis est essentielle à l'aménagement forestier écosystémique, particulièrement dans les régions où le chablis est prédominant dans l'écosystème. Les peuplements post-chablis possèdent plusieurs attributs clés qui n'ont pas encore été décrits dans la forêt boréale de l'est du Canada. Ces attributs sont, entre autres, la composition des plantes de sous-bois, la régénération et les caractéristiques du plancher forestier. De plus, les conséquences écologiques des coupes de récupération qui succèdent aux chablis demeurent inconnues, ce qui démontre l'importance de mettre en place des lignes directrices afin d'assurer le maintien des attributs clés dans les chablis récupérés. Dans cette étude, la végétation de sous-bois, la régénération et le plancher forestier ont été décrits afin de documenter les effets des coupes de récupération sur ces derniers. Nos résultats démontrent que les coupes de récupération affectent la régénération préétablie et diminuent l'hétérogénéité du plancher forestier. De plus, certaines espèces présentes dans les chablis non récoltés étaient absentes suite aux coupes de récupération. Dans une perspective d'aménagement forestier écosystémique, les conditions de sous-bois et les microsites présents dans les chablis laissés intacts pourraient être maintenus en partie en laissant sur les parterres de coupe des îlots de rétention incluant du bois mort au sol, des chicots ainsi que des arbres vivants. Ces îlots pourraient favoriser la régénération et augmenter la richesse en espèces de sous-bois sur les parterres de coupe, aidant ainsi à l'établissement de premiers standards généraux pour les coupes de récupération post-chablis.

Mots clés: attributs clés, pessière à mousses de l'Est, aménagement forestier écosystémique, indice de Shannon, diversité végétale, hétérogénéité du plancher forestier, microtopographie en monticules et en cuvettes, sévérité du chablis.

Introduction

In many parts of the world, major disturbance episodes often lead to salvage logging (often called sanitary logging in Europe, Lindenmayer et al. 2004, 2008). Functionally, salvage logging can be distinguished from other harvest operations in that, with salvaging after natural disturbance, the ecosystem is subjected to two sequential disturbances within a short period (Lindenmayer et al. 2008). Peterson and Leach (2008) suggest that multiple disturbance impacts need to be understood on the basis of cumulative severity. Indeed, recent conceptual advances (e.g. the cusp model of Frelich & Reich 1999, the three-axis model of Roberts 2004, 2007) have begun to address the potential for multiple disturbances to change the trajectory of community development, sometimes in undesirable directions (Paine et al. 1998). Because of the potential for the combined severity of natural disturbance followed by salvaging to yield unwanted 'ecological surprises' (Paine et al. 1998), guidelines are needed for the planning of post-windthrow salvage logging operations. Moreover, these guidelines should be focused on the main processes or forest attributes that are affected by the salvaging activity.

The ecological consequences of this type of forest intervention have been studied, but mostly following fire (Nappi et al. 2004; Purdon et al. 2004; Greene et al. 2006). The few studies that examined post-windthrow salvage logging highlighted the multiple ways that it may influence biological legacies (Elliott et al. 2002; Rumbaitis del Rio 2006; Peterson & Leach 2008; Jonášová et al. 2010). Peterson and Leach (2008) documented differences in relative abundances of microsite types in salvaged vs. unsalvaged windthrow forests of Tennessee. Lang et al. (2009) pointed to the presence of treefall microtopography as a structural legacy allowing establishment of species that would otherwise be rare or locally absent. Rumbaitis del Rio (2006) reported that salvaged areas had lower herbaceous abundance and diversity than unsalvaged areas, and that salvaged areas had widespread mortality of a pre-disturbance dominant shrub *Vaccinium* spp. Fischer et al. (2002), Rumbaitis del Rio (2006), Nelson et al. (2008), Lang et al. (2009) and Fischer and Fischer (2012) have all noted that salvaged areas have greater abundance of ruderal or pioneer species during the initial decades of regeneration.

Disturbance types differ in the legacy imprint they leave on boreal forest ecosystems. Windthrow legacies are characterized by deadwood, pit-and-mound microtopography, remnant trees of various sizes, and diverse seedbed conditions (Vaillancourt 2008; Waldron et al. 2013). Such legacies are involved in tree regeneration process and the maintenance of plant diversity. Soil turnover induced by tree uprooting has been shown to contribute to seedbed heterogeneity following windthrow (Peterson et al. 1990; Clinton & Baker 2000). Furthermore, the change in light and soil conditions following windthrow were shown to increase herbaceous and shrub species diversity (Peterson & Pickett 1990; Palmer et al. 2000; von Oheimb et al. 2007) and influence growth rate of tree regeneration (Ruel & Pineau 2002; Wohlgemuth et al. 2002; Kuuluvainen & Kalmari 2003). Most of these findings come from temperate forest ecosystems (exceptions are Ruel and Pineau 2002 and Kuuluvainen & Kalmari 2003), emphasizing the need to further document their role in boreal forests.

Post-windthrow heterogeneity in forest floor characteristics can favour bryophyte diversity as many species are known to have specific habitat requirements (Jonsson & Esseen 1990). However, harvest operations negatively influence bryophyte diversity by changing the microclimatic conditions and by reducing suitable substrates (Fenton et al. 2003; Jonášová and Prach 2008). Pit-and-mound microtopography could also influence understory plant composition and diversity (Peterson & Campbell 1993). However, the harvest of uprooted trees can make stumps return to their pre-windthrow position (Doyon & Bouffard 2008) and, thus, reduce the pit-and-mound microtopography (Waldron et al. 2013). As demonstrated in previous studies (Peterson & Pickett 1995; Kuuluvainen & Kalmari 2003), seedbed diversity in post-windthrow ecosystems positively affects plant regeneration.

This study characterizes understory species composition, tree regeneration and forest floor heterogeneity, to see whether and how salvage logging affects these post-windthrow attributes. The aims of the study were to 1) characterize post-windthrow undergrowth vegetation, regeneration and seedbeds and 2) compare those attributes with a post-windthrow salvage-logged area.

Materials and methods

Study area

The study was conducted in the eastern black spruce-moss subdomain of the boreal forest in the North Shore administrative region of Quebec, Canada (MRN 2013, Fig. 17). The dominant tree species are black spruce (*Picea mariana* (Mill.) Britton, Sterns & Poggenburg) and balsam fir (*Abies balsamea* (L.) Mill.), but white birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.) are also present. The main succession pattern in the area following fire is the black spruce establishment, with a gradual increasing of balsam fir proportion with the time since fire. This succession pattern can occurs on all soil types. Other succession patterns may occur in the area, but are less frequent. Intolerant hardwoods can establish after fire and be gradually replaced by balsam fir 80 to 100 years after fire or by black spruce 100 to 140 years after fire (De Grandpré et al. 2009). Balsam fir is a shade-tolerant species and can stay many years under the canopy, and rapidly start to grow when canopy opening is created. Balsam fir regeneration can take place on a variety of seedbeds. Black spruce is also considered as relatively shade-tolerant, but less than balsam fir. Black spruce produces small seeds which can establish on Sphagnum, but mineral soil is a preferred seedbed. Layering is also an important means of reproduction for black spruce, especially under existing canopies (Burns & Honkala 1990).

Balsam fir as a mean longevity of 60 to 100 years and the mean longevity of black spruce is between 100 to 200 years (Burns & Honkala 1990). As the main species longevity is shorter than the fire cycle, more than 70% of the stands present an irregular size distribution and a large proportion are old-growth (Boucher et al. 2003; De Grandpré et al. 2009).

Regional topography is complex, including both high elevation sites and deep valleys. Rocky outcrops are very frequent and the main surface deposit is till. Across the study area, mean slope is 14% and mean elevation is 442 m. Annual precipitation averages about 1300 mm, while mean annual temperature ranges between -2.5°C and 0°C (Robitaille & Saucier 1998).

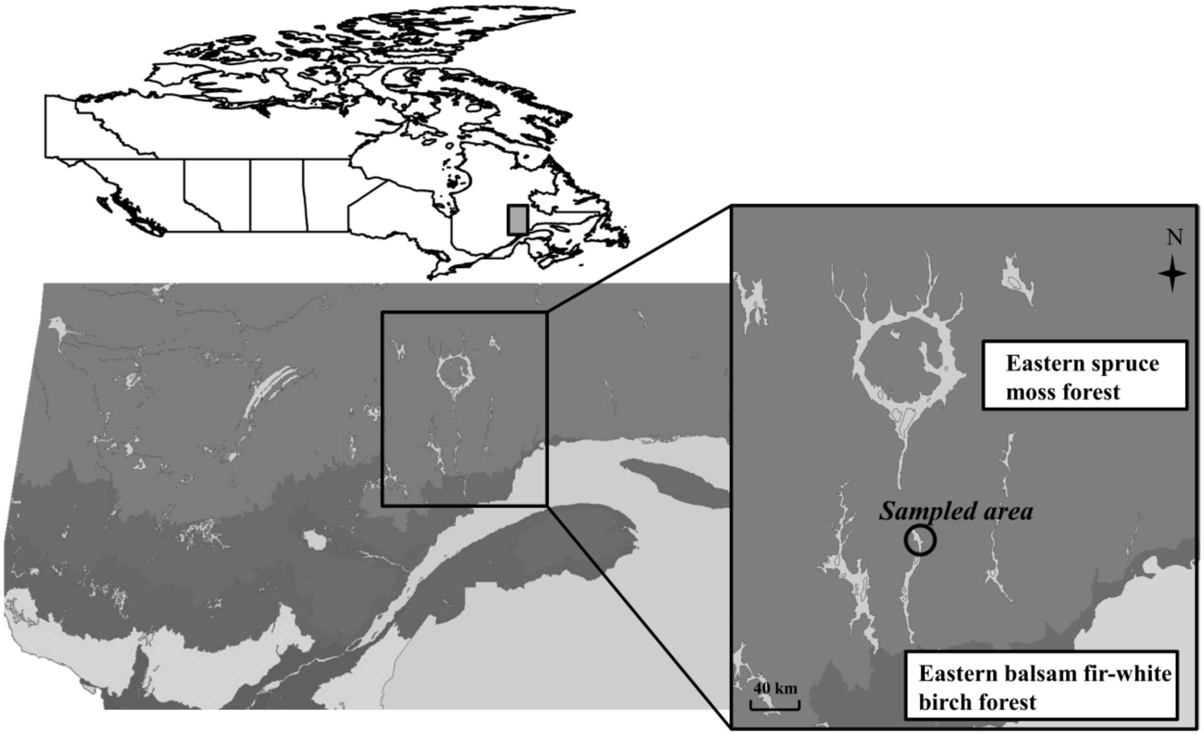

Figure 17: Study area.

This area is characterised by a low frequency of forest fire because of a humid and cold climate (Bouchard et al. 2008). Windthrow and outbreaks of spruce budworm (*Choristoneura fumiferana* (Clem.)) are the main disturbances in this ecosystem (Pham et al. 2004; De Grandpré et al. 2009; Bouchard & Pothier 2010). A few recent windthrow episodes have severely affected the region. A partial windthrow occurred in 2003, which was followed by a major windthrow event in 2006. During this period, more than 88 000 ha were affected by windthrow. A salvage plan followed the 2006 windthrow and covered more than 20 000 ha (Ruel et al. 2010).

In Quebec, following a major natural disturbance, the Quebec Ministry of Natural Resources (MRNQ) allocates wood volume to forest industries that will salvage the affected stands in priority. When executing salvage logging operations, industries can derogate from the RSFM (Regulation respecting standards of forest management for forests in the domain of the State), for the size and spatial repartition of the cutblocks. Also, there is no specific recommendation about the amount of deadwood to be left on the cutblocks during salvage logging operations (MRNF 2012). In the same area, a study about structural attributes after post-windthrow salvage logging showed a reduction of snag density and a homogenization of the decay classes in comparison to unsalvaged windthrow. Also, mean downed deadwood volume after salvage logging was 43.8 m^3/ha in comparison with 80.3 m^3/ha after unsalvaged windthrow. Residual living trees were almost absent in salvaged windthrow (Waldron et al. 2013).

Data collection

Salvage logging plans that had been devised by the forestry company Resolute Forest Products (Baie-Comeau, QC) were used to choose the salvaged sites. Salvaged sites had been harvested in the summer of 2007 or 2008, following the 2006 windthrow episode. We selected salvaged cutblocks where no scarification and reforestation operations had been done. Also, cutblocks chosen for this study were selected on the basis of similar initial stand characteristics and covering a wide range of windthrow severities. Stand composition prior to logging operations was determined with forest inventory maps that were provided by the MRNQ. These maps give information about stand and site characteristics, based upon both photo-interpretation and field verification. High resolution aerial photographs provided by MRNQ, together with ground truthing in the field, were used to determine windthrow severity. Severities were classified into four classes of stand mortality: 1) 0-24%; 2) 25-49%; 3) 50-74%; and 4) 75% or greater. Six cut-blocks of approximately 25 ha were sampled. In each cut-block, sampling followed a systematic approach, with a plot established every 100 m along a transect, for a total of 43 plots.

Based on initial stand and soil characteristics from the MRNQ forest inventory maps, 49 unsalvaged plots, all affected by the 2006 windthrow episode and originating from primary forest, were established within 12 blocks. We selected the unsalvaged plot with the location of the plots of the forest inventory program of the MRNQ, as we know that those plots were relatively accessible. The number of blocks was greater for the unsalvaged treatment, as a systematic location of plots within the unsalvaged area was not possible owing to safety and accessibility issues. A relatively wide range of windthrow severities was represented in the sampled plots, but most plots were restricted to severity classes 1 to 3, because of safety concerns (Table 17).

Tableau 17: Number of salvaged and unsalvaged plots in each windthrow severity class.

Severity classes	Unsalvaged plots	Salvaged plots
1	15	2
2	12	29
3	14	14
4	2	4
Total	43	49

Data were collected during the summer of 2010. A total of 92 plots were sampled, each with a radius of 11.28 m (0.04 ha). Three transects of 19.54 m were positioned to form a triangle within each 0.04 ha plot. One of the corners was oriented northward from the plot centre. On each transect, two subplots of 1.13 m radius (4 m^2) were also established (Fig. 18). Transects without any treefall pit or mound were divided in three equivalent portions and each of these portions was separated by the two subplots. When there were pits and/or mounds crossing the transect, subplots were placed equidistant between those pits and mounds. Thus, we had the same number of subplots on undisturbed forest floor in each plot, regardless of the presence of pit-and-mound microtopography. Pits and mounds are microtopographical features that were formed by tree uprooting, and were associated with an uprooted trunk.

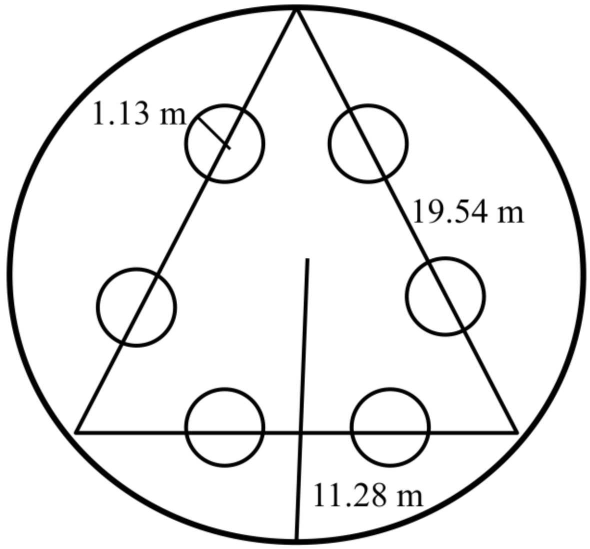

Figure 18: Plot design. Deadwood volume and decay classes were measured in the 11.28 m radius plot; regeneration density, plant diversity and seedbeds on undisturbed forest floor were measured in each 1.13 m subplot; Regeneration density, plant diversity and seedbeds were measured on each pit and mound crossing the 19.54 m transects.

In the main 11.28 m radius plot, all downed coarse woody debris (downed CWD) with diameters ≥ 9 cm and lengths ≥ 30 cm were measured. Wood volume was estimated with Smalian's formula by taking the two end diameters (cm) plus the length (m) for each piece. We chose Smalian's formula because it is computationally straightforward and commonly used by the MRNFQ and Quebec forest industry (Lemieux 2011). When debris on the ground was a whole tree, the butt (large end) diameter was taken and the bole length measured until the diameter had decreased to 9 cm. When the log crossed a plot edge, only the portion within the plot was measured. Downed CWD was also classified using Hunter's decay classes (Hunter 1990; Hunter & Schmiegelow 2011). There are five classes for downed wood material. Class 1 is characterized by an intact bark and wood texture with the presence of twigs. Class 2 also has an intact bark but there are no more twigs on the log. Classes 3 and 4 have lost almost all of their bark and are sagging near the ground or totally on the ground. Finally, class 5 refers to a soft and powdery wood texture partially covered by bryophytes (Hunter & Schmiegelow 2011). CWD with Hunter classes one to three was considered as recent, while that in Hunter classes four or five was considered as old.

In each subplot (1.13 m radius) that had been established on undisturbed forest floor, ground vegetation was recorded. Except for mosses, Sphagnum and lichens, all taxa were recorded at the species level and their cover was visually estimated in 5% classes. Seedbeds were characterised in each of the subplots by visually estimating cover of seedbed types in 5 % classes. Seedbed categories were mosses, Sphagnum, dead mosses, dead Sphagnum, skid trail, rock, organic soil, mineral soil and water. Vegetation and seedbeds were also characterised on each pit and mound crossing a transect.

Regeneration of commercial tree species was counted in each subplot. Since both seedlings and saplings were considered, all stems taller than 5 cm and with a DBH < 9 cm were included. We used 6 height classes to characterize regeneration: 1) 5-30 cm; 2) 30-60 cm; 3) 60-100 cm; 4) 100-200 cm; 5) 200-300 cm; and 6) more than 300 cm. We considered classes 2 to 6 to be advance regeneration, as the sampling was done 2 to 4 years after the disturbance. The tree species was also considered. Regeneration was also counted on pits and mounds.

Analysis

For the analysis, the sum of CWD volume of Hunter classes 1, 2 and 3 (recent CWD) and the sum of the volume of Hunter classes 4 and 5 (old CWD) were used for each plot of 11.28 m radius. For understory vegetation and seedbed cover, the mean value of the six 4 m^2 subplots within each plot was used for the undisturbed forest floor. The mean value of understory vegetation and seedbed cover on pits and on mounds within each plot was also calculated. Finally, for the regeneration density, the mean value per subplot was used.

Vegetation biodiversity and seedbeds characterization

We tested the effect of microtopography of both treatments (salvaged and unsalvaged windthrow) and windthrow severity on species richness (total number of species per subplot) and Shannon diversity index ($H' = - \sum c_i \ln c_i$ where c_i is the proportional cover of the i^{th} species in the subplot) using a mixed model. Blocks and plots were used as nested random factors. We included a different variance term for each treatment in the model to satisfy homoskedasticity (Pinheiro & Bates 2000), given a significant Leven's test. When a significant effect was detected, means comparisons were conducted using post-hoc Tukey tests. These statistical analyses were conducted using nlme version 3.1-109 (Pinheiro et al. 2013), car version 2.10-18 (Fox et al. 2013) and multicomp version 1.2-18 (Hothorn et al. 2013) packages of R, version 3.0.1 (R Core Team 2013).

Multivariate analyses determined which environmental and stand characteristics were the most important in explaining differences in plant species composition and seedbed types among the treatments. Plant species and seedbed data were first Hellinger-transformed with the Vegan package version 2.0-7 (Oksanen et al. 2013) in R to reduce the weight of high cover values and increase the weight of rare species (Legendre & Gallagher 2001; Borcard et al. 2011). Detrended Correspondence Analysis (DCA) was then used to estimate gradient length. As the gradients were under 4, we considered that species and seedbeds were responding linearly to the environmental gradient (Borcard et al. 2011). Given these linear responses, we opted for partial redundancy analyses (partial RDA). Partial RDA was used to control for some site covariables in the analysis. Thus, species and seedbed data could be displayed with other plot characteristics when the effect of the soil and stand factors were kept constant (Borcard et al. 2011). Variance inflation factors (VIF) were calculated prior to RDA using R Vegan package, version 2.0-7 (Oksanen et al. 2013) to ensure that multicollinearity among the predictor variables was avoided (Zuur et al. 2010). We kept variables with VIF smaller than 10 (Borcard et al. 2011). For forest floor characterization, one partial RDA was performed. The seedbed types proportions were included in the analysis, as dependant variable. The covariables included in the analysis were stand composition, age, height, density and soil drainage and were obtained from forest inventory maps provided by the Quebec Ministry of Natural Resources and Wildlife (MRNFQ). This information was originally acquired from photo-interpretation and field verification. The environmental or predictor variables used in this analysis were the treatment, represented by six categorical variables which were forest floor, pits and mounds in unsalvaged windthrow and forest floor, pits and mounds in salvaged windthrow. The other included environmental variable was windthrow severity.

Another partial RDA was used to visualize plant species assemblages on forest floor, pits and mounds for both treatments. Dependent variables were the transformed species cover. The covariables were, as for the seedbed description, the stand composition, age, height, density and soil drainage. Environmental variables that were used were the treatment, represented by the same six categorical variables that we used for seedbed description. Windthrow severity, total volume (m^3/ha) of recent CWD, total volume (m^3/ha) of old CWD, mineral soil cover, and organic soil cover were also used as environmental variables.

Regeneration

The effects of the treatments, microtopography attributes, windthrow severity, and regeneration species on seedlings and saplings were tested using a linear mixed-model. At first, regeneration height classes were included in the model. However, as most of the regeneration was advanced regeneration, height classes had no statistical effect. Thus, the data were pooled without considering height classes. The same random factors selected for diversity analysis were used, with the same packages of R software (R Core Team 2013). We conducted post-hoc Tukey tests to characterize the effect of treatment and microtopographic attributes on the numbers of seedlings and saplings. We compared numbers of seedlings and saplings distributions for the three tree species (black spruce, balsam fir and white birch) among windthrow severity classes using contingency-tables and χ^2tests.

Results

Seedbeds characterization

In order to characterize seedbed heterogeneity, we analyzed a matrix with the different seedbeds cover. These seedbed types, which included mosses, Sphagnum, dead mosses, dead Sphagnum, skid trail, rock, organic soil, mineral soil and water, were the dependant variables. Treatments (forest floor, pits and mounds for salvaged and unsalvaged windthrow) and windthrow severity were used as environmental variables. Covariables were stand composition, age, height, density and soil drainage. The first two axes of the partial RDA explained 16.1% of the variation in forest floor variables (axis 1, 12.0%; axis 2, 4.1%). The first axis was contrasting moss and Sphagnum to dead moss and dead Sphagnum. The first axis was constrained by windthrow severity, and desiccation stress became increasingly more important as windthrow severity increased, as shown by the association between dead moss and dead Sphagnum and windthrow severity vectors. Also, salvaged logging treatment was associated with dead moss and Sphagnum. Mineral and organic soils vectors were positively associated with pits and mounds of unsalvaged treatments. Rock was related to pits and mounds in the salvaged treatment. Skid trails and dead lichen seedbeds were highly associated with forest floor after salvage logging and woody debris and Sphagnum were positively associated with forest floor of unsalvaged windthrow (Fig. 19).

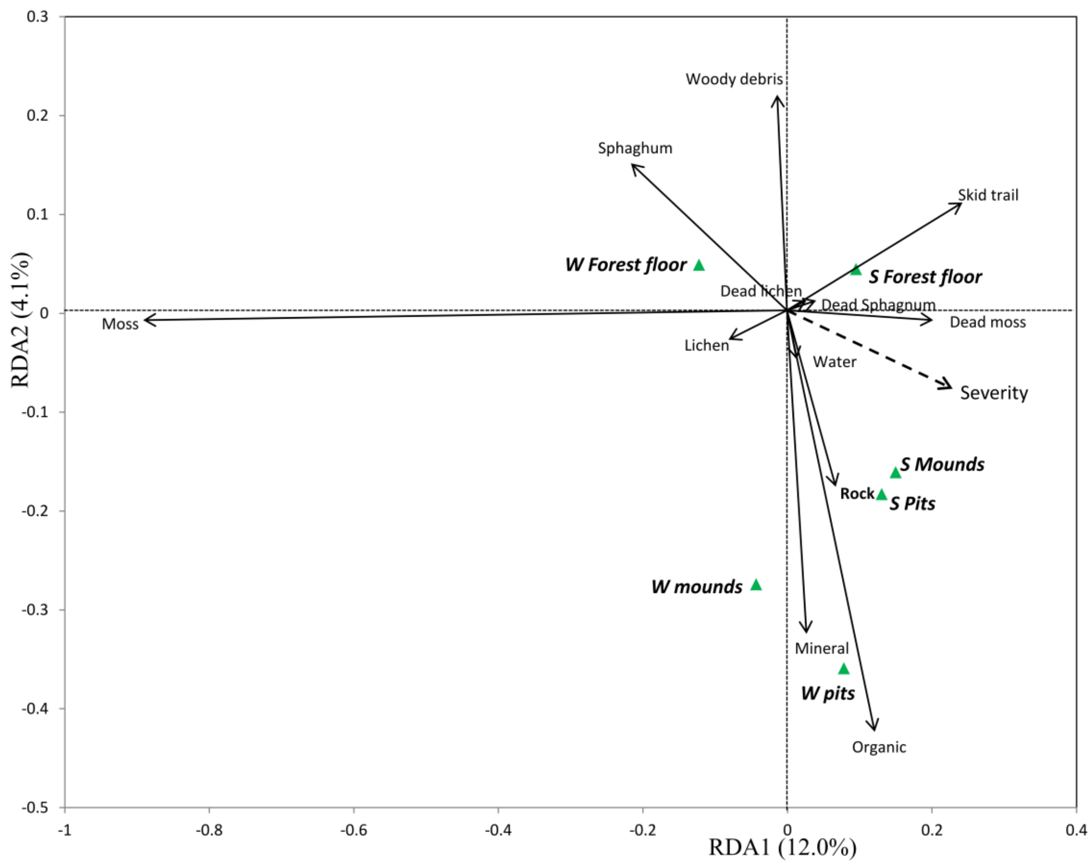

Figure 19: Partial RDA ordination of seedbeds characterization. The seedbeds proportion (dependant variable) is represented by full arrow. The environmental variables were the treatment and windthrow severity. The centroids of the treatment represented by six categorical variables which were forest floor, pits and mounds in unsalvaged windthrow (W) and forest floor, pits and mounds in salvaged windthrow (S) are represented by triangles. The windthrow severity is represented by a dotted arrow. The covariables included in the analysis were stand composition, age, height, density and soil drainage.

Understory species diversity and composition

Microtopography types had a significant effect on the number of species per subplots (F=20.15, df =5, P<0.0001) but windthrow severity did not. Number of species on each microsite type (undisturbed forest floor, pits and mounds) did not differ between salvaged and unsalvaged treatments. For unsalvaged windthrow, mean species number per subplot was significantly higher on forest floor (8.37 ± 0.21) than on mounds (6.56 ± 0.52), which were significantly higher than on pits (5.26 ± 0.56) (Fig. 20). After salvage logging, species richness followed the same trend among microsite types, but the types did not significantly differ from unsalvaged windthrows. Shannon diversity results have not been represented as they followed exactly the same pattern as richness values.

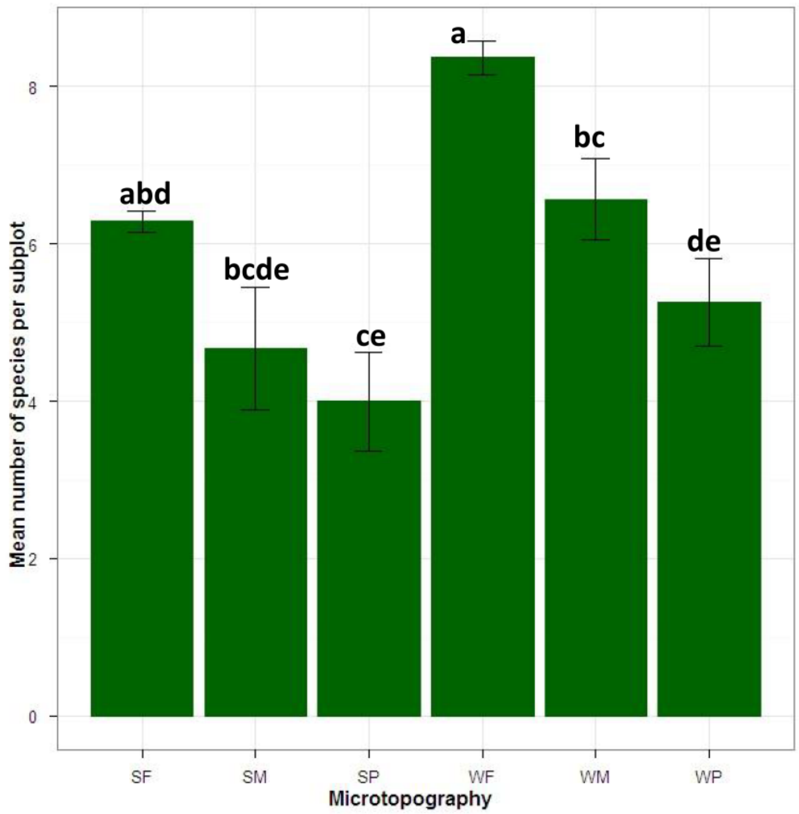

Figure 20: Mean number of species by subplot according to the microtopography. SF: salvaged forest floor, SM: salvaged mound, SP: salvaged pit, WF: unsalvaged windthrow forest floor, WM: unsalvaged windthrow mound and WP: unsalvaged windthrow pit. Means with the same letters do not significantly differ at P = 0.05, according to post-hoc Tukey's test.

In order to characterize species composition, we analyzed a matrix with the different plants cover as dependent variables while controlling for stand composition, age, height, density and soil drainage. The first two axes explained 17.3% of the variation in plant composition (axis 1, 11.9%; axis 2, 5.4%; figure 21). The first axis was constrained by the mineral soil vector. The second axis was constrained by old CWD, recent CWD, and windthrow severity, although the relationship between axes and the latter two categories was weak. In the windthrow treatment (W), forest floor, windthrow pits and windthrow mounds were widely separated from one another. The forest floor of windthrow treatment is the only one on the left side of the first axis. Further, the centroids of the salvaged treatment (S) were closely clustered together (Fig. 21).

Understory species tended to cluster with different attributes. Together with *P. mariana*, the ericaceous species *Vaccinium myrtilloides* Michaux, *V. vitis-idaea* L., *Gaultheria hispidula* (L.) Mühl. ex Bigelow, *Kalmia angustifolia* L., and *Ledum groenlandicum* (Oeder) Kronn & Judd clustered along the left end of axis 1, which is associated with increasing forest floor cover of unsalvaged treatment. *Cornus canadensis* L. was strongly associated with recent CWD. *Betula papyrifera* Marsh., *Oxalis Montana* Raf. and *Maianthemum canadense* Desf. were closely associated with unsalvaged windthrow mounds, with windthrow severity and old CWD. No species were clearly associated with the salvage logging treatment and with unsalvaged pits (Fig. 21).

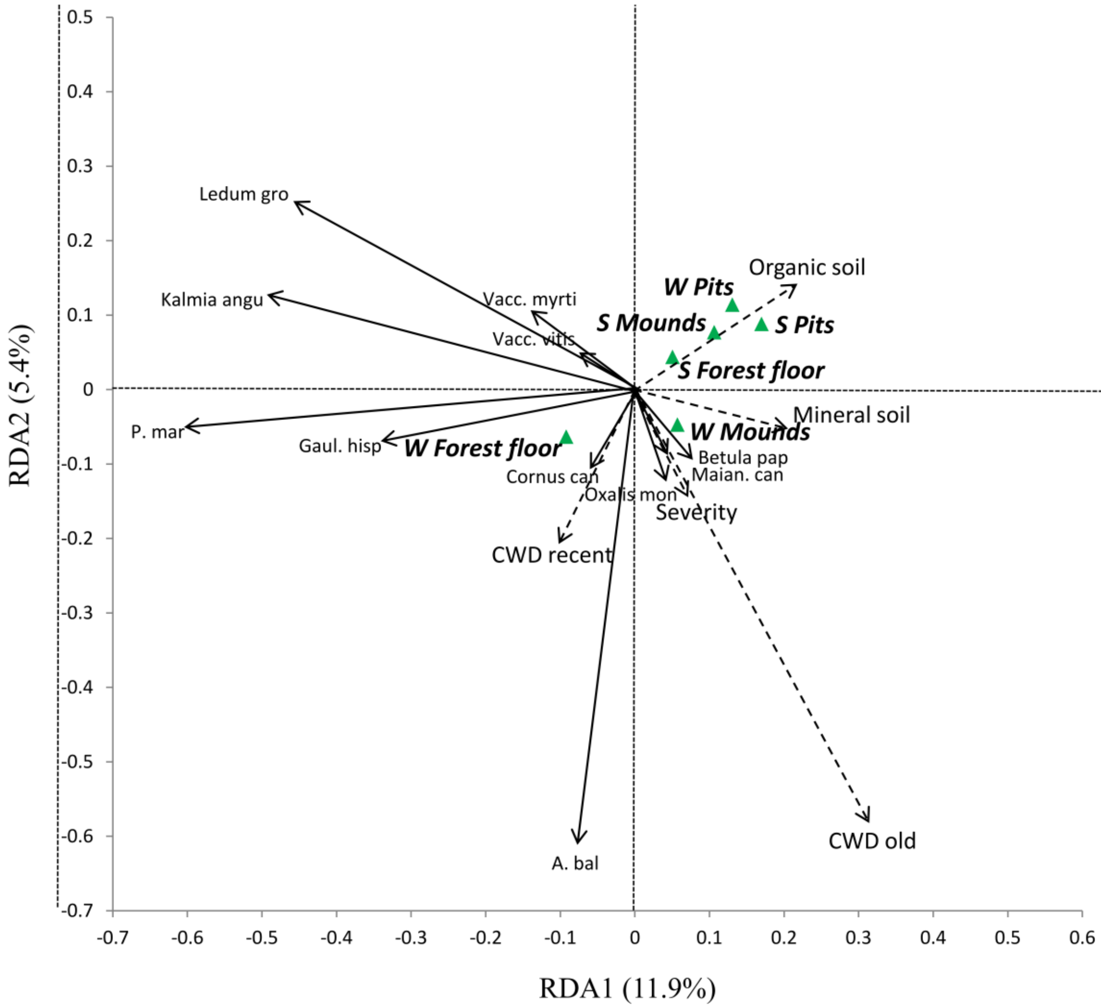

Figure 21: Partial RDA ordination of undergrowth plants cover. The plant cover (dependent variable) is represented by full arrow. The environmental variables were the treatment, windthrow severity, old and recent CWD, mineral and organic soils. The centroids of the treatment represented by six categorical variables which were forest floor, pits and mounds in unsalvaged windthrow (W) and forest floor, pits and mounds in salvaged windthrow (S) are represented by triangles. The other environmental variables are represented by a dotted arrow. The covariables included in the analysis were stand composition, age, height, density and soil drainage.

Commercial species regeneration

As the main commercial species (i.e. balsam fir and black spruce) were not related specifically to pits or mounds (see Figure 21), the seedling and sapling analysis excluded microtopographic features. When mean densities of saplings and seedlings per subplot were compared, we observed significant interactions between treatments and seedling and sapling species and between severity and tree species. There was no significant interaction between treatment and severity classes (Table 18). In other words, the effect of treatment on the density of saplings and seedlings varied between tree species (F=7.95, df=2, p =0.0004) but not between severity classes (F=0.59, df=3, p =6.2). Unsalvaged windthrow had the highest amount of regeneration. Moreover, balsam fir was significantly more abundant (5.0 ± 0.42 stems/plot) in the unsalvaged plots (Fig. 22a). Salvage logging reduced balsam fir density (3.17 ± 0.55 stems/plot) to a level comparable to that of spruce (salvaged treatment, 2.44 ± 0.28 stems/plot; unsalvaged treatment, 3.33 ± 0.34 stems/plot). White birch had the lowest amount of regeneration among tree species, with no difference between salvaged (0.15 ± 0.04 stems/plot) and unsalvaged (0.53 ± 0.11 stems/plot) treatments.

Distribution of seedling and sapling abundances among windthrow severity classes differed between species (χ^2 = 335.27, df = 6, P < 0.001). Partial χ^2 tests between species showed a significant difference for all severity classes (P < 0.001). Windthrow severity classes positively influenced seedling and sapling abundance, at least for balsam fir and white birch regeneration. Indeed, balsam fir seedlings were the most abundant for severity classes 2 to 4. However, the effect of increasing severity on black spruce was not clear, as spruce density was similar in classes 1 to 3, but was the lowest in severity class 4 (Fig. 22b).

Tableau 18: ANOVA summary of the linear mixed-effect model of sapling and seedling quantity. Significant factors (P < 0.05) are shaded.

Effect	Num. df	Saplings and seedlings number	
		F	*p*
Treatments	1	7.87	0.0149
Species	2	73.28	<0.0001
Severity	3	1.70	0.1743
Treat*Species	2	7.95	0.0004
Treat*Severity	3	0.59	0.6222
Severity*Species	6	7.78	<0.0001

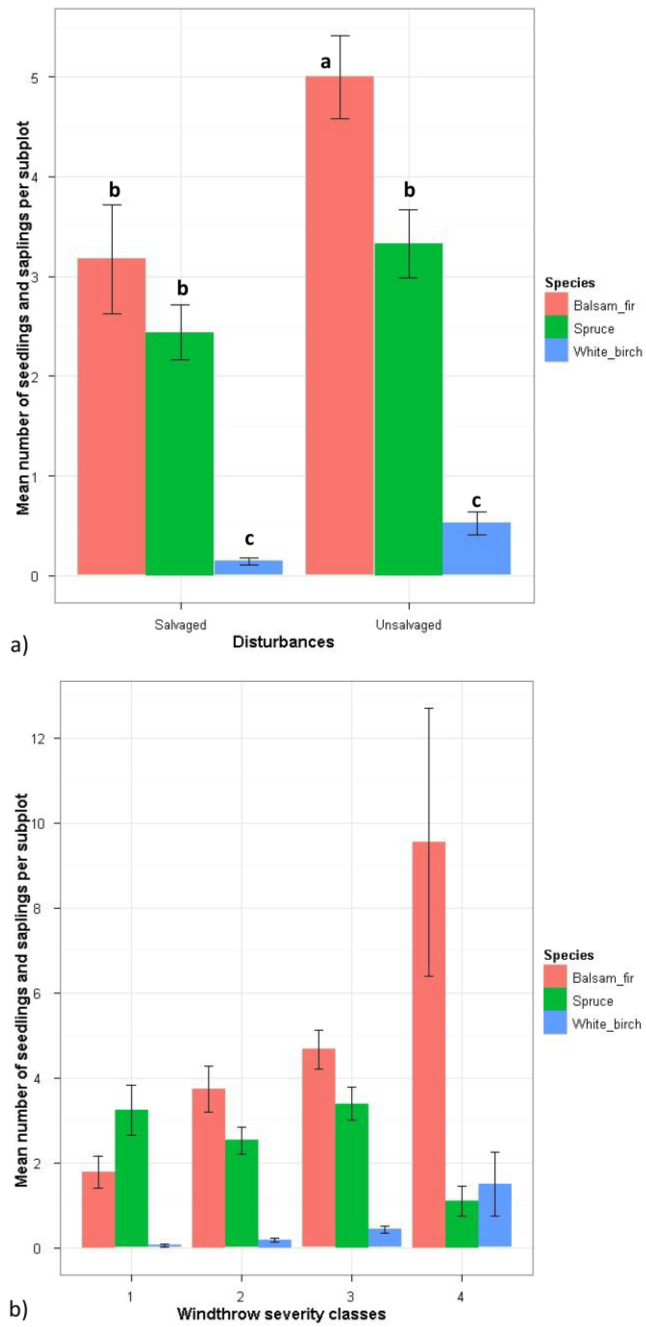

Figure 22: Mean number of seedlings and saplings per subplot for the three main tree species (black spruce, balsam fir and white birch) according to a) disturbance and b) windthrow severity classes. Means with the same letters do not significantly differ at P = 0.05, according to post-hoc Tukey's tests.

Discussion

Although the forest industry did select salvage sites randomly, as the decision to salvage was based mainly on accessibility issues, the differences reported here do not appear to be biased. A comparison of initial forest composition revealed that both treatments had the same pre-disturbance species composition. Also, we used plots in all severity classes and we integrated a block factor in our analysis to control for the effect of differences in site and stand types. Therefore we are confident that the reported results represent differences between the treatments.

Seedbeds characterization

The partial RDA analysis allowed us to measure the variation in seedbed types cover attributable to treatment and gradient of windthrow severity. Our results showed that Sphagnum and moss species were clearly associated with the unsalvaged treatment. Lichen seedbeds were also associated with unsalvaged windthrow forest floors. The first axis was constrained by windthrow severity. The bryophyte cover was the most marked response to winthrow severity. Harvest operations are known to affect bryophyte populations, as they influence microclimatic conditions and substrates (Fenton et al. 2003; Jonášová and Prach 2008). Environmental factors that affect bryophyte and lichen growth are humidity, light, and the quantity of downed CWD and snags (Andersson & Hytteborn 1991). The higher density of standing trees in unsalvaged windthrow in comparison to the salvaged areas (Waldron et al. 2013) may affect environmental conditions. Overstory trees can protect the forest understory from direct sun and desiccation. In the salvaged plots, moss and Sphagnum were found predominantly in a dessicated state. Also, the low volume of downed CWD and low number of snags in the salvaged treatment (Waldron et al. 2013) may affect the presence of bryophytes and lichens. Some studies have shown that non-vascular plants are particularly affected by silvicultural practices that do not allow persistence of large dead wood and snag recruitment (Haeussler et al. 2002). Cryptograms are conspicuous in *P. mariana* stands of the eastern boreal forests of Quebec and they have a strong influence on understory plant regeneration and growth (De Grandpré et al. 2003). Forest floor disturbance due to salvage logging can reduce moss and Sphagnum cover, which may explain the trend of diminishing species number and the absence of specific vegetation after salvage logging when compared to unsalvaged windthrow. One way this might happen is the presence of machinery tracks or skid trails. Skid trails were directly related to salvage logging operations, and they were found in every salvaged plot and in some subplots. In many cases, skid trails were really deep and soil was severely compacted, which could partly explain the absence of vegetation on this type of substrate and also the tendency for a lower mean number of species per subplot.

Tree uprooting in unsalvaged windthrow contributes to the formation of pit-and-mound microtopography and the exposure of mineral and organic soil. However, after salvage logging, many stumps are returned, either partially or completely, to their pre-windthrow position (Doyon & Bouffard 2008), so that organic or mineral soil seedbeds are mostly absent. This phenomenon was observed in our salvaged plots.

Our results confirmed that windthrow created a high diversity of microsites (Peterson & Campbell 1993; Ulanova 2000), which contributes to the heterogeneity of post-windthrow ecosystems. Forest floor heterogeneity may thus explain the presence of some plant species that were specific to unsalvaged windthrows. Salvaged windthrow, with the large proportion of skid trails and dead moss or Sphagnum, had a lower degree of seedbed heterogeneity, and this was also observed by Peterson and Leach (2008).

Understory diversity and composition

The partial RDA analysis allowed us to measure the variation in plant species cover attributable to treatment and gradient of windthrow severity, old and recent CWD as well as mineral and organic soil. Our results showed that, in unsalvaged windthrow, diversity index and number of species are higher on undisturbed forest floor than on pits or mounds. The importance of pits and mounds in post-windthrow vegetation biodiversity has been demonstrated mostly in hardwood or mixed-hardwood forests (Peterson & Pickett 1990; Peterson & Campbell 1993; Ulanova 2000). Plant diversity is higher in these forest ecosystems than in black spruce boreal forests, where the number of species is limited. Moreover, pits and mounds in boreal forest do not have the same properties and size as in more temperate hardwood forests, perhaps due to the superficial root systems produced by black spruce and balsam fir and because of the relatively small size of the trees in the former compared to the latter forests (Clinton & Baker 2000; Doyon & Bouffard 2008; Waldron et al. 2013). This could be a part of the explanation for the absence of specific vegetation and low diversity on pits and mounds. Many studies have shown that pits are not good sites for vegetation establishment (Beatty & Stone 1986; Schaetzl et al. 1989; Peterson et al. 1990; Harrington & Bluhm 2001). Pits generally have lower temperature and light levels than mounds (Clinton & Baker 2000) and seedlings can get buried by soil eroding off the root plate. This could explain why, in the unsalvaged treatment, mounds have a higher species richness and diversity than pits. Moreover, mounds likely supported existing pre-disturbance vegetation, while pits were new sites for colonization. Mounds therefore, might have some diversity immediately after disturbance, while diversity would necessarily have to accumulate from zero in pits.

The only species that was clearly related to microtopography attributes in unsalvaged windthrow was white birch. Our results (Fig. 21) showed that birches were positively associated with mound microtopography. Birch species are known to establish and grow on exposed mineral soil or decomposed coarse woody debris (Perala & Alm 1990). This result is consistent with other studies that showed that pioneer species are likely to be found on mounds (Carlton & Bazzaz 1998; de Chantal et al. 2009). However, this result is a tendency given the fact that the first two axis of our partial RDA analysis explained only 14.0 % of the variance.

Our study was performed between two and four years after windthrow and salvage logging. Most pits and mounds had been created by the most recent windthrow episodes so that most microtopographic features were relatively recent. Pits and mounds are not stable in the initial years following disturbance and their characteristics change over time (Ulanova 2000). Many authors have shown that plant diversity associated with microtopographic features is highest in the first years after disturbance (Palmer et al. 2000; von Oheimb et al.

2007). Although these studies have been done in hardwood forests, they suggest the importance of time since pit-and-mound formation in the development of plant communities. Thus, it would be interesting to see the effects of pit-and-mound microtopography on plant diversity in subsequent years, when pits and mounds have become more stable.

Our study did not take into consideration the diversity of bryophytes, although our results showed that mosses and Sphagnum cover are associated with unsalvaged windthrow. Jonsson & Essen (1990) showed that, in Scandinavian spruce forests, bryophyte diversity was high in forests that have been affected by windthrow, with the high number of species being explained by the microsite diversity caused by tree uprooting (Jonsson & Esseen 1990). In Quebec boreal forest, Desponts et al. (2004) demonstrated that high bryophyte diversity of old-growth stands was explained by the structural heterogeneity of this type of ecosystem. Since our results showed that salvaged logging affected microsite and forest floor characteristics, it would have been useful to characterize moss and Sphagnum species diversity.

The presence of several plant species was positively associated with post-windthrow forest floor rather than with pits and mounds. Most of these plants were ericaceous species. For example, *L. groenlandicum* and *K. angustifolia* are known to spread rapidly after disturbance (Mallik 1994; Jobidon 1995). Given that *L. groenlandicum* is known to grow on humid soil, particularly on Sphagnum site (Jobidon 1995), and that Sphagnum was associated with unsalvaged windthrow forest floor, a positive relationship between *L. groenlandicum* and forest floor in unsalvaged windthrow was not surprising. Further, aggressive competition between black spruce and *K. angustifolia* and *L. groenlandicum* has been well-documented (Mallik 1987; Inderjit & Mallik 1996 a, b), but our results showed that black spruce cover was greater on forest floor. Most spruces that were present on our unsalvaged site were advanced saplings, which could explain the high cover of spruce, despite the presence of *K. angustifolia* and *L. groenlandicum* on unsalvaged forest floor. Most of these ericaceous species are known to grow in the old-growth boreal forests of eastern Canada. The heterogeneity in forest floor composition after windthrow, even if it did not change species composition, may have changed their abundance.

In salvaged windthrow, the mean number of species was not higher on forest floor than pit-and-mound microtopography, unlike the unsalvaged treatment. After salvage logging, light conditions are more homogeneous and there is marked soil disturbance because of the machinery. This homogenization could explain the lack of differences in the number of species among microtopographic features in salvaged plots. However, diversity was higher on salvaged forest floor than on microtopographic features. Pits and mounds are very small after salvage logging, and many are affected by forestry operations (Waldron et al. 2013), which could explain the low biodiversity on microtopographic features after salvage logging. Overall, however, we did not find a significant reduction in species diversity after salvage logging in comparison to unsalvaged plots. In comparison with other studies of salvage logging following windthrow (Elliott et al. 2002; Ilisson et al. 2006; Rumbaitis del Rio 2006), our study area was characterised by a low number of species. This could explain our difficulties in finding differences in species number between treatments. The main effect of salvage logging seems to be related to a reduction of structural heterogeneity more than to a reduction of plant diversity and richness.

Despite the absence of significant differences between treatments in terms of Shannon diversity and species richness per subplot, RDA analysis showed different species assemblages between the treatments. Most species were related to unsalvaged windthrow, while salvage logging treatment was not associated with any specific vegetation, which could be attributed once again to homogenization of the salvaged area. This could be partially explained by the relationship between the volume of recent and old downed CWD and many plant species. Salvaged logging removes wood, so the volume and structure of CWD are modified by this treatment. Even old CWD is reduced after salvage logging, probably because of the machinery impact (Waldron et al. 2013). The presence of CWD could be suitable for some species establishment and growth, for example, *O. montana* (Perala & Alm 1990; Ringius et al. 1997). After unsalvaged windthrow, structural attributes such as living trees and snags are abundant, much more so than after salvage logging

(Waldron et al. 2013). These attributes may play a role in the establishment and growth of some species. Also, the high density of logging trails and the relative structural homogeneity after salvage logging operations may reduce the capacity for plants to establish and germinate. Salvage logging certainly modified light and humidity conditions, which are dominant factors influencing composition and structure of understory vegetation (De Grandpré et al. 2003). Species like *G. hispidula* and *O. Montana* were related to unsalvaged treatment. Those species are known to be associated to old forest environmental conditions, like lower light levels, humid soil conditions, and cool soil temperatures. They persist when soil disturbance is relatively low (De Grandpré et al. 2003), which is not the case in salvaged windthrow. Even if *Vaccinium* spp. tolerate harvest operations, Atlegrim and Sjöberg (1996) showed that *V. myrtillus* decreased after clear-cutting in *Picea abies* forest. Our results trended in the same direction and showed that *Vaccinium* spp. are related to Sphagnum cover and, therefore, to unsalvaged environment.

Regardless of whether the number of species and the Shannon index were affected by salvage logging or not, a specific vegetation pattern could be associated with post-windthrow plots, which was not the case with the salvaged ones. Again, it is important to mention that these results have to be considered as tendencies, given the relatively low percentage of variance explained by the first two ordination axes.

Regeneration

In the unsalvaged treatment, balsam fir had the highest number of saplings and seedlings, followed by black spruce, and lastly, by white birch. RDA revealed that black spruce and balsam fir were related to unsalvaged forest floor, but this analysis also had used species cover percentage. Even if spruce and fir had a high cover after windthrow, the number of saplings and seedlings was relatively low. Thus, most black spruce and balsam fir in the unsalvaged plots were advance regeneration, which had a higher cover than new seedlings. These results are consistent with other studies, which have shown that advanced regeneration in a post-windthrow ecosystem predominated (Wohlgemuth et al. 2002; Jonášová et al. 2010). The low proportion of birch in the original stand probably explains the low number of its seedlings and saplings after windthrow. An additional explanation would be the low pit-and-mound cover, so the lack of adequate seedbeds (Waldron et al. 2013).

For both treatments, our results showed no link between regeneration quantity and microtopographic features, which may be explained by the lack of specialist species in our study area. Thus, it is hard to see a relationship between these species and microtopographic attributes. Overall, the mean number of seedlings and saplings after salvaged windthrows is lower than for the unsalvaged ones. This result could be explained by high soil disturbance during logging operations and a high density of skid trails, which negatively affect advance regeneration (Jonášová et al. 2010; Fischer and Fischer 2012), together with the new recruits. In unsalvaged windthrow, soil disturbance was less severe and, therefore, advance regeneration was not as severely affected as after salvage logging. Our results also showed that balsam fir densities were not significantly higher than those of spruce in salvaged windthrows. These results are interesting, particularly in a context where there are concerns regarding balsam fir overstocking following logging operations (Haeussler & Kneeshaw 2003; Côté 2006).

Windthrow severity affected regeneration in both treatments in the same manner. Yet, the higher numbers of firs with increasing windthrow severity was hard to explain. Since balsam fir are known to be more susceptible to windthrow than black spruce (Ruel & Benoit 1999; Ruel 2000), the most logical explanation of this result would be that, in plots affected by severe windthrow, balsam fir was locally more abundant prior to the episodes of windthrow. This higher importance of fir in the canopy could then favor a higher presence of the species in regeneration of these plots.

Management implications and conclusion

Forest floor composition was affected by salvage logging operations, particularly mosses and Sphagnum cover, which is sensitive to soil disturbance (De Grandpré et al. 2003). This diminution of forest floor heterogeneity, together with the reduction of downed and standing dead wood (Waldron et al. 2013), influenced undergrowth plant composition. However, the volume of down deadwood on the salvaged cutblocks remained relatively high (see Waldron et al. 2013) and the impact of salvage logging on regeneration was low. Thus, we can assume that the salvaged and unsalvaged windthrows will tend to converge over time. Long-term studies on the effects of salvage logging on ecosystem key attributes should be executed in order to verify this assumption.

To maintain post-windthrow forest floor characteristics and thereby diminish the short-term impacts of salvage logging on vegetation, retention patches should be kept on the harvested area. These retention patches should include not only downed and standing deadwood, but also living trees of various sizes, which will maintain a certain degree of structural heterogeneity on the cut-blocks (Kuuluvainen 2002). Indeed, the reduction of structural heterogeneity (living trees, down and standing deadwood) after salvage logging may affect bird species (Lain et al. 2008; Żmihorski 2010), invertebrates (Bouget & Duelli 2004; Żmihorski & Durska 2010) or small mammal populations and species assemblage (Loeb 1999). Our results also showed that salvaged logging operations reduce advance regeneration cover compared to unsalvaged windthrows. Retention patches would also improve the preservation of a certain quantity of advance regeneration on the cut-blocks.

Thresholds on the size and number of patches that should be preserved on cut-blocks in order to maintain key post-winthrow attributes and mitigate the impacts of salvage logging are hard to establish owing to the paucity of studies regarding these attributes and their specific effects on other values, such as wildlife (Vaillancourt 2008). However, In Quebec, retention patch sizes are currently between 150 to 300 m^2 (Leblanc & Pouliot 2011), which is probably an area too small to maintain natural undergrowth conditions (Bradbury 2004; Jönsson et al. 2007). Studies about patch size and post-windthrow structural attributes should be performed to provide some indicators of the minimal acceptable size of patches in the eastern boreal forest of Quebec. Monitoring of biological legacies in retention patches must also be performed and thresholds must be changed where needed (Drapeau et al. 2009; Gauthier et al. 2009). At the stand- and landscape-levels, it is important to ensure that a certain proportion of windthrow areas is kept intact. In Quebec, Nappi et al. (2011)

have suggested that, for salvage logging after fire, at least 30% of fire-affected forest should be left unsalvaged at the management unit scale. This threshold could be applied to windthrow as well, but should be refined via monitoring, which is a key requirement of ecosystem management (Drapeau et al. 2009; Gauthier et al. 2009).

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References

Andersson, L.I. & Hytteborn, H. 1991. Bryophytes and decaying wood: A comparison between managed and natural forest. *Holarctic Ecology* 14: 121-130.

Atlegrim, O. & S¨joberg, K. 1996. Response of bilberry (*Vaccinium myrtillus*) to clear-cutting and single-tree selection harvests in uneven-aged boreal *Picea abies* forests. *Forest Ecology and Management* 86: 39-50.

Beatty, S.W. & Stone, E.L. 1986. The variety of soil microsites created by tree falls. *Canadian Journal of Forest Research* 16: 539-548.

Borcard, D., Gillet, F. & Legendre, P. 2011. Numerical ecology with R. Springer ed. NY, USA.

Bouchard, M. & Pothier, D. 2010. Spatiotemporal variability in tree and stand mortality caused by spruce budworm outbreaks in eastern Quebec. *Canadian Journal of Forest Research* 40: 86-94.

Bouchard, M., Pothier, D. & Gauthier, S. 2008. Fire return intervals and tree species succession in the North Shore region of eastern Quebec. *Canadian Journal of Forest Research* 38: 1621-1633.

Boucher, D., De Grandpré, L. & Gauthier, S. 2003. Développement d'où outil de classification de la structure des peuplements et comparaison de deux territoires de la pessière à mousses du Québec. *The Forestry Chronicle* 79: 318-328

Bouget, C. & Duelli, P. 2004. The effects of windthrow on forest insect communities: a literature review. *Biological Conservation* 118: 281-299.

Bradbury, S. 2004. Understorey plant communities in boreal cutblocks with different sizes and numbers of residual tree patches. *Canadian Journal of Forest Research* 34: 1220-1227.

Burns, R.M. & Honkala, B.H. 1990. Silvics of North America: 1. Conifers. Agriculture Handbook 654, U.S. Department of Agriculture, Forest Service, Washington DC, USA.

Carlton, G.C. & Bazzaz, F.A. 1998. Regeneration of three sympatric birch species on experimental hurricane blowdown microsites. *Ecological Monographs* 68: 99-120.

Clinton, B.D. & Baker, C.R. 2000. Catastrophic windthrow in the southern Appalachians: characteristics of pits and mounds and initial vegetation responses. *Forest Ecology and Management* 126: 51-60.

Côté, G., 2006. Élaboration d'une typologie forestière adaptée à la forêt boréale irrégulière. Master thesis, Laval University, Quebec, Canada.

de Chantal, M., Lilja-Rothsten, S., Peterson, C., Kuuluvainen, T., Vanha-Majamaa, I. & Puttonen, P. 2009. Tree regeneration before and after restoration treatments in managed boreal *Picea abies* stands. *Applied Vegetation Science* 12: 131-143.

De Grandpré, L., Bergeron, Y., Nguyen-Xuan, T., Boudreault, C. & Grondin, P. 2003. Composition and dynamics of the understory vegetation in the boreal forests of Quebec. *In*: Gilliam, F.S. & Roberts, M.R. (eds.) *The herbaceous layer in forests of eastern North America*, pp. 238-261. Oxford University Press, NY, USA.

De Grandpré, L., Gauthier, S., Allain, C., Cyr, D., Périgon, S., Pham, A.T., Boucher, D., Morissette, J., Reyes, G., Aakala, T. & Kuuluvainen, T. 2009. Towards an ecosystem approach to managing the boreal forest in the North Shore region: disturbance regime and natural forest dynamics. *In*: Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. (eds) *Ecosystem management in the boreal Forest*, pp. 229-256, Presses de l'Université du Québec, Montreal, Canada.

Desponts, M., Brunet, G., Bélanger, L. & Bouchard, M. 2004. The eastern boreal old-growth balsam fir forest: a distinct ecosystem. *Canadian Journal of Botany* 82: 830-849.

Doyon, F. & Bouffard, D. 2008. *Étude sur le bois mort, les microsites et la régénération après chablis catastrophiques dans les érablières du Témiscamingue.* Rapport technique, Institut Québécois d'Aménagement de la Forêt Feuillue, Ripon, Canada.

Drapeau, P., Leduc, A., Kneeshaw, D. & Gauthier, S. 2009. An adaptive framework for monitoring ecosystem management in the boreal black spruce forest. *In*: Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. (eds) *Ecosystem management in the boreal Forest*, pp. 343-372, Presses de l'Université du Québec, Montreal, Canada.

Elliott, K.J., Hitchcock, S.L. & Krueger, L. 2002. Vegetation response to large scale disturbance in a southern Appalachian forest: Hurricane Opal and salvage logging. *Journal of the Torrey Botanical Society* 129: 48-59.

Fenton, N.J., Frego, K.A. & Sims, M.R. 2003. Changes in forest floor bryophyte (moss and liverwort) communities 4 years after forest harvest. *Canadian Journal of Botany* 81: 714–731.

Fischer. A. & Fischer, H.S. 2012. Individual-based analysis of tree establishment and forest stand development within 25 years after wind throw. *European Journal of Forest Research* 131: 493-501.

Fischer, A., Lindner, M., Abs, C. & Lasch, P. 2002. Vegetation dynamics in Central European forest ecosystems (near-natural as well as managed) after storm events. *Folia Geobotanica* 37: 17-32.

Fox, J., Weisberg, S., Bates, D.M., Ellison, S., Firth, D., Friendly, M., Gorjanc, G., Graves, S., Heiberger, R., Laboissiere, R., Monette, G., Nilsson, H., Ogle, D., Ripley, B. & Zeileis, A. 2013. car: Companion to Applied Regression. R package version 2.0-18. URL: http://cran.r-project.org/web/packages/car/car.pdf

Frelich, L.E. & Reich, P.B. Neighborhood effects, disturbance severity, and community stability in forests. *Ecosystems* 2: 151-166.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D., Drapeau, P., De Grandpré, L., Claveau, Y. & Paré, D. 2009. Forest ecosystem management: origins and foundations. *In*: Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. & Bergeron, Y. (eds) *Ecosystem management in the boreal Forest*, pp. 13-38, Presses de l'Université du Québec, Montreal, Canada.

Greene, D.F., Gauthier, S., Noël, J., Rousseau, M. & Bergeron, Y. 2006. A field experiment to determine the effect of post-fire salvage on seedbeds and tree regeneration. *Frontiers in Ecology and the Environment* 4: 69-74.

Haeussler, S., Bedford, L., Leduc, A., Bergeron, Y. & Kranabetter, J.M. 2002. Silvicultural disturbance severity and plant communities of the southern Canadian boreal forest. *Silva Fennica* 36: 307-327.

Haeussler, S. & Kneeshaw, D. 2003. Comparing forest management to natural processes. In: Burton, P.J., Messier, C., Smith, D.W. & Adamowicz, W.L. (eds.) *Towards sustainable management of the boreal forest*, pp. 307-368, NRC Research Press, Ottawa, Canada.

Harrington, T.B. & Bluhm, A.A. 2001. Tree regeneration responses to microsite characteristics following a severe tornado in the Georgia Piedmont, USA. *Forest Ecology and Management* 140: 265–275.

Hothorn, T., Bretz, F., Westfall, P., Heiberger, R.M. & Schuetzenmeister, A. 2013. multicomp: Simultaneous Inference in General Parametric Models. R package version 1.2-18. URL: http://cran.r-project.org/web/packages/multcomp/multcomp.pdf

Hunter, M.L. 1990. Wildlife, forests, and forestry: principles of managing forests for biological diversity. Prentice-Hall (ed), Upper Saddle River, USA.

Hunter, M.L. & Schmiegelow, F.K.A. 2011. Wildlife, forests, and forestry : principles of managing forests for biological diversity. 2nd ed. Prentice-Hall (ed), Upper Saddle River, USA.

Ilisson, T., Metslaid, M., Vodde, F., Jõgiste, K. & Kurm, M. 2006. Vascular plant response to windthrow severity in Norway spruce - dominated *Myrtillus* site type forests in Estonia. *Écoscience* 13, 193–202.

Inderjit & Mallik, A.U. 1996a. The nature of interference potential of *Kalmia angustifolia*. *Canadian Journal of Forest Research* 26: 1899-1904.

Inderjit & Mallik, A.U. 1996b. Growth and physiological responses of black spruce (*Picea mariana*) to sites dominated by *Ledum groenlandicum*. *Journal of Chemical Ecology* 22: 575-585.

Jobidon, R. 1995. *Autécologie de quelques espèces de compétition d'importance pour la régénération forestière au Québec.* Revue de littérature. Direction de la recherche forestière, Forêt Québec, Ministère des Ressources naturelles. Mémoire de recherche forestière 117, Quebec, Canada.

Jonásová, M. & Prach, K. 2008. The influence of bark beetles outbreak vs. salvage logging on ground layer vegetation in Central European mountain spruce forests. *Biological Conservation* 141: 1525-1535.

Jonásová, M., Vávrová, E. & Cudlín, P. 2010. Western Carpathian montain spruce forest after a windthrow: Natural regeneration in cleared and uncleared areas. *Forest Ecology and Management* 259: 1127-1134.

Jonsson, B.G. & Esseen, P.-A. 1990. Treefall disturbance maintains high bryophyte diversity in a boreal spruce forest. *Journal of Ecology* 78: 924-936.

Jönsson, M.T., Fraver, S., Jonsson, B.G., Dynesius, M., Rydgård, M. & Esseen, P.-A. 2007. Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. *Forest Ecology and Management* 242: 306-313.

Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fennica* 36: 97-125.

Kuuluvainen, T. & Kalmari, R. 2003. Regeneration microsites of *Picea abies* seedlings in a windthrow area of a boreal old-growth forest in southern Finland. *Annales Botanici Fennici* 40: 401-413.

Lain, E.J., Haney, A., Burris, J.M. & Burton, J. 2008. Response of vegetation and birds to severe wind disturbance and salvage logging in a southern boreal forest. *Forest Ecology and Management* 256: 863-871.

Lang, K.D., Schulte, L.A. & Guntenspergen, G.R. 2009. Windthrow and salvage logging in an old-growth hemlock-northern hardwoods forest. *Forest Ecology and Management* 259: 56-64.

Leblanc, M. & Pouliot, B. 2011. *La coupe avec protection de la régénération et des sols avec rétention de bouquets. Fondements et exécution opérationnelle.* Gouvernement du Québec, Ministère des Ressources naturelles et de la Faune, Quebec, Canada.

Legendre, P. & Gallagher, E.D. 2001. Ecologically meaningful transformations for ordination of species data. *Oecologica* 129: 271-280.

Lemieux, R. 2011. *Méthodes de mesurage des bois. Instructions techniques. Exercice 2011-2012.* Gouverment du Québec, Ministère des Ressources naturelles et de la Faune, Quebec, Canada.

Lindenmayer, D.B., Burton, P.J. & Franklin, J.F. 2008. *Salvage logging and its ecological consequences.* Island Press, Washington DC, USA.

Lindenmayer, D.B., Foster, D.R., Franklin, J.F., Hunter, M.L., Noss, R.F., Schmiegelow, F.A. & Perry, D. 2004. Salvage harvesting policies after natural disturbance. *Science* 303: 1303.

Loeb, S.C. 1999. Responses of small mammals to coarse woody debris in a southeastern pine forest. *Journal of Mammalogy* 80: 460-471.

Mallik, A.U. 1987. Allelopathic potential of *Kalmia angustifolia* to black spruce (*Picea mariana*). *Forest Ecology and Management* 20: 43-51.

Mallik, A.U. 1994. Autecological response of *Kalmia angustifolia* to forest types and disturbance regimes. *Forest Ecology and Management* 65: 231-249.

MRN, 2013. Zones de végétation et domaines bioclimatiques du Québec. Gouvernement du Québec, Ministère des Ressources naturelles du Québec, Canada. URL: http://www.mrn.gouv.qc.ca/forets/connaissances/connaissances-inventaire-zones.jsp

MRNF, 2012. *Document d'information sur les plans spéciaux d'aménagement et l'aide financière à l'intention des bénéficiaires de contrat forestier 2012-2013.* Ministère des Ressources naturelles et de la Faune, Direction du soutien aux opérations Faune et Forêts Secteur des opérations régionales, Quebec, Canada.

Nappi, A., Drapeau, P. & Savard, J.-P.L. Salvage logging after wildfire in the boreal forest: Is it becoming a hot issue for wildlife? *The Forestry Chronicle* 80: 67-74.

Nappi, A., Déry, S., Bujold, F., Chabot, M., Dumont, M.-C., Duval, J., Drapeau, P., Gauthier, S., Brais, S., Peltier, J. & Bergeron, I. 2011. *La récolte dans les forêts brûlées - Enjeux et orientations pour un aménagement écosystémique.* Ministère des Ressources naturelles et de la Faune, Direction de l'environnement et de la protection des forêts, Quebec, Canada.

Nelson, J.L., Groninger, J.W., Battaglia, L.L. & Ruffner, C.M. 2008. Bottomland hardwood forest recovery following tornado disturbance and salvage logging. *Forest Ecology and Management* 256: 388-395.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. 2013. vegan: Community Ecology Package. R package version 2.0-8. URL: http://cran.r-project.org/web/packages/vegan/vegan.pdf

Paine, R.T., Tegner, M.J. & Johnson, E.A. 1998. Compounded perturbations yield ecological surprises. *Ecosystems* 1: 535-545.

Palmer, M.W., McAlister, S.D., Arévalo, J.R. & DeCoster, J.K. 2000. Changes in the understory during 14 years following catastrophic windthrow in two Minnesota forests. *Journal of Vegetation Science* 11: 841-854.

Perala, D.A. & Alm, A.A. 1990. Reproductive ecology of birch: A review. *Forest Ecology and Management* 32: 1-38.

Peterson, C.J. & Campbell, J.E. 1993. Microsite differences and temporal change in plant communities of treefall pits and mounds in an old-growth forest. *Bulletin of the Torrey Botanical Club* 120: 451-460.

Peterson, C.J., Carson, W.P., McCarthy, B.C. & Pickett, S.T.A. 1990. Microsite variation and soil dynamics within newly created treefall pits and mounds. *Oikos* 58: 39-46.

Peterson, C.J. & Leach, A.D. 2008. Salvage logging after windthrow alters microsite diversity, abundance and environment, but not vegetation. *Forestry* 81: 361-376.

Peterson, C.J. & Pickett, S.T.A. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *Journal of Vegetation Science* 1: 657-662.

Peterson, C.J. & Pickett, S.T.A. 1995. Forest reorganization: a case study in an old-growth forest catastrophic blowdown. *Ecology* 76: 763-774.

Pham, A.T., De Grandpré, L., Gauthier, S. & Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. *Canadian Journal of Forest Research* 34: 353-364.

Pinheiro, J.C. & Bates, D.M. 2000. *Mixed-effects models in S and S-plus.* Springer (ed.), NY, USA.

Pinheiro, J.C., Bates, D.M., DebRoy, S. & Sarka, D. 2013. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-110. URL: http://cran.r-project.org/web/packages/nlme/nlme.pdf

Purdon, M., Brais, S. & Bergeron, Y. 2004. Initial response of understorey vegetation to fire severity and salvage-logging in the southern boreal forest of Québec. *Applied Vegetation Science* 7: 49-60.

R Core Team, 2013. R: a language and environment for statistical computing. R Project for Statistical Computing. Vienna, Austria. URL: http://www.r-project.org/

Ringius, G.S., Sims, R.A. & Meades, S.J. 1997. *Indicator plant species in Canadian forests.* Natural Resources Canada, Canadian Forest Service, Ottawa, Canada.

Roberts, M.R. 2004. Response of the herbaceous layer to natural disturbance in North American forests. *Canadian Journal of Botany* 82: 1273-1283.

Roberts, M.R. 2007. A conceptual model to characterize disturbance severity in forest harvests. *Forest Ecology and Management* 242: 58-64.

Robitaille, A. & Saucier, J.-P. 1998. *Paysages régionaux du Québec méridional.* Direction de la gestion des stocks forestiers et Direction des relations publiques, Ministère des ressources naturelles du Québec, Quebec, Canada.

Ruel, J.-C. 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. *Forest Ecology and Management* 135: 169-178.

Ruel, J.-C., Achim, A., Herrera, R.E., Cloutier, A. & Brossier, B. 2010. Wood degradation after windthrow in a northern environment. *Forest Products Journal* 60: 200-206.

Ruel, J.-C. & Benoit, R. 1999. Analyse du chablis du 7 novembre 1994 dans les régions de Charlevoix et de la Gaspésie, Québec, Canada. *The Forestry Chronicle* 75: 293-301.

Ruel, J.-C. & Pineau, M. 2002. Windthrow as an important process for white spruce regeneration. *The Forestry Chronicle* 78: 732-738.

Rumbaitis del Rio, C.M. 2006. Changes in understory composition following catastrophic windthrow and salvage logging in a subalpine forest ecosystem. *Canadian Journal of Forest Research* 36: 2943-2954.

Schaetzl, R.J., Burns, S.F., Johnson, D.L. & Small, T.W. 1989. Tree uprooting: review of impacts on forest ecology. *Vegetatio* 79: 165-176.

Ulanova, N.G. 2000. The effects of windthrow on forests at different spatial scales: a review. *Forest Ecolo*gy and Management 135: 155-167.

Vaillancourt, M.-A. 2008. Effets des régimes de perturbation par le chablis sur la biodiversité et les implications pour la récupération. Ministère des Ressources naturelles et de la Faune, Direction du développement socio-économique, des partenariats et de l'éducation et Service de la mise en valeur de la ressource et des territoires fauniques. Quebec, Canada.

Von Oheimb, G., Friedel, A., Bertsch, A. & Härdtle, W. 2006. The effects of windthrow on plant species richness in a Central European beech forest. *Plant Ecology* 191: 47-65.

Waldron, K., Ruel, J.-C. & Gauthier, S. 2013. Forest structural attributes after windthrow and consequences of salvage logging. *Forest Ecology and Management* 289: 28-37.

Wohlgemuth, T., Kull, P. & Wüthrich, H. 2002. Disturbance of microsites and early tree regeneration after windthrow in Swiss mountain forests due to the winter storm Vivian 1990. *Forest, Snow and Landscape Research* 77: 17-47.

Żmihorski, M. 2010. The effect of windthrow and its management on breeding bird communities in a managed forest. *Biodiversity and Conservation* 19: 1871-1882.

Żmihorski, M. & Durska, E. 2010. The effect of contrasting management types on two distinct taxonomic groups in a large-scaled windthrow. *European Journal of Forest Research* 130: 589-600.

Zuur, A.F., leno, E.N. & Elphick, C.S. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1: 3-14.

Conclusion générale

Bien que méconnu au Québec comparativement aux feux ou aux épidémies d'insectes, le chablis est une perturbation naturelle importante en forêt boréale, particulièrement dans les régions où le cycle de feu est long (De Grandpré et al. 2008; Gauthier et al. 2010). Ainsi, cette thèse avait comme principal objectif de dresser un portrait global de la dynamique du chablis en forêt boréale irrégulière dans un contexte d'aménagement forestier écosystémique.

La plage de variabilité naturelle des perturbations naturelles est souvent décrite grâce à trois axes, soit l'axe temporel, spatial et intrinsèque (Bergeron et al. 2007; Vaillancourt et al. 2008). Plus spécifiquement, la répartition de taille de la perturbation, sa sévérité ainsi que son cycle. Cependant, bien qu'adéquate pour le feu, qui tend à agir sur tous les types de peuplements sans discrimination, cette représentation n'est pas totalement appropriée au chablis. Ainsi, en plus de décrire ces trois axes, cette thèse en a aussi évalué la spécificité, qui est une caractéristique intrinsèque importante à considérer dans la description du chablis. De plus, les attributs clés post-chablis ont été quantifiés vu leur importance pour le maintien de la biodiversité (Gauthier et al. 2008).

Synthèse des principaux résultats

À l'échelle du paysage, plusieurs facteurs peuvent influencer la susceptibilité d'un peuplement au chablis. Une comparaison de modèles composés de variables de peuplement, géoclimatiques et édaphiques démontre que les variables ayant le meilleur pouvoir prédictif quant à la probabilité de chablis sont l'épaisseur du dépôt de surface, le topex et la pente. Un topex faible, une pente de catégorie intermédiaire et un dépôt épais favorisent le chablis à l'échelle du paysage. À l'inverse, les sites les moins susceptibles au chablis sont ceux possédant un topex élevé, une pente nulle et un dépôt mince ou d'épaisseur intermédiaire. Sur la période de 30 ans couverte par l'étude, 6,1% du territoire a été affecté par un chablis partiel et 0,65% par un chablis total. En d'autres mots, 0,20% du territoire sera affecté par le chablis partiel annuellement, ce qui est comparable au cycle de feu du territoire d'étude. Cependant, il faut être prudent dans le calcul du cycle de chablis puisque l'échelle temporelle utilisée pour le calcul demeure relativement courte.

Les caractéristiques spatiales des chablis partiels, des chablis totaux et des coupes totales (CPRS) à l'échelle du paysage ont été décrites pour trois zones de la pessière à mousses de l'Est. D'abord, une tendance est observée par rapport à la distance du voisin le plus proche. Les chablis partiels sont plus rapprochés les uns des autres que ne le sont les chablis totaux. De plus, les chablis partiels présentent une variété de tailles plus importante que les chablis totaux, qui eux, sont en moyenne plus petits. Les coupes possèdent une plus grande variété de tailles que les chablis. À l'échelle du polygone, ou à l'intérieur d'un peuplement perturbé, on dénote encore une fois plusieurs différences spatiales entre les chablis partiels et totaux. Un polygone affecté par un chablis partiel possède en moyenne plus de 60% de sa superficie couverte par des arbres vivants résiduels alors que les chablis totaux possèdent moins de 15% de leur superficie en arbres vivants résiduels. Bien que le niveau de complexité de la forme des îlots résiduels soit relativement faible, les chablis partiels possèdent des îlots d'arbres résiduels avec une forme plus complexe que les chablis totaux. En ce qui a trait aux polygones de coupes, plus de 60% de leur superficie est récoltée en totalité et, en moyenne, moins de 10% des polygones sont recouverts par des arbres vivants résiduels. Le pourcentage moyen du polygone non perturbé, donc recouvert par les arbres vivants résiduels, ne diffère pas entre les coupes et les chablis totaux.

À l'échelle du peuplement, le chablis crée des attributs structuraux clés dans l'écosystème forestier, qui sont modifiés par les coupes de récupération post-chablis. Le bois mort au sol suite à un chablis est présent à différentes classes de dégradation. Cependant, lorsque le chablis est suivi d'une coupe de récupération, le bois mort fortement décomposé est quasi absent des sites. La répartition de densité de chicots entre les différentes classes de dégradation est différente après chablis de ce qui est retrouvé après coupe de récupération. Les coupes entrainent une réduction de la densité de chicots et une homogénéisation entre les différentes classes de dégradation. De plus, les arbres vivants résiduels sur les parterres de coupes de récupération sont rares et lorsque présents, ils appartiennent aux petites classes de DHP. Le nombre de monticules et de cuvettes est supérieur dans les chablis laissés intacts. Les coupes de récupération n'affectent pas la taille des monticules mais les cuvettes sont plus petites dans les coupes de récupération que dans les chablis laissés intacts.

Bien que le nombre d'espèces de sous-bois soit peu affecté par les coupes de récupération, la composition en espèces varie. Par exemple, les mousses et les sphaignes sont associées aux chablis intacts. De plus, on remarque que la richesse en espèces est plus importante sur le parterre forestier que sur les cuvettes et les monticules lorsque le chablis n'est pas récolté. Après coupe de récupération, la densité de semis et de gaules de sapin baumier est aussi élevée que celle retrouvée dans les chablis qui n'ont pas été récoltés. Par contre, dans les chablis intacts, la densité de régénération en sapins est plus élevée que celle en épinettes.

Application des principaux résultats

La raréfaction des vieilles forêts associée à une modification de la structure d'âge de la matrice forestière fait partie des enjeux de biodiversité et de résilience actuels (Jetté et al. 2008; Hunter et Schmiegelow 2011) et ce, particulièrement sur la Côte-Nord. En effet, plus de 70% de la superficie recouverte par les résineux est formée de peuplements âgés de plus de 120 ans (De Grandpré et al. 2008). Dans le contexte où les feux, bien que relativement rares dans la pessière et la sapinière de l'Est, brûlent de larges superficies (De Grandpré et al. 2008) en plus des CPRS et des coupes de récupération, qui sont les types de coupe les plus effectuées, un rajeunissement de la matrice forestière est à craindre. Les résultats de cette thèse illustrent bien l'importance du chablis dans cet écosystème. En ajoutant à cela les épidémies de tordeuse des bourgeons de l'épinette qui frappent la région (Bouchard et Pothier 2010), on peut affirmer que la gestion équienne ne devrait pas être aussi dominante sur la Côte-Nord. Les résultats présentés ci-haut démontrent que le chablis partiel présent dans le paysage maintiendra une quantité importante d'arbres sur pied et donc, n'engendrera pas un peuplement de première cohorte (*sensu* Bergeron et al. 2002) comme le ferait un feu de forêt ou un chablis très sévère. En effet, le chablis partiel maintient l'hétérogénéité structurale des peuplements, non seulement de par les arbres vivants résiduels, mais aussi grâce aux différentes strates de végétation présentes, aux chicots et au bois mort au sol. De plus, l'intervalle de retour relativement élevé du régime de perturbation par chablis ne favorisera pas le rajeunissement de la matrice forestière. Ainsi, l'utilisation de différents types de coupes partielles permettrait de diminuer la conversion de vieux peuplements en peuplements de première cohorte, tout en ayant des conséquences plus similaires au chablis partiel pour ce qui est de la structure d'âge de la matrice forestière à l'échelle du paysage. Pour se rapprocher du régime de perturbation par chablis partiels, les gestionnaires possèdent une certaine latitude quant à leurs interventions sylvicoles. En effet, des assiettes de coupes de tailles variées avec la rétention de différents niveaux d'arbres vivants résiduels sont possibles.

Un autre enjeu actuel relié à la gestion des forêts québécoises est celui de la simplification de la structure interne des peuplements (Jetté et al. 2008; Hunter et Schmiegelow 2011). En effet, les résultats présentés dans cette thèse ont démontré que les chablis, surtout partiels, sont caractérisés par une densité importante d'arbres vivants résiduels de différents diamètres, en plus des chicots et du bois mort au sol. Les CPRS et les coupes de récupération telles que pratiquées actuellement simplifient cette structure. La rétention d'arbres vivants sur les parterres de coupe est une option qui pourrait permettre le maintien d'une certaine hétérogénéité structurale dans les peuplements aménagés. Cependant, les normes actuelles font que les ilots laissés sur place sont petits et ne recouvrent qu'une faible superficie des parterres de coupe (Leblanc et Pouliot 2011), ce qui est probablement insuffisant au maintien des attributs structuraux caractéristiques des forêts post-chablis (Bradbury 2004; Jönsson et al. 2007). De plus, le maintien d'îlots comprenant divers éléments structuraux (arbres vivants, bois mort au sol, chicots, attributs microtopographiques) suite aux coupes de récupération pourrait augmenter l'hétérogénéité des peuplements. Évidemment, l'aménagement écosystémique passe par le principe d'adaptabilité, c'est-à-dire qu'un suivi doit être effectué suite aux différentes pratiques forestières afin de modifier, au besoin, les normes ou critères établis (Gauthier et al. 2008).

Perspectives de recherches

Les résultats de cette thèse décrivent les attributs clés post-chablis, et les écarts existant avec les chablis récoltés. Par contre, ces résultats ne permettent pas l'établissement de seuils à respecter quant aux attributs à maintenir dans les peuplements aménagés. En effet, pour que l'établissement d'un seuil soit possible, des études reliant les attributs à des espèces fauniques devraient être effectuées dans la région. Les espèces parapluies pourraient permettre de fixer des seuils de bois mort, qui seraient par la suite validés sur d'autres espèces (Hunter et Schmiegelow 2011). Une autre approche pourrait être de s'inspirer de ce qu'on retrouve en forêt naturelle n'ayant pas subi de perturbation (Hunter et Schmiegelow 2011). Par exemple, dans la zone étude, la densité de chicots dans les vieilles forêts varie de 132±45 tiges/ha (Aakala et al. 2008) à 155±54 tiges/ha (Pham et al. 2004). Ces valeurs pourraient donc servir à établir des seuils de densité de chicots. Bref, d'autres études seront nécessaires afin de mettre en place des seuils écologiques quant aux attributs post-chablis.

Après un épisode de chablis, les données sont souvent prises de façon ponctuelle, et aucun suivi n'est effectué dans le temps. Cependant, certaines études démontrent que les caractéristiques présentes dans un écosystème post-chablis pourraient varier dans les années qui suivent la perturbation (Duelli et al. 2002; Lain et al. 2008). Dans cette optique, il serait pertinent d'étudier les attributs décrits dans les chapitres III et IV quelques années après chablis, afin, entre autres, de comprendre la dynamique du bois mort dans le temps (apport de bois mort, taux de dégradation) ainsi que celle des autres attributs clés.

Références

Aakala, T., Kuuluvainen, T., Gauthier, S., and De Grandpré, L. 2008. Standing trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. Forest Ecol. Manage. 255: 410-420.

Bergeron, Y., Leduc, A., Harvey, B.D., and Gauthier, S. 2002. Natural fire regime: a guide for sustainable management of the boreal forest. Silva Fenn. 36(1): 81-95.

Bergeron, Y., Drapeau, P., Gauthier, S., and Lecomte, N. 2007. Using knowledge of natural disturbances to support sustainable forest management in the northern Clay Belt. For. Chron. 83(3): 326-337.

Bouchard, M., and Pothier, D. 2010. Spatiotemporal variability in tree and stand mortality caused by spruce budworm outbreaks in eastern Quebec. Can. J. For. Res.40: 86-94

Bradbury, S. 2004. Understorey plant communities in boreal cutblocks with different sizes and numbers of residual tree patches. Can. J. For. Res. 34: 1220-1227.

De Grandpré, L., Gauthier, S., Allain, C., Cyr, D., Périgon, S., Pham, A.T., Boucher, D., Morissette, J., Reyes, G., Aakala, T., et Kuuluvainen, T. 2008. Vers un aménagement écosystémique de la forêt boréale de la Côte-Nord. Régime des perturbations et dynamique naturelle. *Dans*: Aménagement forestier écosystémique en forêt boréale. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpre, L., Kneeshaw, D.D., Morin, H., Drapeau, P., et Bergeron, Y. (eds), Presses de l'Université du Québec, Montréal, Canada, pp. 241-268.

Duelli, P., Obrist, M. K., and Wermelinger, B. 2002. Windthrow-induced changes in faunistic biodiversity in alpine spruce forests. For. Snow Landsc. Res. 77(1/2): 117-131.

Gauthier, S., Vaillancourt, M.-A., Kneeshaw, D., Drapeau, P., De Grandpré, L., Claveau, Y., et Paré, D. 2008. Aménagement forestier écosystémique. Origines et fondements. *Dans*: Aménagement forestier écosystémique en forêt boréale. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P., et Bergeron, Y. (eds). Presses de l'Université du Québec, Montréal, Canada, p. 13-40.

Gauthier, S., Boucher, D., Morissette, J., et De Grandpré L. 2010. Fifty-seven years of composition change in the eastern boreal forest of Canada. J. Veg. Sc. 21: 772-785.

Hunter, M.L., and Schmiegelow, F.K.A. 2011. Wildlife, forests, and forestry: principles of managing forests for biological diversity. 2nd ed, Prentice Hall (Ed.), Upper Saddle River, NJ, USA, 259 p.

Jetté, J.-P., Vaillancourt, M.-A., Leduc, A., et Gauthier, S. 2008. Les enjeux écologiques de l'aménagement forestier. *Dans*: Aménagement forestier écosystémique en forêt boréale. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. et Bergeron, Y. (eds). Presses de l'Université du Québec, Montréal, Canada, p. 1-10.

Jönsson, M.T., Fraver, S., Jonsson, B.G., Dynesius, M., Rydgård, M., and Esseen, P.-A. 2007. Eighteen years of tree mortality and structural change in an experimentally fragmented Norway spruce forest. Forest Ecol. Manage. 242: 306-313.

Lain, E.J., Haney, A., Burris, J.M., and Burton, J. 2008. Response of vegetation and birds to severe wind disturbance and salvage logging in a southern boreal forest. Forest Ecol. Manage. 256: 863-873.

Leblanc, M., and Pouliot, B. 2011. La coupe avec protection de la régénération et des sols avec rétention de bouquets. Fondements et exécution opérationnelle. Gouvernement du Québec, Ministère des Ressources naturelles et de la Faune, Québec, Canada, 9 p.

Pham, A.T., De Grandpré, L., Gauthier, S., and Bergeron, Y. 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. Can. J. For. Res. 34: 353-364.

Vaillancourt, M.-A., De Grandpré, L., Gauthier, S., Leduc, A., Kneeshaw, D., Claveau, Y., et Bergeron, Y. Comment les perturbations naturelles peuvent-elles constituer un guide pour l'aménagement forestier écosystémique? *Dans*: Aménagement forestier écosystémique en forêt boréale. Gauthier, S., Vaillancourt, M.-A., Leduc, A., De Grandpré, L., Kneeshaw, D., Morin, H., Drapeau, P. et Bergeron, Y. (eds). Presses de l'Université du Québec, Montréal, Canada, p. 41-59.

Appendix A: Description of tree species categories used in chapter I

Tree species categories	Description of the category
Hardwood	White/grey birch stand, Intolerant hardwoods, Quaking aspen stand
Mixed conifer-hardwood	White/grey birch stand with conifers, Intolerant hardwoods with conifers, Quaking aspen stand with conifers, Intolerant hardwoods with white pine
Black spruce	Pure black spruce stand, Spruce stand (no dominant companion species)
Mixed conifer-black spruce dominant	Black spruce stand with white pine, Black spruce stand with balsam fir or white spruce
Balsam fir	Pure balsam fir stand
Mixed conifer-balsam fir dominant	Balsam fir stand with black/red spruce, Balsam fir stand with Eastern white cedar
Other	Larch stand, Jack pine stand, Jack pine stand with black/red spruce

Appendix B: Description of the FRAGSTATS metrics that were used in chapter II

Metric	Abbreviation	Metric descriptions
Total Area (ha)	TA	Total area of the landscape (landscape level) or patch (patch level).
Class Area (ha)	CA	Sum of areas of all patches belonging to a given class.
Area-Weighted Mean Patch Fractal Dimension	AWMPFD	Shape complexity measurement adjusted by individual patch area weighting, as larger patches tend to be more complex. Values are between 1 and 2, where 1 is a simple shape and 2 is for more complex shapes.
Mean Nearest-Neighbour (m)	MNN	Mean of the shortest distance (edge to edge) between an individual patch and a similar patch.
Shannon Diversity Index	SDI	Relative patch diversity. Will be 0 if there is only one patch and increases with the number of patches or proportional distribution of patch types.
Number of Patches	NP	Number of patches in each class.
Mean Patch Size (ha)	MPS	Mean patch size of each class.
Patch Density (no./ha)	PD	Number of patches in an area of 1 ha. Equivalent to NP/TA.