UNIVERSITÉ DU QUÉBEC À MONTRÉAL

CARACTÉRISATION DES PERTURBATIONS NATURELLES DE PETITE ENVERGURE DANS DES PEUPLEMENTS DE *PICEA ABIES* DU NORD-EST DE LA FINLANDE

MÉMOIRE
PRÉSENTÉ
COMME EXIGENCE PARTIELLE
DE LA MAÎTRISE EN BIOLOGIE

PAR
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DÉCEMBRE 2007

REMERCIEMENTS

Dans un premier temps, je veux remercier mon directeur, Daniel Kneeshaw, et mon co-directeur, Louis de Grandpré, pour leur appui à la fois académique et moral tout au long de ma maîtrise. Un merci tout spécial à l'enthousiasme contagieux de Dan et à l'humour pince-sans-rire de Louis. Je tiens aussi à remercier Timo Kuuluvainen en tant que conseiller finlandais au sein du projet, et plus particulièrement lors de mon séjour en Finlande.

Pour la planification du travail de terrain, merci à Tuomas Aakala et Tuomo Wallenius pour leurs judicieux conseils. Un énorme merci à mon équipe de terrain multiculturelle: Jordana Soderman (Canadienne), Juha Petäjäniemi (Finlandais) et Volker Bulder (Allemand). Je garde de merveilleux souvenirs de ces semaines passées en camping au cœur de la forêt boréale finlandaise sous le soleil de minuit. Un double merci à Hannu Herva pour son aide sur le terrain et son partage de connaissance sur la dendrochronologie.

Kiitos paljon à toute l'équipe du centre de recherche Metlä de Kolari qui ont rendu mon séjour au cercle polaire une expérience très enrichissante et épanouissante. Heikki Kauhanen, mon père adoptif finlandais, requière un merci à part entière, car grâce à lui la Finlande demeura pour toujours un deuxième chez moi. Aussi, *kiitos* Marja-Leena Niva pour tous les bons repas du midi et les incroyables petits pains chauds du matin. Aussi, je rends grâce à chacun des saunas que la Finlande m'a offerts.

Un gros merci à l'équipe du Centre Forestier des Laurentides. Merci à Dominique Boucher, pour son appui en statistique et sa disponibilité à m'aider sur toutes sortes de questions écologiques, mais surtout pour les ballades à l'heure du dîner. Mon ex-collègue de bureau, Frank Grenon, mérite un beau gros merci pour son oreille attentive et ces valeureux conseils.

Finalement, merci à mes parents, mes proches et mes ami(e)s. À mes parents et mes proches, merci pour votre patience et vos encouragements. Mes ami(e)s, merci de votre support moral constant tout au long de ma maîtrise. À Sophie Brugerolle, je te remercie sincèrement d'avoir écouté mes moments de délire de maîtrise. Ce n'est pas que la maîtrise m'est rendue dingue, mais...

AVANT-PROPOS

Ce document de mémoire se divise en deux chapitres rédigés sous forme d'articles scientifiques. En tant que candidate à la maîtrise, j'ai procédé à la récolte et à l'analyse des données écologies, ainsi qu'à la rédaction des articles dont je suis la première auteure. Ces deux articles seront soumis à des revues scientifiques arbitrées: 1) Characterisation of the gap attributes of moist *Picea abies* (L. Karst) dominated stands located in the Pallas-Ylläs Tunturi National Park in north-eastern Finland 2) Reconstructing small and large scale disturbances in old-growth *Picea abies* (L. Karst) dominated stands located in north-eastern Finland. Mon directeur de recherche, Daniel Kneeshaw, mon co-directeur, Louis de Grandpré, ainsi que Timo Kuuluvainen, en sont les co-auteurs.

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RÉSUMÉ

Il demeure peu de peuplements forestiers anciens en Finlande. Il ne tarde donc à comprendre le développement et le maintien de ces peuplements afin de les conserver, mais aussi de restaurer les forêts dégradées et d'établir des plans d'aménagement écosystémique. L'objectif général de cette étude était de documenter la dynamique de trouées de peuplements anciens dominés par *Picea abies* (L. Karst) au nord de la Finlande. L'étude se divise en deux volets. Un volet caractérise la dynamique de trouées de peuplements dominées par *P. abies* du nord de la Finlande sur trois aspects: (1) la taille et la fraction des trouées, (2) les arbres créateurs de trouées, et (3) la régénération des trouées. Le second volet porte sur une reconstruction historique de la dynamique des troués en établissant la distribution de création de trouées et en estimant l'ouverture annuel de la canopée.

L'aire d'étude se situe dans le Parc National de Pallas-Ylläs Tunturi (67°30-67°44' N, 24°00-24°55'E) au nord-est de la Finlande, où l'on retrouve des peuplements anciens de *P. abies*. Les trouées ont été recensées sur six transects de 400m. Des données concernant la taille, la portion ouverte, les arbres créateurs de trouées et la régénération ont été récoltées. Avec des échantillons d'arbres créateurs de trouées, nous avons daté les trouées et établi une rétrospective des perturbations des dernières 300 années en utilisant des analyses dendrochronologiques sur les patrons de croissances des cernes.

La taille moyenne des trouées est plus grande que les études passées, supportant ainsi la faible densité et productivité de la location septentrionale de l'étude. La prédominance des vents sud-ouest a influencé la direction de chute des arbres créateurs de trouées. Bien que le recrutement se constitue principalement d'espèces tolérantes à l'ombre dans les trouées, leur petite taille suggère que la fermeture d'une trouée est lente. De plus, le recrutement ne semble pas influencé par les microsites engendrés par les arbres créateurs de trouées étant donné que la majorité des semis recensées dans les trouées sont établis sur des microsites non-perturbés. La distribution irrégulière des périodes de création de trouées et l'absence de pic distinct d'année créatrice de trouées confirment l'occurrence continue d'un régime de perturbation de trouées de petite envergure dont le temps de rotation est estimé à 250 années. Bien qu'aucune perturbation de grande échelle connue n'ait pris cours sur le territoire, les patrons de croissances de plusieurs *P. abies* ont enregistré de forte reprise de croissance. La plus importante période de reprise de croissance eut lieu de 1816-1826. Une perturbation intermédiaire est probablement tenue en cause. En conclusion, nos résultats démontrent que la dynamique de trouées est continue dans le temps malgré son asynchronisme et que la plupart des *P. abies* ressentent moins une reprise de croissance au cours de leur existence.

Un aménagement forestier fait sur de longue rotation avec de multiples interventions est donc suggéré pour les peuplements dominés par *P. abies*; par contre la viabilité économique est peu probable. En termes d'écologie forestière, ce travail suggère que la dynamique de trouées est difficilement de mener des généralisations pour l'ensemble de la forêt boréale.

Mots clés : Dendrochronologie, dynamique de trouées, Finlande, forêt boréale, *Picea abies*, reprise de croissance

SUMMARY

There are few old-growth stands remaining in Finland. Gaining knowledge about the development and maintenance of these forest stands is primordial in order to conserve them, but also to restore degraded forests and to develop ecosystem management planning. The general objective of this study is to document gap dynamics of old-growth *Picea abies* (L. Karst) dominated stands in northern Finland. The study is divided into two chapters. The first chapter characterises three aspects of the gap dynamics of *P. abies* dominated stands of northern Finland: (1) gap size and fraction, (2) gapmakers, and (3) gap fillers. The second chapter reconstructs gap dynamics history by establishing the timing of gap creation and by estimating the annual canopy opening.

The study area is located in the National Park Pallas-Ylläs Tunturi (67°30-67°44' N, 24°00-24°55'E) north-eastern Finland where some old-growth *P. abies* stands still remain. Gaps were inventoried along six 400m long transects. Data about gap size, open canopy portion, gapmakers and gap fillers were collected. Sample disks were removed from gapmakers from which we dated gaps and established a reconstruction of disturbances over the past 300 years from dendrochronological analysis of the growth ring patterns.

Average gap size is higher in comparison to other gap boreal studies which support the low Average gap size is higher in comparison to other boreal gap studies due most likely to the low stand density and the poor site productivity associated with this northern location. The direction of the fallen boles of gapmakers was affected by the predominant south-west wind in the region. Even though shade-tolerant gap fillers were abundant, their small size suggests that gap closure is slow and probably not sustainable over the long term, because very few tall seedlings were found inside gaps. Furthermore, the presence of disturbed gap microsites does not seem to influence seedling recruitment as most of the seedlings were found on undisturbed microsites. The irregular temporal distribution of gap creation and the absence of distinct periods of gap creation confirm the continuous occurrence of gap disturbances for which we estimated a rotation period of 250 years. Even though, no large-scale disturbances have been recorded for this territory, several *P. abies* recorded some years of major growth release over their lifetime. The most important growth release lasted from 1816-1826. It is likely that a disturbance of intermediate scale occurred around this decade. In conclusion, our results show that gap dynamics is continuous in time notwithstanding its non-synchronicity, and that most of the *P. abies* experienced at least one important growth release during their lifespan.

Forest management planning should be done over long rotation periods using multiple small cutting interventions for *P. abies* dominated stands; however its economical viability is low. In terms of forest ecology, this work suggests that the influence of gap dynamics is specific to each stand and therefore forest management cannot be to done based on generalised concepts on the influence of small-scale disturbance on stand development.

Keywords: Boreal forest, dendrochronology, Finland, gap dynamics, growth release, *Picea abies*

INTRODUCTION GÉNÉRALE

La dynamique des peuplements en forêt boréale

Définies comme un événement dans le temps qui perturbe soit un écosystème, une communauté ou une population et qui change les ressources, la disponibilité du substrat ou encore l'environnement physique (White et Pickett, 1985), les perturbations naturelles jouent un rôle prépondérant dans la dynamique des peuplements forestiers. Le remue-ménage occasionné par une perturbation naturelle oriente des changements à la fois dans la composition en espèces, la structure, et les processus et fonctions écologiques d'un peuplement. Conséquemment, l'état actuel d'un peuplement est une réponse à une perturbation antérieure en concordance avec les conditions biotiques et abiotiques du milieu (Chapin, Matson et Mooney, 2002; Landres, Morgan et Swanson, 1999). L'omniprésence des perturbations naturelles dans l'écosystème forestier engendre une réorganisation continuelle, empêchant l'atteinte d'un état d'équilibre stable du peuplement, (Sprugel, 1991), parlant plutôt d'un état d'équilibre dynamique. Cette réorganisation varie selon l'intensité, le type, la sévérité et la fréquence des perturbations (Chapin, Matson et Mooney, 2002; Frelich, 2002). Donc, le développement d'un peuplement est dynamisé dans l'espace et dans le temps par des perturbations détruisant de grandes étendues (ex. un feu de forêt) ou de petites étendues (ex. sénescence d'un arbre) (Kuuluvainen, 1994).

En forêt boréale, le feu est considéré comme l'agent principal de perturbation (Bergeron *et al.* 1998; Esseen *et al.* 1997; Johnson, 1979; Zackrisson, 1977). Selon l'intensité et la sévérité du feu, il lui est possible de décimer plusieurs hectares de forêt entraînant le remplacement de peuplement entier. L'ouverture du couvert forestier et la perturbation du sol sur de vastes étendues suivant le passage d'un feu favorise l'établissement d'une première cohorte composée d'arbres d'espèces intolérantes à l'ombre, dites aussi pionnières (ex. *Betula spp.*, *Populus spp.*, *Pinus spp.*). S'établissant sensiblement à la même période, cette première cohorte d'arbres se caractérise par une structure régulière où les individus sont relativement semblables en termes d'âge et de taille.

Commun et fréquent sur une grande partie du territoire boréal, le feu contribue au maintien d'une mosaïque de peuplements à différents stades de rétablissement post-feu. L'état de rétablissement de ses peuplements est influencé selon le temps depuis le dernier feu qui est fortement lié avec les conditions climatiques régionales. Par exemple, les régions ayant un climat sec ont un cycle de feu court, tandis que les régions de climat maritime et humide peuvent avoir un retour de feu allant au-delà de la longévité des arbres (Kneeshaw et Gauthier, 2003; Gauthier *et al.* 2001; Johnson, 1992; Heinselman, 1981). Conséquemment, le paysage boréal est constitué de peuplements à différents stades de rétablissement selon le temps écoulé depuis le dernier feu.

Lorsque le temps entre deux feux dépasse la longévité moyenne des arbres de la première cohorte, des changements dans la composition et dans la structure s'opèrent au sein d'un peuplement au fil des ans. Les espèces pionnières intolérantes à l'ombre de la première cohorte cèdent leur place à des espèces tolérantes à l'ombre (ex. *Picea spp., Abies ssp.*). Ces espèces ont la capacité de demeurer opprimées en sous-couvert jusqu'à la venue des conditions optimales de croissance et elles s'établissent généralement avant le déclin de la première cohorte (Oliver et Larson, 1996). Le remplacement d'espèces débute progressivement par le biais de perturbations autres que le feu, soit des perturbations de petite envergure (ex. insectes, pathogènes, sénescence ou chablis) qui n'affectent que quelques individus à la fois (c'est-à-dire de 1 à 10 arbres) (Kneeshaw et Gauthier, 2003; Kuuluvainen, 1994). Ces perturbations engendrent des ouvertures dans le couvert forestier de tailles restreintes qui sont éventuellement refermées par les arbres post-établis en sous-couvert. Toutefois, des arbres nouvellement établis peuvent aussi intervenir dans le processus de fermeture. Ce processus de remplacement d'arbres par des perturbations de petite envergure est reconnu comme la dynamique de trouées (Drobyshev, 1999; Kneeshaw et Bergeron, 1998).

En plus des changements dans la composition en espèces, le prolongement du temps depuis le dernier feu apporte des modifications dans la structure du peuplement. La mortalité étant dispersée dans le temps, de nouveaux arbres s'établissent à différent moment; passant ainsi d'une structure régulière et équienne à une structure irrégulière et inéquienne (Oliver et Larson, 1996). En effet, un peuplement sous l'influence de perturbation de petite envergure est peuplé d'arbres se trouvant à différent stade de développement; c'est-à-dire que ces peuplements regroupent à la fois des semis, des gaules et des arbres matures, surannés et moribonds. Les arbres sénescents succèdent au state mort debout et chicot avant de s'accumuler au sol, menant au développement d'un vieux peuplement au fur et à mesure que le temps depuis le feu dernier s'allonge (Frelich et Reich, 2003; Kneeshaw et Gauthier, 2003; Mosseler, Thompson et Pendrel, 2003; Kneeshaw et Burton, 1997; Spies et Franklin, 1988). Ces vieux peuplements permettent l'établissement de certaines espèces de plantes vasculaires, de lichens épiphytes et de bryophytes qui ont des longs cycles reproductifs et que seul les vieilles forêts leurs offrent le substrat ou le microclimat qui convient à leur établissement (Esseen *et al.* 1997). La présence de ces espèces contribue non seulement à la complexité de la structure d'un peuplement, mais aussi à l'augmentation de la diversité bêta et gamma des écosystèmes boréaux.

La dynamique de trouées en forêt boréale

La reconnaissance de la dynamique de trouées est récente en forêt boréale, bien qu'elle fût largement étudiée en forêt tropicale et tempérée (McCarthy, 2001). Dans les zones tempérées et tropicales, il a été démontré que les perturbations par trouées jouent un rôle essentiel au sein du développement et du maintien des caractéristiques et des fonctions d'un peuplement (ex.: Runkle, 1985; Brokaw 1985; Denslow 1985). Tandis que dans la zone boréale, l'ubiquité du feu a conduit à une surévaluation du rôle de ce dernier dans la dynamique de développement (McCarthy, 2001; Bergeron *et al.* 1998; Johnson, Miyanishi et Weir, 1998; Kuuluvainen 1994). En plus du feu, l'occurrence d'épidémie d'insecte et de chablis sur de grandes étendues ont contribué au paradigme de la dynamique de 'patch' pour expliquer le développement des peuplements boréaux (McCarthy, 2001); c'est-à-dire des perturbations de grande envergure qui mènent au replacement de tout un peuplement. C'est la reconnaissance de peuplements de structure irrégulière et inéquienne qui a éventuellement mené au constat que des perturbations par trouées affectent le développement d'une certaine portion des peuplements forestiers boréaux (Boucher, De Grandpré et Gauthier, 2003; De Grandpré, Morisette et Gauthier, 2000; Kneeshaw et Bergeron, 1998; Sirèn, 1955). Les absences prolongées de feu sont principalement rencontrées dans les zones les plus humides du biome boréal.

En forêt boréale, la dynamique de trouées entraîne notamment une complexité de la structure au sein d'un peuplement, tandis que la composition demeure relativement semblable étant donné le nombre peu élevé d'espèces d'arbres, soit une prédominance des espèces tolérantes à l'ombre (Harper *et al.* 2003; De Grandpré, Morisette et Gauthier, 2000). Les arbres créateurs de trouées occasionnent la création de microsites propices à l'établissement de la régénération lors de leur chute au sol (de Chantal *et al.* 2003; Kuuluvainen et Kalamari, 2003; Jäderlund *et al.* 1997, Kuuluvainen, 1994). Par exemple, un arbre déraciné qui engendre l'exposition du sol minéral devient un lit de germination opportun, et même qu'un arbre en décomposition représente un emplacement de recrutement intéressant étant que l'humidité du substrat favorise la germination des graines. Toujours selon le mode de création de trouées, la quantité de semis recrutés est influencée. C'est ainsi qu'un arbre déraciné qui perturbe une plus grande étendue qu'un arbre mort debout (Putz *et al.* 1983), laisse un espace plus vaste pour le recruitement. À long terme, la dynamique de trouées d'intervient non seulement dans l'établissement de la régénération, mais elle fournit des niches écologique à des espèces fauniques et florales qui sont confinées qu'aux peuplements anciens (Esseen *et al.* 1997).

Par la caractérisation de la dynamique de trouées, il est possible d'identifier les processus qui interviennent dans le maintien et le développement d'un peuplement. Étant donné la reconnaissance récente de la dynamique de trouées en forêt boréale, l'étude des régimes de trouées boréaux n'a débuté que depuis quelques années. La plupart des recherches ont porté quasi-essentiellement sur les attributs physiques des perturbations par trouées, tels que la portion et la grandeur des trouées, le nombre d'arbres créateurs de trouées, le mode de mortalité des arbres créateurs de trouées, et ce en utilisant des techniques d'échantillonnage inspirés des travaux faits en forêt tropicale et tempérée. En Suède, en Russie et au Canada, différentes études ont porté sur les attributs physiques des trouées boréales (Pham *et al.* 2004; Bartemucci *et al.* 2002; Drobyshev, 1999; Kneeshaw et Bergeron, 1998; Liu et Hytteborn, 1991; Leemans, 1990), dont McCarthy (2001) a fait un article revue.

Les forêts de *Picea abies* (L. Karst) du nord de la Finlande

Le nord de la Finlande fait partie de la zone boréale nord Fenno-scandinave (N 65° - N 68°). Le climat froid et relativement humide de cette portion de la Finlande (Bonan et Shugart 1989; Ahti *et al.* 1968) est plus clément que le climat du Canada ou de la Russie Sibérienne à la même latitude. Cette différence entre ces pays septentrionaux est causée par l'influence du courant marin chaud du Golf Stream (Varmola *et al.* 2004) qui réchauffe toute la côte Atlantique du continent européen. En plus du climat maritime, l'abondance de lacs et de milieux humides sur l'ensemble du territoire finlandais accentue la présence de milieux forestiers mésiques.

La présence de sites à haute teneur en humidité est favorable à l'établissement de *Picea abies* (L. Karst), une espèce non-adaptée au feu (Burns et Honkala, 1991; Sirén, 1955). Les sites dominés par *P. abies* accumulent beaucoup d'humus (3-10 cm) à cause de la forte podzolisation qu'engendre le haut taux d'humidité, d'où leur appellation humus épais ou encore '*Hylocomium-Myrtillus* type' (HMT) (Bonan et Shugart, 1989; Norokorpi, 1979). Dominée par *Picea abies, Betula pubescens* Ehrh. est la seconde espèce en abondance, suivi de loin par *Pinus sylvestris* L.. La strate arbustive et herbacée se compose de *Sorbus aucuparia* L., *Salix caprea* L., *Vaccinium vitis-idaea* L. Et *Vaccinium myrtillus* L. et les mousses *Hylocomium splendens* (Hedw.) et *Pleurozium schreberi* (Brid.) recouvrent le sol forestier (Esseen *et al.* 1997).

Les peuplements HMT sont reconnus pour leur long cycle de feu, au-delà de 300 ans (Kuuluvainen, 1994; Sirèn, 1955). Par exemple, la région de Kivalo est reconnue pour n'avoir eu que quatre feux au cours des 1700 dernières années (Hyvärinen et Sepponen, 1988). Conséquemment, les peuplements HMT se développent et se maintiennent par la dynamique de trouées ayant ainsi une structure irrégulière et inéquienne (Kuuluvainen, 1994; Havas et Kubin, 1983). En plus d'échapper au feu, les peuplements de HMT du nord de la Finlande ne sont pas sujets aux épidémies d'insectes ou de pathogènes. Les arbres semblent mourir de manière non-contagieuse. La principale cause de mortalité est la sénescence, rendant les arbres plus sensibles aux perturbations allogéniques (ex. vent, fardeau de neige ou de glace, insecte défoliateur ou mineur) (Kuuluvainen, 1994; Norokorpi, 1979).

En plus d'influencer la structure des peuplements de HTM, la dynamique de trouées est très importante à la régénération de ces peuplements (Kuuluvainen et Kalmari, 2003; Hofgaard, 1993*a*; Sirén, 1955). La chute éventuelle des arbres vivants ou morts debout créent une foule de microsites, c'est-à-dire : débris ligneux fin et gros, fosses, buttes, exposition du sol minéral (Harmon *et al.* 1986), qui offrent des emplacements propices à l'établissement de la régénération au sein des peuplements (Kuuluvainen et Kalmari 2003; Hofgaard, 1993*a*; Sirén, 1955). L'importance de ces microsites est due au fait que l'épaisse couche de mousse au sol n'assure pas à l'établissement à long terme des semis *P. abies*, car une fois la graine germée les racines ont peine à toucher le sol minéral (de Chantal *et al.* 2003; Jäderlund *et al.* 1997). Toutefois, mis à part ces études sur les microsites, les peuplements dominés par *P. abies* du nord de la Finlande demeurent peu étudiés en ce qui a trait à la dynamique de trouées.

Importance de l'étude

En Finlande, il ne reste que très peu de peuplements anciens à cause des activités anthropogéniques qui ont pris cours sur presque la totalité du territoire (Östlund *et al.*, 1993; Essen *et al.*. 1992). Les conséquences de l'utilisation de la ressource forestière ont mené à une augmentation du nombre d'espèces boréales en danger, tant floristique que faunique (Bernes 1994). L'établissement d'aires protégées permet de maintenir la biodiversité en déclin, toutefois les secteurs protégés se retrouvent principalement au nord de la Finlande (Association Finlandaise de la Forêt 2001). Des solutions alternatives, telles que l'aménagement écosystémique ou la restauration de forêts dégradées, sont donc nécessaires afin de préserver la biodiversité sur de plus vastes étendues. Toutefois, l'implantation de telles solutions requière une bonne connaissance des processus écologiques qui régissent la dynamique naturelle du développement et maintien des peuplements forestiers.

Les perturbations naturelles sont au cœur de la dynamique des peuplements forestiers (Chapin, Matson et Mooney, 2002; Oliver et Larson, 1996). Étant donnée leur rôle dans le développement des peuplements, les perturbations naturelles sont considérées comme un modèle à s'inspirer dans l'élaboration de plan d'aménagement durable, soit un aménagement écosystémique. Le développement d'une sylviculture basée sur les perturbations naturelles requiert toutefois une bonne compréhension de ces dernières dans divers milieux. Regarder en quoi différentes régions boréales se ressemblent et diffèrent permet l'amélioration de la compréhension de la complexité des perturbations naturelles et une meilleure conceptualisation de celle-ci (White et Jentsch, 2001). Conséquemment, ces connaissances écologiques évitent de développer des approches d'aménagements trop générativistes.

Différents études faites sur en milieux boréaux ont caractérisé les perturbations par trouées dans divers types de forêt selon les attributs des trouées (Pham *et al.* 2004; Bartemucci *et al.* 2002; Drobyshev, 1999; Kneeshaw et Bergeron, 1998; Liu et Hytteborn, 1991; Leemans, 1990), sans toutefois s'attarder à l'aspect temporel, mise à part l'étude de Kneeshaw et Bergeron (1998) faite selon une chronoséquence. Les études ont porté principalement sur la portion sud du territoire et sur la dimension de la création de microsites de germination (de Chantal *et al.* 2003, Kuuluvainen et Kalmari 2003; Jäderlund *et al.* 1997). Bien que la régénération des trouées fasse partie intrinsèque de la dynamique de trouées, il n'en demeure pas moins que des informations sur les attributs spatiaux et temporels de la dynamique demeurent essentielles à la compréhension de ce régime de perturbation.

Objectifs de l'étude

L'objectif général de cette étude vise à documenter la dynamique de trouées de peuplements anciens dominés par *P. abies* au nord de la Finlande afin de mieux comprendre comment les perturbations de petite envergure interagissent en milieu boréal. Cette étude de maîtrise se divise en deux chapitres écrits en anglais sous la forme d'article scientifique.

Le premier chapitre documente les attributs de la dynamique de trouées dans des peuplements de *P. abies*, plus précisément du type de forêt *Hylocomium-Myrtillus* située dans le Parc National de Pallas-Ylläs Tunturi au nord-est de la Finlande. Les attributs sur lesquels l'étude s'attarde sont : la taille des trouées, la portion du peuplement en trouées, et une description exhaustive des arbres créateurs de trouées, soit espèce, quantité, état de dégradation, état de mortalité et orientation de la chute du tronc. Ce même chapitre aborde aussi la l'établissement de la régénération à l'intérieur des trouées selon la présence de microsites. En général, les résultats espérés devraient être similaires aux études passées sur la caractérisation des trouées faites dans des types similaires de peuplements boréaux ainsi que dans des types différents.

Le deuxième chapitre porte sur la caractérisation temporelle de la dynamique de trouées effectué dans le même parc national. L'objectif est de faire une reconstruction de l'historique de la dynamique récente des troués en établissant la distribution de création de trouées et en estimant l'ouverture annuel de la canopée. De plus, nous évaluons comment les perturbations par trouées influences les patrons de croissances des *P. abies.*

L'atteinte de ces objectifs permettra une meilleure compréhension du développement et du maintien des forêts boréales qui sont soumises à de longs régimes de feu. Ces connaissances pourront à la fois servir de base pour l'aménagement et écosystémique ainsi qu'à la revalorisation de forêts boréales dégradées.

CHAPITRE I

CHARACTERISATION OF THE GAP ATTRIBUTES OF MOIST *PICEA ABIES* DOMINATED STANDS LOCATED IN THE PALLAS-YLLÄS TUNTURI NATIONAL PARK IN NORTH-EASTERN FINLAND

1.1 Abstract

We characterised gap dynamics of moist *Picea abies* (L. Karst) dominated stands, more specifically the *Hylocomium-Myrtillus* forest type located in Pallas-Ylläs Tunturi National Park in north-eastern Finland Three particular attributes were investigated: (1) gap size and fraction, (2) gapmakers, and (3) gap fillers. The objectives were to determine the gap features of these forests and to elaborate on how they influence stand dynamics. We investigated all gaps intersecting six 400m linear transects established in the park. Average gap size is higher in comparison to other boreal gap studies which reflect the low stand density and the poor site productivity caused by the northern location of study area. The direction of the fallen boles of gapmakers was affected by the predominant south-west wind in the region. The different states of decay of the gapmakers support asynchronous gap creation. Even though shade-tolerant gap fillers were abundant, their small size suggests that gap closure is slow and probably not sustainable over the long term, because very few tall recruits were found inside gaps. Furthermore, the presence of disturbed gap microsites does not seem to influence seedling recruitment as most of the seedlings were found on undisturbed microsites. In terms of forest ecology, this work suggests that the influence of gap dynamics is specific to a region and that therefore forest management cannot be done based on generalisations about stand development under the influence of small-scale disturbances.

Key words: Boreal forest, disturbance, Finland, gap dynamics, *Picea abies*

1.2 Résumé

Nous avons caractérisé la dynamique de trouées de peuplements dominées par *Picea abies* (L. Karst), plus précisément du type de forêt *Hylocomium-Myrtillus* située dans le Parc National de Pallas-Ylläs Tunturi au nord-est de la Finlande. Trois attributs ont été investigués: (1) la taille et la fraction des trouées, (2) les arbres créateurs de trouées, et (3) le recrutement. Les objectifs étaient de déterminer les caractéristiques des trouées et d'élaborer comment ces dernières influencent la dynamique du peuplement. Dans le parc, nous avons recensé toutes les trouées interceptant six transects linéaires de 400m. La taille moyenne des trouées est plus grande que les études passées ce qui supporte la faible densité et productivité de la location septentrionale de l'étude. La prédominance des vents sud-ouest a influencé la direction de chute des arbres créateurs de trouées, et les différents états de décomposition des arbres créateurs de trouées suggèrent que la création de trouées est asynchrone. Bien que le recrutement se constitue principalement d'espèces tolérante à l'ombre dans les trouées, leur petite taille suggère que la fermeture d'une trouée est lent, voire faible. De plus, le recrutement ne semble pas influencé par les microsites engendrés par les arbres créateurs de trouées étant donné que la majorité des semis recensés dans les trouées sont établis sur des microsites non-perturbés. En terme d'écologie forestière, ce travail suggère que la dynamique de trouées est spécifique, et qu'il est donc difficile de mener des généralisations pour l'ensemble de la forêt boréale.

Mots clés : Dynamique de trouées, Finlande, forêt boréale, perturbation, *Picea abies*

1.3 Introduction

In temperate and tropical forests small-scale disturbances have been acknowledged for decades to be key factors in controlling the development and maintenance of stand characteristics such as an irregular tree-size structure, an uneven-aged structure, an accumulation of coarse woody debris, and variations in ground microtopography (Brokaw 1985; Denslow 1985). In the boreal forest, the omnipresence of large-scale fires has led to the landscape being viewed as a mosaic of regular tree-size and even-aged stands of different post-fire successional stages (Johnson 1992). However, it is now recognised that in some parts of the boreal forest, the period between fires may exceed tree longevity leading to the development of stands driven by small-scale gap disturbances (Kneeshaw & Gauthier 2003; Kneeshaw 2001; McCarthy 2001; Kuuluvainen 1994) and which results over time, in stands having an irregular and uneven-aged structure with an important accumulation of woody debris (Oliver & Larson 1996). This may be more frequent than previously thought especially in boreal regions with either high annual precipitation or on very mesic soils, such as in the boreal Fennoscandian forest (Engelmark 1999; Esseen *et al.* 1997).

Sirèn (1955) was the first to recognize the influence of small-scale disturbances in the development and maintenance of moist *Picea abies* (L. Karst) dominated stands, in northern Finland, that have not burned for long periods (> 300 years). In these stands, dead trees are replaced by pre- or post-established seedlings, and as these dead trees fell over and decomposed, they eventually become appropriate microsites for tree recruitment. More recently, the importance of small-scale disturbances was re-investigated in Finland, demonstrating their role in the development of irregular and uneven-aged stand structure, and in the creation of disturbed ground microtopography for tree establishment (Kuuluvainen 1994). Ground microtopography is influencing for gap recruitment (de Chantal *et al.* 2003; Hörnberg *et al.* 1997; Jäderlund *et al.* 1997). Similar stand structural patterns were also observed in other studies conducted in stands characterised by a long fire interval in other parts of Fennoscandia as well as in the boreal forests covering Russia and Canada (McCarthy & Weetman 2006; Boucher *et al.* 2003; Svensson & Jeglum 2001; De Grandpré *et al.* 2000; Kuuluvainen *et al.* 1998; Linder *et al.* 1997; Hörnberg *et al.* 1995; Hofgaard 1993*ab*).

Despite the important consequences of small-scale disturbances on the development of *P. abies* dominated stands, many gap characteristics have yet to be described unlike other boreal forest (e.g. Pham *et al.* 2004; Bartemucci *et al.* 2002; Drobyshev 1999; Kneeshaw & Bergeron 1998; Liu & Hytteborn 1991; Leemans 1990). A number of generalities about gap attributes can be identified from these other boreal studies: gaps were found to be caused by less than 10 individuals, to be about the same size (around 100 m^2) and to have a skewed distribution toward small gaps (Pham *et al.* 2004; Bartemucci *et al.* 2002; McCarthy 2001; Liu & Hytteborn 1991). However, gap recruitment appears to vary from stand type to stand type (McCarthy 2001).

The aim of this study is to characterize gap attributes of moist *P. abies* dominated stands, more specifically the *Hylocomium-Myrtillus* forest type located in Pallas-Ylläs Tunturi National Park in north-eastern Finland, to determine its gap features and to elaborate on how they influence stand dynamics. Gap characteristics were evaluated in particular: (1) gap size and fraction, (2) gapmakers (tree(s) responsible for the canopy opening), and (3) gap fillers. We wanted to know to which extent these particular factors contribute to the gap regime individually and how or whether they interact. This study will provide a better understanding of how small-scale gap disturbances contribute to the development and maintenance of *P. abies* dominated stands, and thus will provide a better conceptualization of boreal forest dynamics in stands that have not burned for a long period of time. The information gathered from this study could serve as a benchmark for the development and improvement of ecosystem forestry, restoration of degraded forests, and protection planning.

1.4 Site

The study area was in the northern Fennoscandian boreal vegetation zone, between N65° and N68° (Ahti *et al.* 1968). The Pallas-Ylläs Tunturi National Park in north-eastern Finland (67°30-67°44' N, 24°00-24°55'E), covering 1 020 km^2, was chosen because of a few remaining old-growth *P. abies* stands corresponding to *Hylocomium-Myrtillus* forest type are present there (Fig. 1.1). The northern location of Pallas-Ylläs Tunturi National Park limits the growing season to 100-140 days. The mean annual temperature is around -0.8°C and the annual amount of precipitation is about 500 mm with 45% of it falling as snow (Varmola *et* *al.* 2004). The park encompasses many lakes and is surrounded by rocky mounts with the highest elevation being Pallas Tunturi which culminates at 807 m. Protected by the Finnish government since the mid 1930's, some forestry activities took place in earlier periods in part of the park with the exception of the Pyhäjärvi and Pallasjärvi sectors.

Soils in this area originate from glacial till and tend to podzolize easily, which promotes the accumulation of raw humus on the most mesic sites (Bonan & Shugart 1989); giving rise to the *Hylocomium-Myrtillus* forest type (HMT) sensu Cajander (1926). The high moisture associated with the HMT forest favours the establishment of *Picea abies* (L. Karst), which is the dominant species followed by *Betula pubescens* Ehrh. and *Pinus sylvestris* L. to a lesser extent (Essen *et al.* 1997; Norokorpi 1979). The shrub layer includes *Sorbus aucuparia* L. and *Salix caprea* L., while the dwarf-shrub layer is dominated by both *Vaccinium vitis-idaea* L. and *Vaccinium myrtillus* L. (Esseen *et al.* 1997).

1.5 Methods

1.5.1 Sampling

Six sites within the Pallas-Ylläs Tunturi National Park were chosen based on the following criteria: 1) part of the *Hylocomium-Myrtillus* forest type, 2) having snags and down wood, heterogeneous vertical structure, and large living and dead trees, 3) relatively flat topography, 4) no signs of human impact and 5) no signs of recent severe disturbance. Four sites were located in the Pyhäjärvi area (7521971N; 2525787E) and the two others were in the Pallasjärvi sector (7548709N; 2508749E). The two areas are about 150 km apart.

At each of the 6 sites, one 400 m linear transect was established in the direction that allowed such length transect to fit into. We used the line intersect method, which has been commonly used in gap studies in the boreal forest (Pham *et al.* 2004; Bartemucci *et al.* 2002; Kneeshaw & Bergeron 1998; Liu & Hytteborn 1991), which consisted of investigating all gaps that intersected a linear transect. A gap was considered to be a canopy opening created by the death of a few trees where the regeneration height was less than two thirds of the dominant canopy height and bordered by living trees having a DBH over 9 cm (Pham *et al.* 2004; Kneeshaw & Bergeron 1998).

For each encountered gap, both canopy and expanded gap portion intersecting the transect were measured. Gap fraction corresponds to the total gap length (canopy or expanded gap) divided by the total transect length (ratio method) (Runkle 1992; 1982). The canopy gap is the land surface area directly under the canopy opening (i.e. from tree crown to tree crown) (Runkle 1982); while an expanded gap is measured from the tree base to tree base of trees forming the opening (i.e. from trunk to trunk) (Runkle 1992; 1982). However, the expanded gap portions were not measured for one transect (i.e. transect 1).Using the canopy gap definition, gap surface area was assessed by measuring the longest axis of the gap (A_{major}) and the widest point perpendicular to the longest axis (A_{minor}). The area was calculated with the ellipsoid formula, i.e. gap area = π (A_{major} * A_{minor}) / 4 where A_{major} equals the length of the longest axis while A_{minor} is the length of the shortest axis perpendicular to the A_{major} axis (Runkle 1992; 1982). Measurements were taken with a Vertex (Haglöf, Langsele, Sweden) to the nearest 0.1m.

Even though the ellipsoid formula tends to over-estimate the area of irregular gaps (de Lima 2005; Battles *et al.* 1996), a correction factor was not applied because when we used an alternative gap surface assessment method that we developed, which consisted on calculating gap surface from mapping the trees delimiting the gap, we did not obtain a significant difference in estimating gap area between the two methods (see appendix B). This mapping gap method was applied on a random selected sub-sample of the inventoried gaps.

A gapmaker was defined as a dead tree with a DBH greater than 9 cm which contributed to gap formation (Pham *et al.* 2004). We inventoried each gapmaker in every gap where the following information was gathered: species, diameter at breast height (DBH), state of mortality (standing, snapped or uprooted), orientation of downed bole for both snapped and uprooted trees, and we assigned them to one of the five decay states (Table 1.1).

Sampling for recruitment was performed in every fifth gap for which regeneration was present. We considered as recruitment tree any trees smaller than 9 cm DBH and below two-thirds of the dominant canopy were identified to species and their growing space was classified as a disturbed or undisturbed microsites. A disturbed microsite was considered a habitat that a gapmaker had altered the initial condition by either exposing the mineral soil or by accumulating woody debris (from coarse to fine). Finally, the height and last three years of growth of all the recruitment trees were measured to the nearest centimetre.

Finally to have a site description, we identified to species and measured both height (Vextex) and DBH (calliper, at the nearest 1cm) of all living and dead trees greater than 9 cm DBH in each 400 m x 40 m transect. Laasasenaho (1982) taper equations were used to calculate volumes for *P.abies*, *B. pubescens* and *P. sylvestris*. Wood volumes for others species were not calculated as they represent less than 2% of the whole study area. In the case of snapped trees, snapped height was used as the actual height which led to a slight overestimation of the dead wood volume. An importance value (IV) was calculated for the spruces, birches and the other species. Importance value calculations were performed as the average of the sum of the relative frequency of each species in term of basal area and density.

1.5.2 Statistical analysis

A series of chi-square tests (PROC FREQ, SAS 9.1) using a one-way contingency table were performed to evaluate the distribution of different variables concerning gapmaker attributes, such as the number of gapmakers per gap and their state of degradation. Orientation of downed boles was also tested using a chi-square test to verify whether their direction boles were oriented in the direction of the prevailing wind, i.e. south-west. Tree fall direction was split into four groups: north-west, north-east, south-west and south-east. Uprooted trees were pooled with snapped trees because of the low number of uprooted trees found in the field. Two-way contingency tables were used to verify whether the state of mortality interacted with decay state and tree species. The number of gapmakers was also correlated (Pearson correlation) with gap size.

To determine whether disturbed or undisturbed microsites provided the most favourable growing microsites inside a gap, an analysis of variance (PROC GLM, SAS 9.1) was performed on the height growth of the three last years. The recorded data on growth length had to be log-transformed in order to respect the assumptions of ANOVA (Sokal & Rohlf 1995). Linear regression analysis (PROC GLM, SAS 9.1) was performed to test whether the abundance of seedlings was due to gap size or the numbers of gap-makers present in a gap.

1.6 Results

1.6.1 Stand description

Tree density, basal area and living tree volume varied from site to site for both living and dead trees. Living tree density recorded the largest variability ranging from 365.6 trees/ha to 516.9 trees/ha for an average of 457.0 ± 51.8 trees/ha. For living trees, the average basal area was 15.5 ± 2.3 m^2/ha and mean wood volume was 104.2 ± 15.8 m^3/ha (Table 1.2). Dead tree density varied from 69.8 trees/ha to 112.5 trees/ha for a mean of 94.2 ± 15.4 trees/ha (Table 1.2). Average dead wood basal area was 5.0 ± 2.1 m^2/ha and average dead wood volume was 14.7 ± 2.7 m^3/ha. We encountered on average one dead tree for every five living trees (i.e. a ratio of dead to living trees of 0.21; Table 1.2). However, dead wood occupies a greater proportion of the study area than the ratio suggested as down wood was not considered in this analysis.

P. abies was the dominant species with an importance value varying from 60 to 84% while *B. pubescens* varied from 12 to 31% (Table 1.2). *P. abies* were the dominant dead tree species with an average of 62 ± 4%, a slightly lower importance value compared to the importance of living trees, while the importance value of dead birches was slightly higher compared to the living ones (32 ± 10%; Table 1.2).

1.6.2 Gap attributes

A total of 128 gaps were sampled, for an average of 21.3 ± 1.8 gaps per 400 m transect with one gap roughly every 19 m and an average canopy and expanded gap fraction of 43.1 ± 7.5% and 53.4 ± 9.4 % respectively (Table 1.3). Gap size distribution ranged from 25 m^2 to 1 600 m^2 (Fig. 1.2). Average gap size was 221 ± 198 m^2 whereas the median was nearly 180 m^2. The presence of two gaps greater than 1 000 m^2 increased the average gap size considerably. While only 20% of the gaps were smaller than 100 m^2, nearly 85% of them were less than 300 m^2 (Table 1.3). Only one transect had nearly 40% of its gaps smaller than 100 m^2, while in the other transects, less than 20% of the gaps were less than 100 m^2 (Table 1.3). Thus, gap size distribution tended to be log distributed.

1.6.3 Gapmaker attributes

In total, 556 gapmakers were inventoried for an average of 92.7 ± 16.8 gapmakers per transect, and 4.3 gapmakers per gap (Fig. 1.3). There was a significant difference in the frequency of occurrence of the number of gapmakers per gap for the whole study area (χ^2=62.4252; df=10; p<0.0001). Less than 4% of the gaps had more than 10 gapmakers; only one gap had 20 gapmakers, and two gaps had no gapmakers at all. Even though the number of gapmakers per gap had a low variability, a positive correlation was obtained between gap size and the number of gapmakers (Pearson: 0.46252, n=127, p<0.0001).

Gapmaker species were composed of 72% *P. abies,* 21% *B. pubescens* and 4% *P. sylvestris* (Table 1.4). The observed state of mortality was significantly different among species (χ^2=32.4952; df=4; p<0.0001). Both *P. abies* and *B. pubescens* were commonly found snapped (74% and 89% respectively); while *P. sylvestris* had 47.5% of its stems snapped, 9.5% standing and 43% uprooted (Table 1.4).

The five decay states were unequally distributed (Fig. 1.4; χ^2=274.6582; df=4; p<0.0001). For instance, around 40% of the gapmakers were in an advanced decay state, and less than 10% of gapmakers were in an early to intermediate-early decay state. There was a significant difference in the frequency of occurrence of decay state in relation to the state of mortality (χ^2=86.7451; df=8; p<0.0001) (Fig. 1.5). It was observed that the amount of standing dead trees decreased continuously as decay increased, while the number of uprooted and snapped trees increased as decay increased.

The downfall direction of 466 down boles was significantly different among the four directions tested (north-west, north-east, south-east and south-west; χ^2=91.2189; df=3; p<0.0001; Fig. 1.6). The two dominant downfall directions were north-east (30%) and south-east (40%) while the direction of the prevailing regional wind is south-west.

1.6.4 Gap fillers

More than 90% of the gaps had both gapmakers present and regeneration growing; then most gaps corresponded to the developmental gap definition of both Bartemucci *et al.*

(2002) and Runkle (1992; 1982) where both gapmakers and regeneration are present inside a gap.

A total of 23 gaps were inventoried for tree recruitment, equal to a total surface area of 3 972 m^2. We approximated 1 gap filler per 7 m^2 in gaps which suggested that regeneration was not over crowded. The number of gap fillers per gap ranged from 4 to 162, for an average of 24.2 ± 33.9 gap fillers per gap and a median of 13.5. Exactly 78% of the gaps had between 1 to 30 seedlings growing and the rest had more (Fig 1.7). The gap having 162 trees recruited is considered an outlier and has been excluded from the linear regression of gap size and number of gapmakers.

Of the 533 recorded gap fillers, 94% of them were *P. abies*. The 6% remaining were mainly *B. pubescens*, although there were a few *P. sylvestris*. The regeneration was representative of the dominant canopy species, i.e. *P. abies*. Most of the gap fillers were small with 89% of them being less than 1 m tall (Fig. 1.8).

Nearly 70% of the *P. abies* gap fillers were found growing on undisturbed microsites. In fact, there was a significant difference between the amount of gap fillers found in the undisturbed and disturbed classes (χ^2=75.76, df=1, p<0.0001). Even though undisturbed microsites supported more recruitment, height growth over the three last years was not significantly different between undisturbed and disturbed microsites (F=0.29, df=1; p<0.5881). Neither gap size nor quantity of gapmakers per gap had an effect on the abundance of gap filler recruitment (Fig 1.9 and Fig 1.10 respectively; r^2=0.31, p=0.6166 and r^2=0.17, p=0.5888 respectively).

1.7 Discussion

1.7.1 Gap attributes

In the old-growth *Hylocomium-Myrtillus* forest type located in Pallas-Ylläs Tunturi National Park in north-eastern Finland both gap fraction and gap size distribution were higher than what has previously been observed in similar stand types dominated by *P. abies* in the Fennoscandian boreal forest zone (Drobyshev 1999; Liu & Hytteborn 1991). The calculated mean gap area of this study is about two-times greater than what was found in similar *P. abies* dominated stands of central Sweden (Liu & Hytteborn 1991; Leemans 1990). This discrepancy may result in part from the stand location. The northern location of the study sites leads to low tree density and low site productivity which slows down the gap filling process, and therefore increases the probability of observing larger gaps. Northern locations have a shorter growing season, slower growth rates and persistent snow pack (Lertzman *et al.* 1996). Differences in gap fraction for a same type of forest were also observed in mixed boreal stands in Quebec by Messier *et al.* (2005) who recorded a higher gap fraction in the western part of the province (Temiscamingue) compared to the eastern part (Gaspesie), which they partly attributed to differences in spruce budworm outbreaks in each region. In the tropics, even similar forest types observed from sites within a same region demonstrated gap size variability due to different soil types (Kapos *et al.* 1990). Thus, for a same forest type, depending gap dynamics shapes a stand according the local environmental factors driving the disturbance. Generalisations based of stand types should thus be made carefully.

Gap size divergences also occur when contrasting our work with studies done in different boreal stand types of North America (Périgon 2006; Pham *et al.* 2004; Kneeshaw & Bergeron 1998). Stand species composition is one potential explanation for the divergences. The physiological difference between tree species, such as mean tree size, crown shape or tree sensitivity to disturbances (e.g. insect host), directly influences gap formation process. For example, Pham *et al.* (2004) observed differences in gap forming processes between *P. mariana* and *A. balsamea* dominated stands in eastern Quebec, Canada. *P. mariana* stands tended to have smaller openings which were attributed to the narrower and more conical crown of *P. mariana* compared to *A. balsamea.* Stand dynamics is thus species dependent.

1.7.2 Gapmaker attributes

Even though gaps are larger than what has usually been found in the boreal forest, the number of trees creating a gap is low, ranging from 2-5 trees (Fig. 1.3). For instance, gaps formed in northern Finland respected the gapmaker threshold (i.e. 1-10 trees per gap) established by Liu & Hytterborn (1991). But, the predominance of snapped gapmakers in the study area may have partially contributed to the formation of larger gaps. As a matter of fact, the fallen crown of a snapped tree frees more canopy space in comparison to a standing dead tree. For instance, in studies where standing gapmakers predominated, gaps were fairly small (Pham *et al.* 2004; Lertzman & Krebs 1991).

The predominance of the snapped state of mortality of gapmakers also seems to be influenced by the dominance of *P. abies*. With increasing age, *P. abies* is more likely to be affected by butt rot (Norokorpi 1979) which weakens the tree, enhances decay, and then makes the tree more sensitive to exogenous disturbance, such as strong winds or heavy snow loads (Kuuluvainen 1994). Tree sensitivity to wind is shown in our results with the great proportion of downed boles being oriented in the opposite direction to the south-west predominant wind, i.e. north-east. Again species appears to play an important role in the type of mortality that was observed. For example, *P. sylvestris* degrades slowly after death and remains standing dead for years, even for several decades while *P. abies* gapmakers were mainly found snapped which confirms similar findings by Liu & Hytteborn (1991),.

The presence of different decay classes suggests that gap formation is not due to a single event, but rather to a continuous series of small mortality events, as suggested by both Pham *et al.* (2004) and Lertzman and Krebs (1991). Gap forming processes in the study area are therefore asynchronous.

1.7.3 Gap fillers

The high proportion (91%) of gaps having gap fillers in *P. abies* dominated stands in northern Finland suggests that seedlings establish readily in gap dynamics stand (Kuuluvainen & Kalmari 2003; Drobyshev 1999; Hofgaard 1993*a*). However, even though each gap contains an average of 25 gap fillers, long term establishment seems to be relatively low as a small proportion of the gap fillers (11%) are taller than 1m. Thus, seedlings establish, but long-term recruitment to eventually close the canopy seems poor. Further investigation will be needed in order to evaluate more precisely gap filling success over the years.

The abundance of gap fillers per gap is neither influenced by gap size nor by the number of gapmakers. Furthermore, there was no difference in the last three years of growth between trees growing on disturbed or undisturbed microsites which suggest that both undisturbed and disturbed microsites provide equivalent growing conditions. Gap fillers growing on undisturbed microsites were more numerous, for instance 70% of seedlings were growing on undisturbed microsites. In contrast to a controlled experiment (Hörnberg *et al.*1997; Jäderlund *et al.* 1997), the abundance of microsites favours gap filler establishment, and competition from *V. myrtillus* limits recruitment success. However, we cannot tell whether seedlings previously germinated on exposed soil or decomposed trunk microsites as time may have erased any sign of past disturbed microsites.

The dominance of *P. abies* recruitment in gaps supports the idea that small-scale disturbances promote regeneration of shade tolerant species and leads to the decline of shade intolerant species, for instance *B. pubescens* and *P.sylvestris* which are shade-intolerant species are found in low numbers (Liu & Hytteborn 1991). As a matter of fact, *B. pubescens* is decreasing in number since our data show that there was a higher proportion of dead birch than living ones. Furthermore, the decline of *B. pubescens* supports a shift in composition.

1.8 Conclusion

This study demonstrates that generalisation about gap dynamics in the boreal forest cannot be made easily even for similar stand types across regions. Local environmental factors greatly influence stand responses to disturbance. Our results show that the gaps formed in old-growth *Hylocomium-Myrtillus* forest type located in Pallas-Ylläs Tunturi National Park in north-eastern Finland are larger than elsewhere in the boreal forest even though only a few individuals are involved in the process. This is probably a result of the low stand density and the poor site productivity associated with the northern location.

The predominant south-west wind influences the direction of the fallen boles of the gapmakers which suggest that most gapmakers were senescent or already dead when they fell. Furthermore, the presence of different state of decay supports those disturbances are asynchronous.

Even though shade-tolerant gap fillers were abundant, their small size shows that gap closure may be slow or not sustainable over the long term because very few tall gap-fillers were found. Furthermore, the presence of disturbed gap microsites does not seem to influence seedling recruitment as most of the seedlings were growing on undisturbed microsites.

In terms of forest ecology, this work suggests that the influence of gap dynamics is specific to each stand and therefore forest management cannot be done based on some generalisation about stand development under the influence of small-scale disturbance. The management recommendations from our study are to restrict the cutting intervention to a few individuals, to leave some dead wood and to protect gap fillers. But as this might not be economically viable, no intervention would be the best option.

1.9 Acknowledgements

We are grateful to Volker Bulder, Hannu Herva, Juha Petäjäniemi and Jordana Soderman for assistance with the field work. Financial support was provided by NSERC.

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Table 1.1 Description of the five different decay states used to qualify gapmakers (Adapted from Hunter 1990).

Decay Class	Description
Early	Recently dead, bark intact, small twigs and big branches remain; red to brown foliage can remain and wood is hard
Early-Intermediate	Bark partly intact, some small twigs might be remaining, big branches present, no foliage present and wood is hard
Intermediate	Bark partly intact, small twigs absent, big branches are present, softening of the wood
Intermediate-advanced	Bark mostly gone, big branches are more or less intact, wood soft, wood breaks down in big chunks and shape of the log is still round
Advanced	Often without bark, big branches might remain, wood soft, wood breaks down into small chunks, has lost its shape

Table 1.2 Stand descriptions with minimum, maximum, average and standard deviation for the study area

Stand descriptive criterions	Minimun	Maximum	Average	Stdev
Living stem density (trees/ha)	365.9	516.9	457.0	51.8
Dead stem density (trees/ha)	68.8	112.5	94.2	15.4
Living basal area (m^2/ha)	12.9	19.4	15.5	2.3
Dead basal area (m^2/ha)	2.8	5.1	5.0	2.1
Living wood volume (m^3/ha)	84.6	119.3	104.4	15.8
Dead wood volume (m^3/ha)	12.0	18.5	14.7	2.4
Ratio dead / living trees	0.15	0.22	0.21	0.03
Importance value (%)				
Living spruce	60	84	71.3	8.7
Living birch	12	31	24.3	8.5
Living other species	0	9	4.2	3.9
Dead spruce	56	66	62.2	4.0
Dead birch	19	42	32.2	9.7
Dead other species	0	14	5.7	7.3

Table 1.3 Gap descriptions with minimum, maximum, average and standard deviation for the whole study area

Gap descriptive criterions	Minimun	Maximum	Average	Stdev
Canopy gap fraction (%)	32	50	43.1	7.5
Expanded gap fraction (%)	42	63	53.4	9.4
Mean gap size (m^2)	153.7	164.8	235.5	254.5
Median gap size (m^2)	113.3	162.2	170.2	202.2
Range gap size (m^2)	25-514	49-401	70-693	75-1599
% gaps < $100m^2$	5.3	39.1	17.7	11.9
% gaps < $300m^2$	76.2	76.2	84.4	7.9
Number of intercepted gaps	19	24	21.3	1.8

Table 1.4 Number of snapped, standing and uprooted gapmakers according to species

	Snapped	Standing	Uprooted	Total
P.abies	297 (74%)	28 (7%)	76 (19%)	401 (72%)
P.sylvestris	10 (48%)	2 (10%)	9 (43%)	21 (4%)
B.pubescens	117 (89%)	5 (4%)	9 (7%)	131 (23%)
Others	4 (80%)	0 (0%)	1 (20%)	5 (1%)

Figure 1.1 Location of the study area in the Pallas-Ylläs Tunturi National Park, Lapland, Finland, in northern Fennoscandia forest.

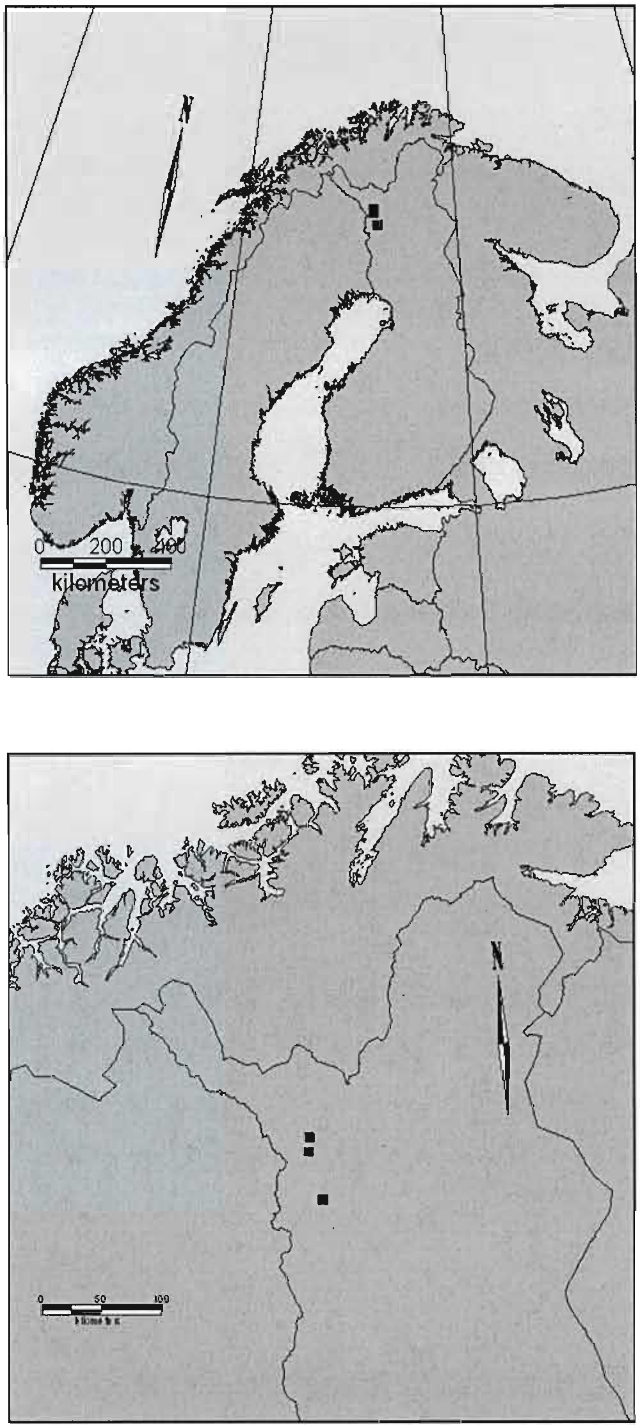


Figure 1.2 **Relative gap area frequencies**

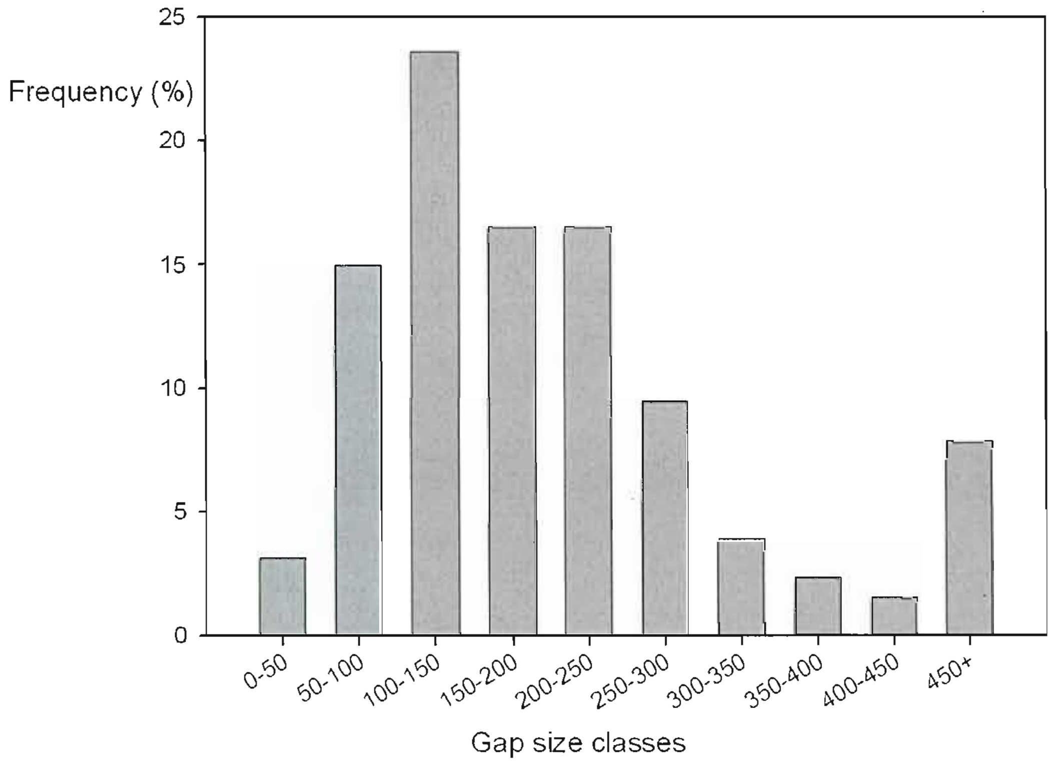


Figure 1.3 Relative frequency of the numbers of gapmakers per gap obtained in *P. abies* dominated stands of northern Finland.

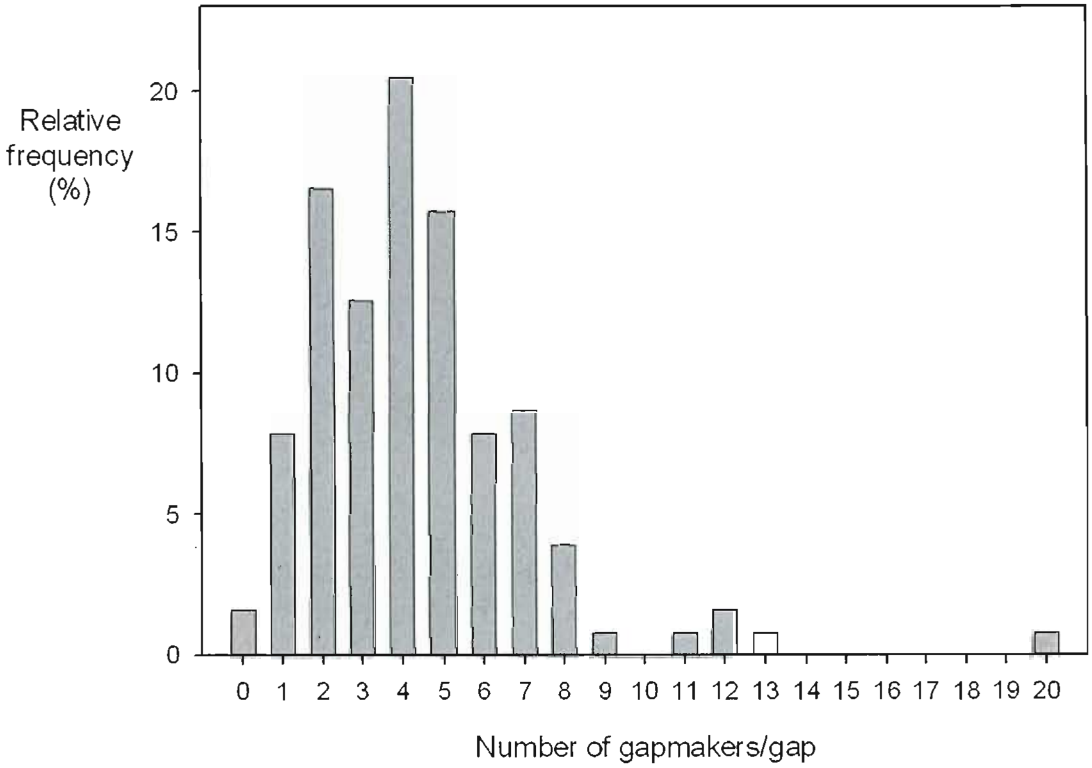


Figure 1.4 Relative frequency of decay class distribution of gapmakers in *P. abies* dominated stands of northern Finland.

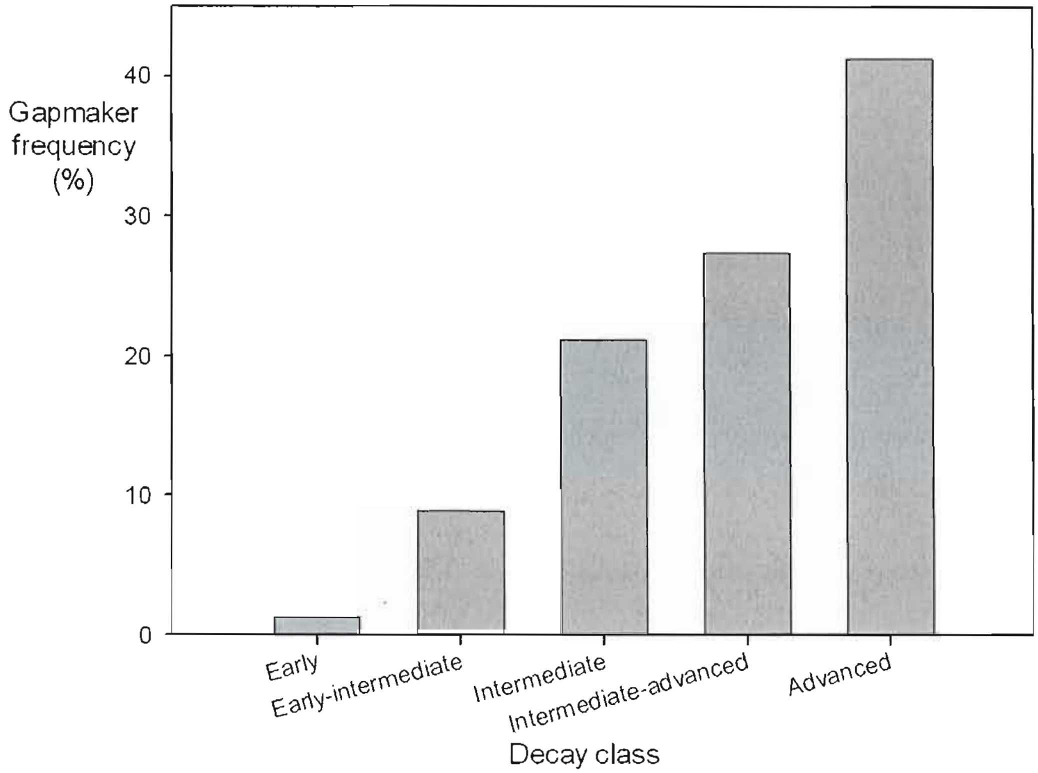


Figure 1.5 Gapmaker frequency distribution in respect to the mode of mortality and decay state

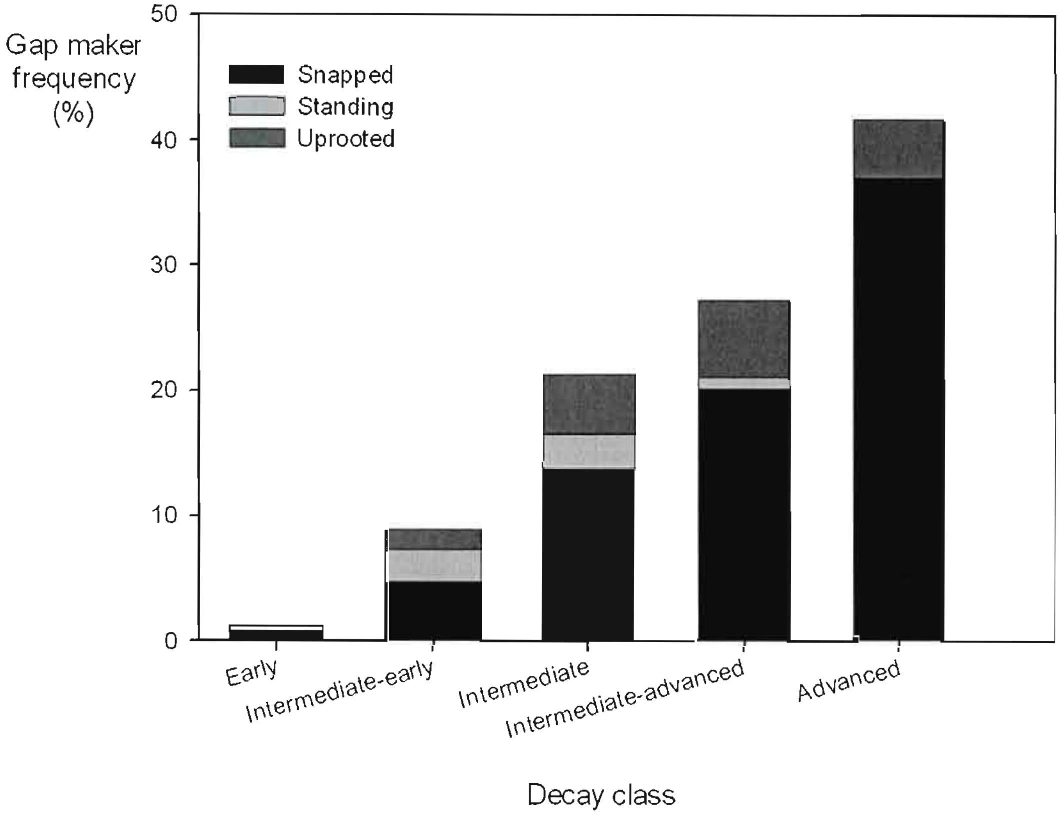


Figure 1.6 Absolute frequency of the number of gapmakers according to their direction of fall

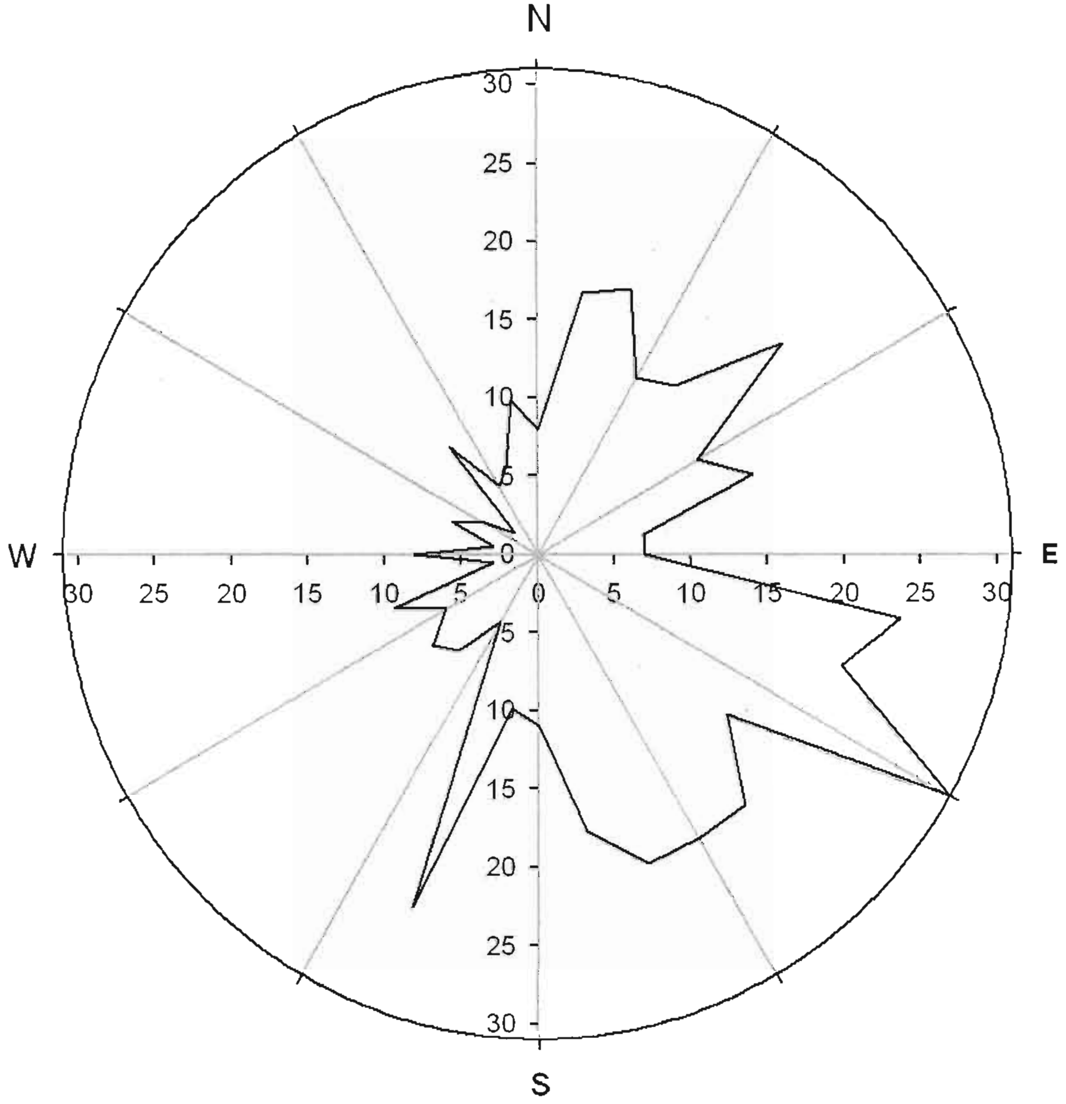


Figure 1.7 Relative frequency distribution of the number of gap fillers per gap

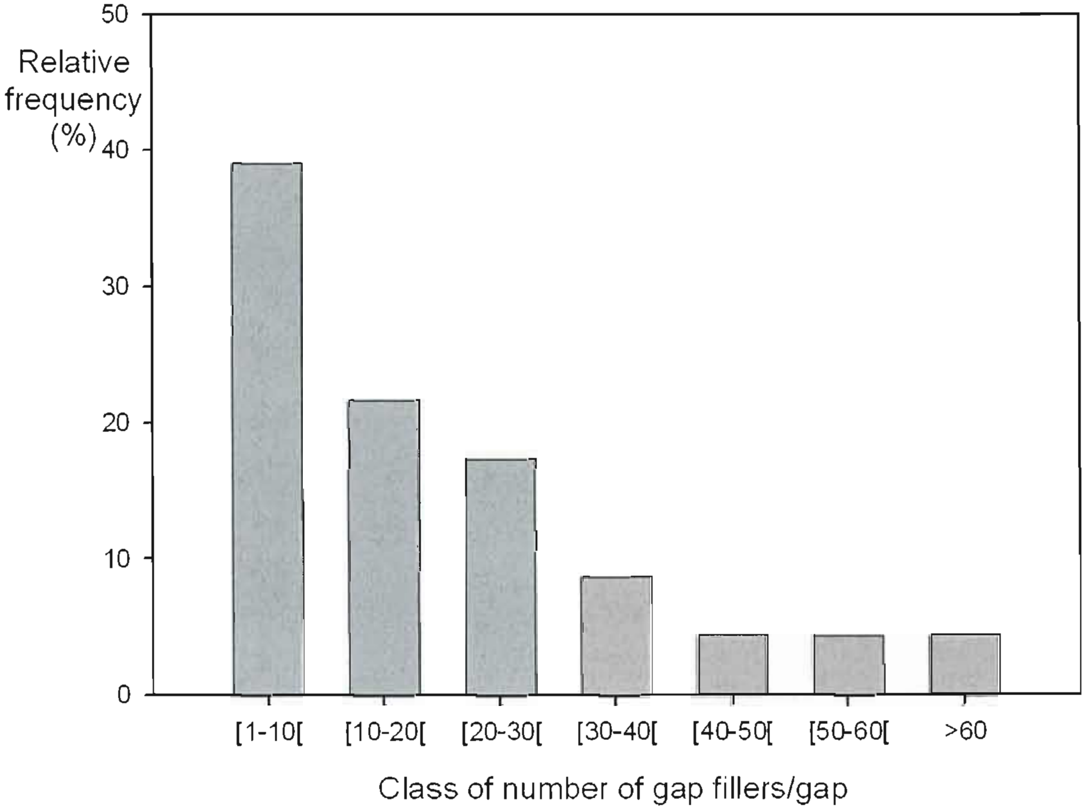


Figure 1.8 Gap filler height distribution

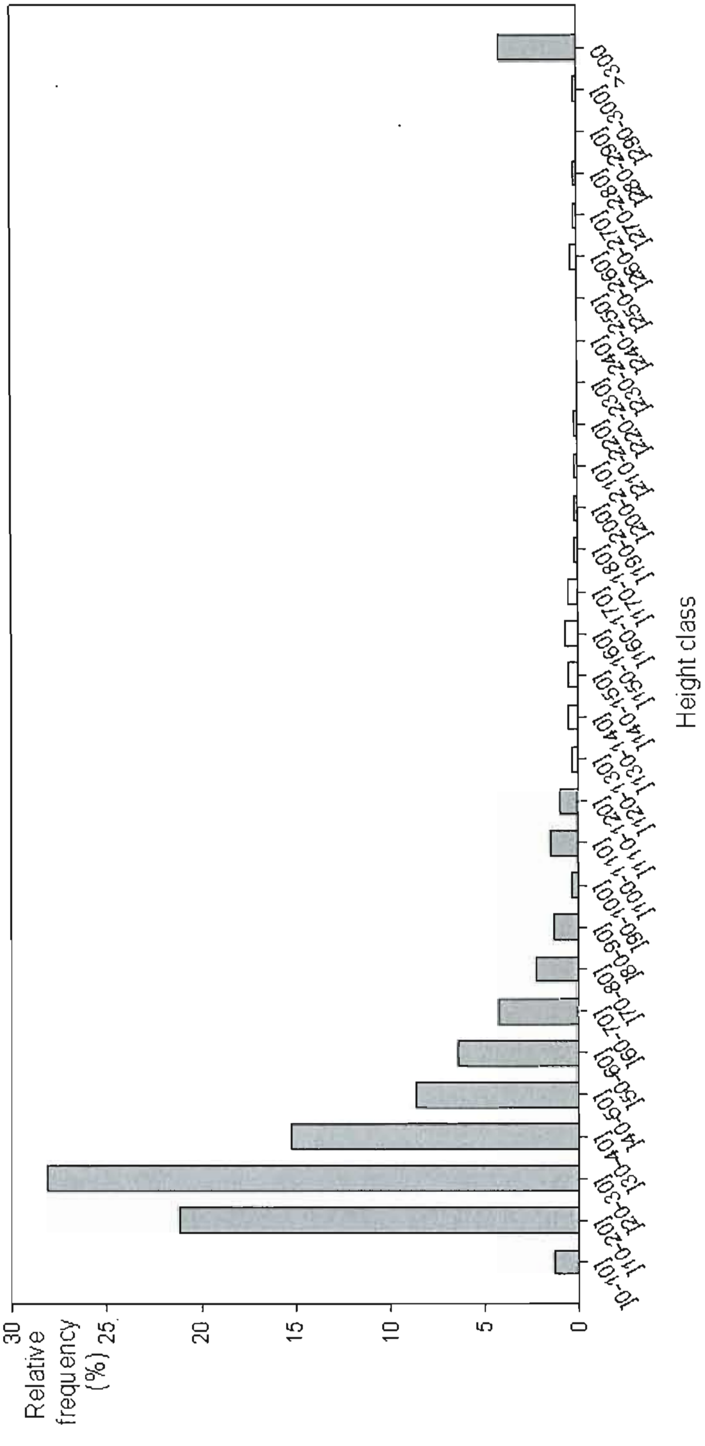


Figure 1.9 Relationship between the numbers of seedlings and gap size (r^2=0.31, p=0.6166)

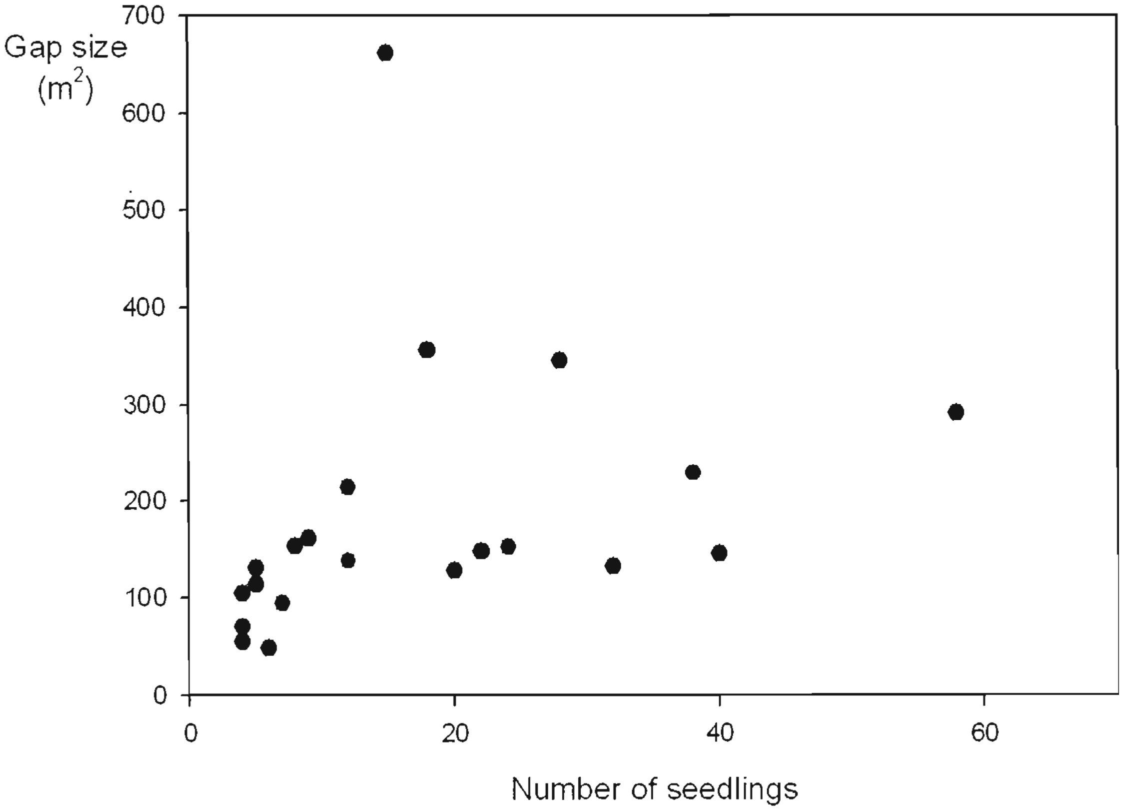
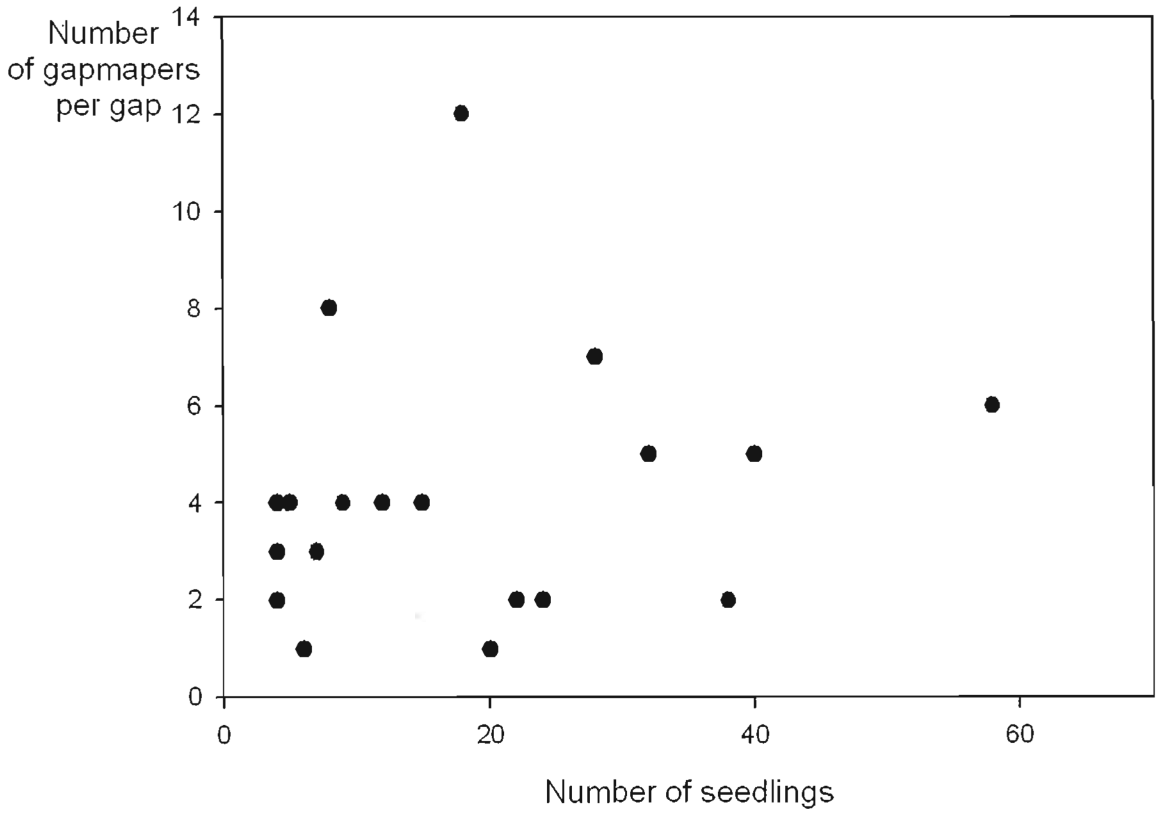


Figure 1.10 Relationship between the number of seedlings and the number of gapmakers per gap (r^2=0.17, p=0.5888)



CHAPITRE II

RECONSTRUCTING SMALL AND LARGE SCALE DISTURBANCES IN OLD-GROWTH *PICEA ABIES* (L. KARST) DOMINATED STANDS LOCATED IN NORTH-EASTERN FINLAND

2.1 Abstract

We reconstructed the disturbance history of old-growth *Picea abies* located in Pallas-Ylläs Tunturi National Park because; few of these stands remain and their stand dynamics through time are poorly understood. The objectives were to reconstruct the recent small-scale disturbance history and to characterise the radial growth of *P. abies* in order to detect past canopy disturbance. On six 400m line transects, intersecting gaps were aged by cross-dating in the laboratory tree ring series taken from gapmakers. The irregular temporal distribution of gap creation and the absence of distinct periods of gap creation confirm the continuous occurrence of gap disturbances for which we estimated a rotation period of 250 years. Even though, no large-scale disturbances have been recorded for this territory, several *P. abies* recorded some years of major growth release over their lifetimes. The most important growth release decade was 1816-1826. It is likely that a disturbance of intermediate scale occurred around this decade. In conclusion, our results show that gap dynamics is continuous in time notwithstanding its non-synchronicity, and that most of the *P. abies* experience at least one important growth release during their lifespan

Key words: Dendrochronology, disturbance, Finland, gap dynamics, growth release, *Picea abies*

2.2 Résumé

Nous avons reconstruit l'historique des perturbations de vieux peuplements de *Picea abies* dans le parc national de Pallas-Ylläs Tunturi parce que peu de ces peuplements sont encore présents et que leur dynamique temporelle demeurent peu comprise. Les objectifs étaient de déterminer le taux annuel de formation de trouées et de caractériser la croissance radiale de *P. abies* afin de détecter des perturbations de la canopée communes dans les patrons de croissance sur l'ensemble du territoire à l'étude. La distribution irrégulière des périodes de création de trouées et l'absence de pic distinct d'année créatrice de trouées confirment l'occurrence continue d'un régime de perturbation de trouées de petite envergure dont le temps de rotation est estimé à 250 années. Bien qu'aucune perturbation de grande échelle connue n'ait pris cours sur le territoire, les patrons de croissances de plusieurs *P. abies* ont enregistré de forte reprise de croissance. La plus importante période de reprise de croissance eut lieu de 1816-1826. Une perturbation intermédiaire est probablement tenue en cause. En conclusion, nos résultats démontrent que la dynamique de trouées est continue dans le temps malgré son asynchronisme et que la plupart des *P. abies* ressentent moins une reprise de croissance au cours de leur existence.

Mots clés: Dendrochronologie, dynamique de trouées, Finlande, perturbation, *Picea abies*, reprise de croissance

2.3 Introduction

Fire is the major natural disturbance in the boreal forest (Johnson 1979; Zackrisson 1977). Its omnipresence has let to an overestimation of its influence on boreal stand dynamics (McCarthy 2001; Bergeron *et al.* 1998; Johnson *et al*, 1998; Kuuluvainen 1994). However, parts of the boreal forest can escape fire for hundreds of years due to particular environmental conditions (Engelmark 1999; Esseen *et al.* 1997), such as sites with high annual precipitation or with very mesic soil. Where the period between fires exceeds tree longevity, stand dynamics are driven by small-scale disturbances such as tree senescence and damage due to insects, pathogens, windthrow, and snow or ice loads (Kneeshaw & Gauthier 2003; Kneeshaw 2001; McCarthy 2001; Kuuluvainen 1994). Under small-scale disturbances, mortality occurs at the scale of the individual tree which leads to the development and maintenance of irregular and uneven-aged stand structure with an important accumulation of woody debris (Oliver & Larson 1996). This results in stands having old-growth forest characteristics (Mosseler *et al.* 2003; Franklin *et al.* 1987, Harmon *et al.* 1986).

In Finland, such as for the whole Fennoscandian boreal zone, few old-growth forests remain due to anthropogenic activities (Östlund *et al.* 1993; Essen *et al.* 1992). This had led to an increase of both endangered Fennoscandian boreal flora and fauna species (Svensson 1996; Bernes 1994). Protected areas offer one way of maintaining biodiversity but these are mainly located in northern areas. For instance, in Finland, the majority the 344 000 ha of protected old-growth forests are found in the northernmost part of the country (Finnish Forest Association 2001). Alternative solutions, such as ecosystem management or restoration planning, can be used to conserve boreal biodiversity in areas where it may be more difficult to establish protected zones such as in the south of Finland. Consequently, knowledge of boreal stand dynamics from the few untouched old-growth forests needs to be gained in order to implement appropriate and adequate alternative solutions in the Fennoscadian boreal forest.

Recently acknowledged in the boreal forest, gap dynamics have been studied principally for their influence on stand structure development (McCarthy & Weetman 2006; Hofgaard 1993*ab*), gap attributes (i.e. gap size and fraction, qualifying and quantifying gapmakers, light availability) (Pham *et al.* 2004; Bartemucci *et al.* 2002; Liu & Hutteborn 2001), and creation of favourable recruitment microsites (Kuuluvainen & Kalmari 2003; Drobyshev 1999; Hofgaard 1993*a*). Little has been studied on the influence of boreal gap dynamics on stand development and maintenance through time. Permanent plots would be appropriate for evaluating gap dynamics on a long term basis, but they require several inventories at different time intervals. Dendrochronological techniques offer an interesting alternative method as disturbance historical reconstruction can be done based on a single inventory.

In the temperate forest, scientists have used dendrochronological analysis to qualify and quantify gap dynamics through time (Nowacki & Abrams 1997; Payette *et al.* 1990; Frelich & Lorimer 1989; Lorimer 1980). Apart from climate, tree-ring patterns are influenced by the occurrence of disturbances (Schweingruber 1996; Fritt & Swetman 1989). Tree-ring chronologies can be used to reconstruct stand dynamics history with the use of different techniques: identifying growth release periods induced by disturbances (Black & Abrams 2004; Nowacki & Abrams 1997; Lorimer & Frelich 1989), dating fire scars (Buell *et al.* 1954), analysing stand age structure (Foster 1988) or cross-dating dead trees (Fritts 1976).

In this study, we documented the disturbance regime of old-growth *Hylocomium-Myrtillus* forest type located in Pallas-Ylläs Tunturi National Park in north-eastern Finland through a dendrochronological disturbance reconstruction. This forest type is dominated by *Picea abies* (L. Karst). Specifically, the objectives were to reconstruct the recent disturbance history and to characterise the radial growth of *P. abies* in order to detect both small and large past canopy disturbances common in the tree-ring growth patterns of the study area. Because old-growth *P. abies* stands are known to have a long fire interval (over 300 years) and no recorded pest outbreaks (Norokorpi 1979; Sirèn 1955), we expected gap formation to be homogenous through time and there to be an absence of large-scale disturbance. From this work, better knowledge about the small scale boreal disturbance regime would be determined which could contribute to the improvement of forest ecosystem management as well as for restoration of the forests in the Fennoscandian zone.

2.4 Site

The study area was in northern Fennoscandian boreal vegetation zone, between N65° and N68° (Ahti *et al.* 1968). The Pallas-Ylläs Tunturi National Park in north-eastern Finland (67°30-67°44' N, 24°00-24°55'E), covering 1 020 km^2, was chosen because of a few remaining old-growth *P. abies* stands corresponding to *Hylocomium-Myrtillus* forest type are present there (Fig. 2.1). The northern location of Pallas-Ylläs Tunturi National Park limits the growing season to 100-140 days. The mean annual temperature is around -0.8°C and the annual amount of precipitation is about 500 mm with 45% of it falling as snow (Varmola *et al.* 2004). The park encompasses many lakes and is surrounded by rocky mounts with the highest elevation being Pallas Tunturi at 807 m. Protected by the Finnish government since the mid 1930's, some forestry activities took place in part of the park with the exception of the Pyhäjärvi area and parts of Pallasjärvi sector which have never been harvested.

Soils in this area originate from glacial till and tend to podzolize easily, which promotes the accumulation of raw humus on the most mesic sites (Bonan & Shugart 1989); giving rise to the *Hylocomium-Myrtillus* forest type (HMT) sensu Cajander (1926). The high moisture associated with the HMT forest favours the establishment of *Picea abies* (L. Karst), which is the dominant species followed by *Betula pubescens* Ehrh. and *Pinus sylvestris* L. (Essen *et al.* 1997; Norokorpi 1979). The shrub layer includes *Sorbus aucuparia* L. and *Salix caprea* L., while the dwarf-shrub layer is dominated by both *Vaccinium vitis-idaea* L. and *V. myrtillus* L. (Esseen *et al.* 1997).

2.5 Methods

2.5.1 Sampling

Six sites within the Pallas-Ylläs Tunturi National Park were chosen based on the following criteria: 1) part of the *Hylocomium-Myrtillus* forest type, 2) having snags and down wood, heterogeneous vertical structure, and large living and dead trees, 3) relatively flat topography, 4) no signs of human impact and 5) no signs of recent severe disturbance. Four sites were located in the Pyhäjärvi area (7521971N; 2525787E) and the two others were in the Pallasjärvi sector (7548709N; 2508749E). The two areas are about 150 km apart.

At each of the 6 sites, one 400 m linear transect was established in the direction that allowed such length transect to fit into. We used the line intersect method, which has been commonly used in gap studies in the boreal forest (Pham *et al.* 2004; Bartemucci *et al.* 2002; Kneeshaw & Bergeron 1998; Liu & Hytteborn 1991), which consisted of investigating all gaps that intersected a linear transect. A gap was considered to be a canopy opening, i.e. from tree crown to tree crown (Runkle 1992, 1982), created by the death of a few trees where the regeneration height was less than two thirds of the dominant canopy height and bordered by living trees having a DBH over 9 cm (Pham *et al.* 2004; Kneeshaw & Bergeron 1998). We measured the length of the intersecting canopy gap portion that was crossed by the transect which served in the gap rotation period calculation.

The dendrochronological analysis is based on gapmakers sampled from the inventoried gap encountered along the six transects. We considered a gapmaker to be a dead tree with a DBH greater than 9 cm which created the gap. From 1 to 3 gapmakers were sampled randomly per gap independently of the species. In some cases, it was impossible to sample any of the gapmakers found in a gap, because their state of decay was too advanced to remove a suitable disk. Ideally, bark had to remain attached to the sample disk as the outermost ring was used as the reference point for assessing the year of mortality, and thus the minimal year of gap creation. A total of 130 trees (111 *P. abies*, 9 *P. sylvestris* and 10 *B. pubescens*) were sampled. We eliminated 17 *P. abies* and one *P. sylvestris* because of indistinct tree-rings, making them unsuitable for dendrochronological analysis.

2.5.2 Dendrochronological measurements

All disks were sanded to even out the surface, and then two radii were traced and carved with a razor blade. The choice of radius was based on the absence of reaction wood and the presence of bark at the edge of the disk. Water and magnesium powder were added to the carved radii to better expose the cells under the binocular. For each radius, ring widths were counted and measured to the nearest 0.01 mm using a sledge table interface with a computer.

Assessment of the year of tree death was done by cross-dating with the computer program COFECHA (Grissino-Mayer 2001; Holmes 1983). Basically, the computer program

COFECHA superimposes an unknown tree-ring series of a dead tree with a standardized master chronology tree-ring series, finds the best statistical match between the two according to Pearson correlations, and then suggests one to several years of death (Holmes 1983). As prior to death, trees may not produce full annual tree-rings; two radii provide a more accurate approximation. In case of discrepancy between counts for the two radii, the most recent year was selected as the year of death. In our case, a master chronology already existed for both *P. abies* and for *P. sylvestris* of the study region (Tinomen & Herva, personal communication). However, we kept the results of *P. abies* only, because there were too few *P. sylvestris* sampled to be considered as representative. As there was not master chronology for *B. pubescens,* we attempted to build one from living increment core taken in the study area, but poor correlations were obtained in cross-dating *B. pubescens*. The site growth sensitivity of birch might have interfered with the construction of a reliable birch master chronology. Consequently, tree-ring information from birch was not used.

Even though COFECHA informs about measurement quality control, a graphical visual verification was done by plotting the two radii tree-ring series against the master chronology with the characteristic years (pointer years), i.e. 1902, 1928, 1931, 1948-1951, and 1981-83 which were narrow rings (personnel observations; Mäkinen *et al.* 2000), to verify whether tree-ring series followed a similar growth trend.

2.5.3 Statistical methods

The ecological question about the timing of gap creation was examined using a chi-square test (PROC FREQ, SAS 9.1) with a one-way contingency table. This specific analysis was restricted to the gapmakers that died after 1965, because prior to this time there were too few data.

The gap rotation period, which corresponds to the amount of time needed to disturb an equivalent area to the one under study (Frelich 2002), was calculated with a truncated time-since-the oldest gap distribution. This analysis was derived from the truncated time-since-fire analysis of Johnson & Gutsell (1994). Using a truncated distribution allows us to consider gaps that could not be dated by using the oldest gapmaker. To construct the truncated time since oldest gap, the oldest gap was determined for each transect from which the cumulative open section was related to the time since the transect experienced its first observable opening (i.e. the age of the oldest gap). The approximation was obtained with a Maximum Likelihood estimator 'b' which gives the rotation time in years and which corresponds to a negative exponential distribution. The maximum likehood estimator for the gap rotation calculation was obtained from the equation:

$$b = \frac{(a_i x_i)^{+} + \sum_{i=1}^{r} a_i x_i}{N}$$

where b is rotation period in number of years, $(a_i x_i)^+$ is the time-of the oldest gap aged (x_i) in which the data is truncated multiplied by the area (a_i) in age x_i in the study which was under closed canopy, ($a_i x_i$) is the time-since-the oldest gap aged multiplied by the area in each age which was open, *r* is the total number of aged gaps recorded and *N* is the total area which was opened during the study.

2.5.4 Growth release analysis

Investigating tree-ring growth patterns can be used to examine past disturbances in the case of suppressed canopy trees. A disturbance in the dominant canopy layer provokes a subsequent growth increase (i.e. percent growth change) due to the alteration in the availability of growth resources (Schweingruber 1996; Fritt & Swetnam 1989). In this study, the percent-increase method proposed by Nowacki & Abrams (1997) was applied to detect growth releases, and hence to evaluate past gap disturbances for a period of time going back as far as the 18th century. The analysis was only performed on *P. abies* because the sample size of both *P. sylvestris* was not sufficient.

Using the percent-increase method, a growth threshold from the relation between percent growth change and prior growth had to be first established from the resulting average of the two tree-ring radii for each of the 94 *P. abies* sampled gapmakers. Percent growth change was calculated according to the following formula: $[(M_2\text{-}M_1)/\ M_1] \times 100$, where M_1 corresponds to the average radial growth of the 10 preceding years (including the evaluated year), and M_2 equals the average radial growth of the 10 succeeding years (excluding the analysed year). Then, prior growth was calculated as the average growth over the 10 preceding years (excluding the analysed year). The pre- and post 10-year window is a common window length used in the literature for quantifying growth change for a given year, because this window length filters out tree-ring response to short-term changes caused by annual fluctuations in temperature and precipitation (Black & Abrams 2004, 2003; Nowacki & Abrams 1997; Lorimer & Frelich 1989).

By plotting the average of the top 10 percent growth changes against 0.05 mm classes of prior growth (e.g. 0-0.05, 0.1, 0.15, 0.2...2.0 mm), the best fit curve (highest significant R^2) (using the statistical option in SigmaPlot 8.0) obtained from that relationship corresponded to the maximum boundary line, the maximum growth threshold. Only the top 10 percent growth changes were considered to even out the sample size classes of each prior growth segment. Major growth releases were considered as any point of the relation percent growth change versus prior growth falling above 50 % of the maximum threshold line while a moderate growth release was located at 20 % of the maximum threshold (Black & Abrams 2004). This said, the maximum growth threshold obtained from 94 *P. abies* between percent growth change and prior growth was fit to a negative linear regression ($y = -98.8219x + 163.3876$; $R^2 = 0.88$; Fig. 2.2). Major and moderate growth thresholds were derived from this relationship, where they respectively equalled 50 % and 20 % of the maximum threshold of percent growth change. Major growth release indicates a transition from understorey to a canopy position, while a moderate growth release signals an increase in growing space for trees already in the canopy as well as the end of a period of suppression (Frelich 2002). All major and moderate growth changes recorded were then compiled by year of occurrence, in order to establish the growth release time period distribution.

2.6 Results

2.6.1 Recent gap creation

A total of 128 gaps were intersected along the six transects for an average 5 gaps per 100 m. The total proportion of the forest that was open varied from 127.9 to 200.0 for each

400-m-long transect, leading to an average of 172.2 ± 27.3 m (Table 2.1). Therefore, mean open fraction equals approximately 50%.

It was possible to age 59 gaps, a little less than half of the total number of inventoried gaps. The other gaps, with the exception of the two that had no gapmakers, could not be aged since gapmakers were too decayed for dendrochronological analysis. The youngest gap was formed in 2005 (the survey year), and the oldest gap was created in 1922. 75% of the gaps were less than 40 years old (i.e. created after 1965) (Fig. 2.3).

Gap creation for the period 1965-2005 was irregularly distributed ($\chi^2 = 21.0847$, df = 8, p = 0.007) (Fig. 2.3). Gap creation was greatest during the period 1980-1985 with 17.0% of the gaps being created. It also included the year (1983) with the greatest number of new gaps created (5). The period 1970-1975 was the second highest period of gap creation (15.3%). The lowest number of gaps created occurred between 2000-2005 (1.7%). The other time periods contained between 5 and 10% of the total dated gaps. No peak in gap creation occurred across the whole study area. Year of gap creation was highly variable from transect to transect, and no common trend was observed for all transects (Fig. 2.4).

The actual gap opening in the transects varied from 63.6 to 111.8 m for a mean of 87.3 ± 16.9 m (Table 2.1). The truncated time-since-the creation of the oldest gap and the distribution derived from the open aged fraction allowed us to estimate the rotation period which ranged from 173.6 to 333.6 years with an average rotation period of 248.2 ± 55.8 years for the whole study area (Table 2.1). It would then take nearly 250 years to have an area equivalent to our study area entirely disturbed at least once.

2.6.2 Disturbances since the 1700's and growth release

94 sample trees were used for the growth release analysis. The number of tree rings per disk varied from 80 to 295 with an average of 197 ± 49. 80% of the trees had more than 160 tree rings, and less than 3% of the trees had fewer than 100 tree rings (Fig. 2.5). Even though age could not systematically be estimated because disks were not removed at the tree base depending on tree decomposition, the tree ring counts showed that gapmakers were mature and even over-mature trees.

Due to the length of the tree ring series collected, growth release analysis could be carried out as far back as 1690 (Fig.2.6 and Fig. 2.7). Moderate growth release was observed in all trees at least once during their lifetime. Moderate growth releases were evenly distributed with most decades represented by at least 60% of the tree disks (Fig 2.6). Decades represented by less than 60% of the disks occurred in most part prior to 1800 which was also the time period with the lowest number of trees available for the analysis.

At least one major growth release was recorded in 68 sample trees (i.e. 72%). The time distribution of major growth releases was irregularly distributed and some peak decades were observed (Fig. 2.7). For instance, the periods, 1810-1819 and 1820-1829, had the highest number of trees with a major growth release, respectively 32% and 44% of the sampled trees. Furthermore, major growth releases occurred predominantly in the decade 1810-1819, but more intensively in transect 5 and 6. 1820-1829 stood out but to a lesser extent (Fig. 2.8). Thus, two episodes of high major growth release were found in the study area.

For the period 1810-1829, we observed that the number of trees experiencing major growth release rapidly increased from 1816 to 1821, culminated in 1821, and then slowly decreased till 1826 (Fig. 2.9). The disturbance event causing the period of major growth release between 1816-1826 influenced tree ring growths patterns over several years.

2.7 Discussion

2.7.1 Historical reconstruction of gap disturbance

As hypothesised, the old-growth *Hylocomium-Myrtillus* forest type located in Pallas-Ylläs Tunturi National Park in north-eastern Finland had no distinct peak of gap creation during their recent history from 1965 to 2005. The irregularity in the timing of gap creation and the maximum 8% of gap creation in a single year suggest that no peak in disturbance occurrence occurred over the study period in either Pyhäjärvi or Pallasjärvi areas. This absence of a peak in gap creation concords with past stand dynamics studies done in different forest types dominated by *P. abies* in Fennoscandia which suggest that the development and maintenance of such stands result from the occurrence of continuous small-scale disturbances interspersed by a limited number of large-scale disturbances (Lilja *et al.* 2006; Kuuluvainen 1994; Norakorpi 1979; Sirèn 1955). When looking at gap formation on a site by site basis, gap creation periods differ from one transect to another, thus there appears to be no synchronicity of gap creation among the sites. Consequently, gap formation would be more likely caused by local site small disturbance events.

The quasi-constant gap creation observed in old-growth *P. abies* dominated stands differs from the gap creation pattern occurring in the boreal forest of Quebec, Canada where peaks in gap formation, as well as peaks in mortality, have been identified in the years following a spruce budworm (*Choristoneura fumiferana* (Clemens)) outbreak in both *Picea mariana* Mill. and *Abies balsamea* (L.) stands (Aakala *et al.* 2007; Périgon 2006; Kneeshaw & Bergeron 1998). *A. balsamea* stands had a higher number of gaps created during the outbreak in comparison to *P. mariana* stands (Périgon, 2006). These findings support the fact that old-growth *P. abies* dominated stands are not subject to pest outbreaks in our study area. The Finnish literature also does not report any important pest outbreaks (Kuuluvainen 1994; Norakorpi 1979; Sirèn 1955). The absence of pests leads to a more continuous occurrence of gap creation caused by small-scale disturbances in our study area.

Furthermore, this absence of pest outbreaks may partially explain the long rotation period of nearly 250 years that we obtained. Périgon (2006) calculated a much lower rotation period ranging from 60 to 105 years in both *P. mariana* and *A. balsamea* stands in eastern Quebec, and Kneeshaw & Bergeron (1998) obtained similar estimations for the coniferous boreal forest of western Quebec. The presence of spruce budworm outbreaks in Quebec's boreal forest is more likely to accelerate the occurrence of openings and shorten rotation periods. However, other mechanisms such as tree longevity are also important to consider. For instance, both *P. mariana* and *A. balsamea* have a lifespan of 100-200 years (Burns & Honkala 1990) while *P.abies* can live for 200-300 years (Sirèn 1955). Our data support long living trees as the minimum age of most of the *P. abies* gapmakers (80%) was evaluated as at least 160 years old. Consequently, these trees are more likely to die with increasing age as they approached to senescence and became more susceptible to small exogenous disturbances such as snow loads or strong winds (Kneeshaw & Gauthier 2003; Kneeshaw 2001; McCarthy

2001; Kuuluvainen 1994). This point is further supported by the asynchronous timing of gap creation that we observed.

Compared with other Fennoscandian *P. abies* stands, we assume that gap opening and gap filling process happen at the same rate in our study area as found by Liu & Hytterborn (1991). The obtained turnover varies from 173 to 333 years in our study area, being higher than turnover in central Sweden which was found to range from 170-228 years (Liu & Hytterborn 1991). Since pest outbreaks are not common in the *P. abies* of central Sweden, the northernmost latitude of our study area may explain the discrepancy. As a matter of fact, northern locations have a shorter growing season, slower growth rates and persistent snow pack (Lertzman *et al.* 1996). Consequently, the higher site productivity in the south is more likely to accelerate gap closing process. Further investigation about gap filling is needed to test this hypothesis, (e.g the success of establishment).

2.7.2 Disturbances since the 1700's and growth release tree patterns

Our growth release analysis allowed the detection of multiple canopy disturbances for a time period covering nearly three centuries, i.e. from 1710 to 1995. Overall, most *P. abies* (72%) underwent at least one major growth release, while all *P. abies* recorded one to several moderate growth releases. This difference in frequency of occurrence between major and moderate growth releases is probably due to the fact that major growth release may indicate a transition from an understorey position to a canopy position, while a moderate growth release is associated with an increase in growing space for trees in the understory, subcanopy or canopy and can thus easily occur more than once in a lifetime (Frelich 2002). Our results thus support the occurrence of several dispersed episodes of canopy disturbances that were severe enough to permit suppressed trees to reach the canopy.

Our results also suggest that larger disturbances may also have taken place almost two centuries ago. Even though major growth release was found in trees across the study area at a relatively low frequency; there are two decades that stood out (1810-1819 and 1820-29) in terms of the high frequency of trees recording major growth releases (respectively 32 % and 44 % of the sampled trees) (fig. 2.7). These distinct peaks are observed at both sites in each transect (fig 2.8). The disturbance event is thus probably common to both the Pyhäjärvi and Pallasjärvi areas. Stands took a few years to recover from the disturbance event, as the number of trees having recorded major growth release increases rapidly from 1816 to 1821, then culminate, and finally slowly decrease till the late 1920's.

Identifying the disturbance agent causing these major growth release period is not easy as little information exists about forest history for that time period. As the growth release patterns are found in all the sites, even the ones which are 150 km apart from each other, the disturbance would probably have originated from an exogenous event. Unusual climate conditions might be one possibility. The great eruption of the Tambora volcano in 1815 which has been hypothesized as having important consequence around the globe leading to cooler climate conditions (Harrington 1992) might be one explanation for the observed patterns in concordance with timing of the growth patterns.

Other disturbances affecting multiple trees over great distance, such as windthrow or ice-storms may be more likely candidates for this important period (1816-1826) of major growth releases. Wildfire and human caused surface fires should also be considered as different studies have shown that fires were more frequent prior to the 1800's in Fennoscadia (Wallenius *et al.* 2005; Zackrisson 1977). Charred stumps, charcoal or pollen analysis in their respective transects or their neighbourhood, if present, could provide supplemental information about the fire dynamics history of the area. A final possibility could be a cohort shift in dominant trees. For instance, an initial post stand-disturbed cohort may have been at its point of decline when weather conditions or some stress may have helped synchronise a massive death of individuals, leading to major growth releases from the suppressed second tree cohort (Senecal *et al.* 2004). A post-disturbed cohort, having established at the same time, could die in great numbers around the same period, leaving plenty of growing space and resources for suppressed trees to reach the canopy. Therefore, several different explanations are possible, but this period of major growth release observed in many trees suggests that *P. abies* dominated stands are subject to infrequent larger canopy disturbance.

2.8 Conclusion

In conclusion, our data shows that small-scale disturbances influence the development of the old-growth *Hylocomium-Myrtillus* forest type located in Pallas-Ylläs

Tunturi National Park in north-eastern Finland, while large disturbance events are infrequently occurring at the century scale. According to the recent history disturbance reconstruction, the irregular distribution of gap creation through time and the absence of a distinct peak period of gap creation support a continuous occurrence of small gap disturbances since 1965. From this data, the rotation period was estimated at about 250 years. The long rotation period that we observed may be due to the low site productivity and the absence of insect outbreaks in this northern area.

According to the recent disturbance reconstruction, the results from this study suggest that forest management planning for *P. abies* dominated stands should be done over long rotations with several small cutting interventions in order to have the least impact. Such forest management is not economically sustainable, therefore more investigation would be needed about the past larger disturbance event of the 1810's which could allow a more rentable forest management and more sustainable for both the forest and the industry.

2.9 Acknowledgements

We are grateful to Volder Bulder, Hannu Herva, Juha Petäjäniemi and Jordana Soderman for assistance with the field work. Hannu Herva deserves additional thank for his dendrochonogical advice. Financial support was provided by NSERC. We would also like to thank Marilou Beaudet for her helpful comments.

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Table 2.1 Canopy fraction (%), time since first gap formation (year) and gap rotation (year) by transect and mean for the entire study area

Transect	Total open section (m)	Open aged section (m)	Oldest gap years	Rotation years
1	195.4	96.3	59	209.0
2	127.9	70.9	32	173.6
3	143.1	63.6	48	277.3
4	176.4	81.1	74	333.6
5	190.6	111.8	83	260.5
6	200.0	99.8	67	234.9
Mean	**172.2**	**87.3**	**60.5**	**248.2**
Stdev	27.3	16.9	16.9	55.8

Figure 2.1 Location of the study area in the Pallas-Ylläs Tunturi National Park, Lapland, Finland, in northern Fennoscandia forest.

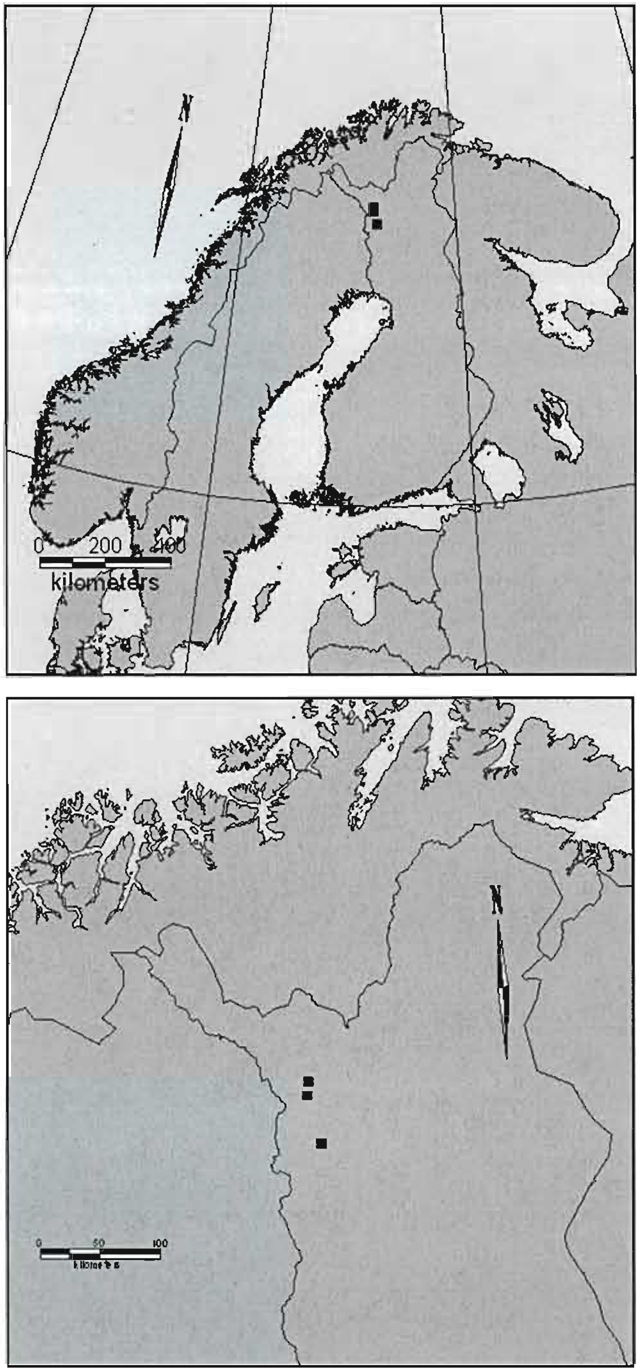


Figure 2.2 Percent growth change threshold with respect to prior growth for the top 10 percent growth changes in *P. abies*, where each dot represents a tree-ring. The triangles and the corresponding line represent the maximum %GC threshold, the circles and the corresponding line show 50% of the maximum threshold, and the squares and corresponding line set show 20% of the maximum threshold.

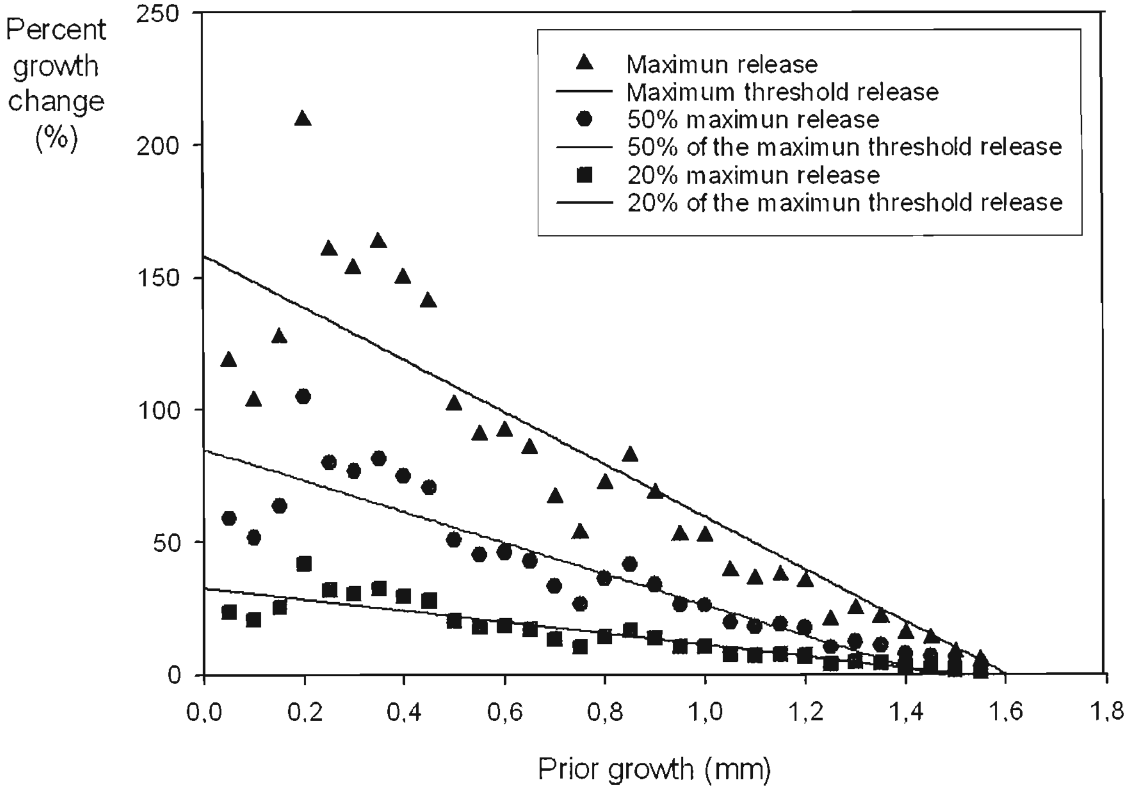


Figure 2.3 Temporal distribution of gap creation in five year classes for all transects combined (n = 59).

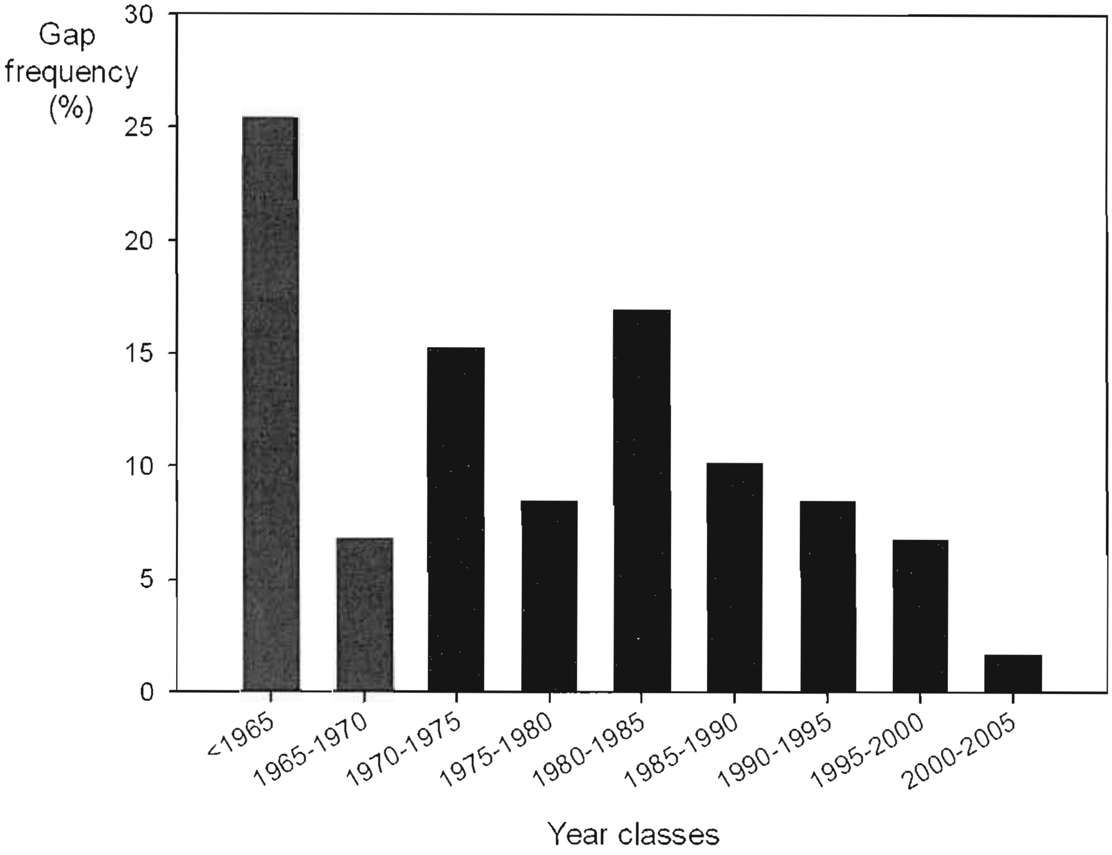


Figure 2.4 Temporal distribution of gap creation in five year classes by transect for the post 1965 period (Tr1: n =11; Tr2: n = 10; Tr3: n = 9; Tr4: n = 11; Tr5: n = 9; and Tr6: n = 9).

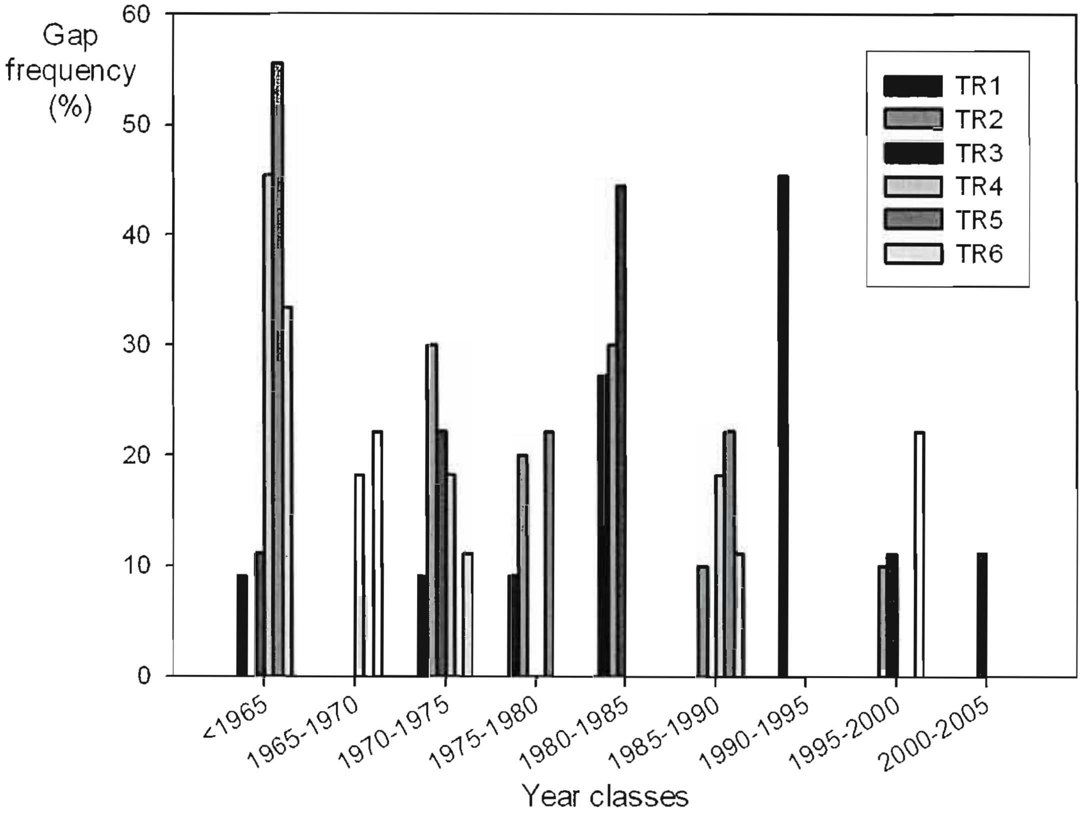


Figure 2.5 Percentage of gapmaker trees having a minimum age (i.e. number of ring widths per tree)

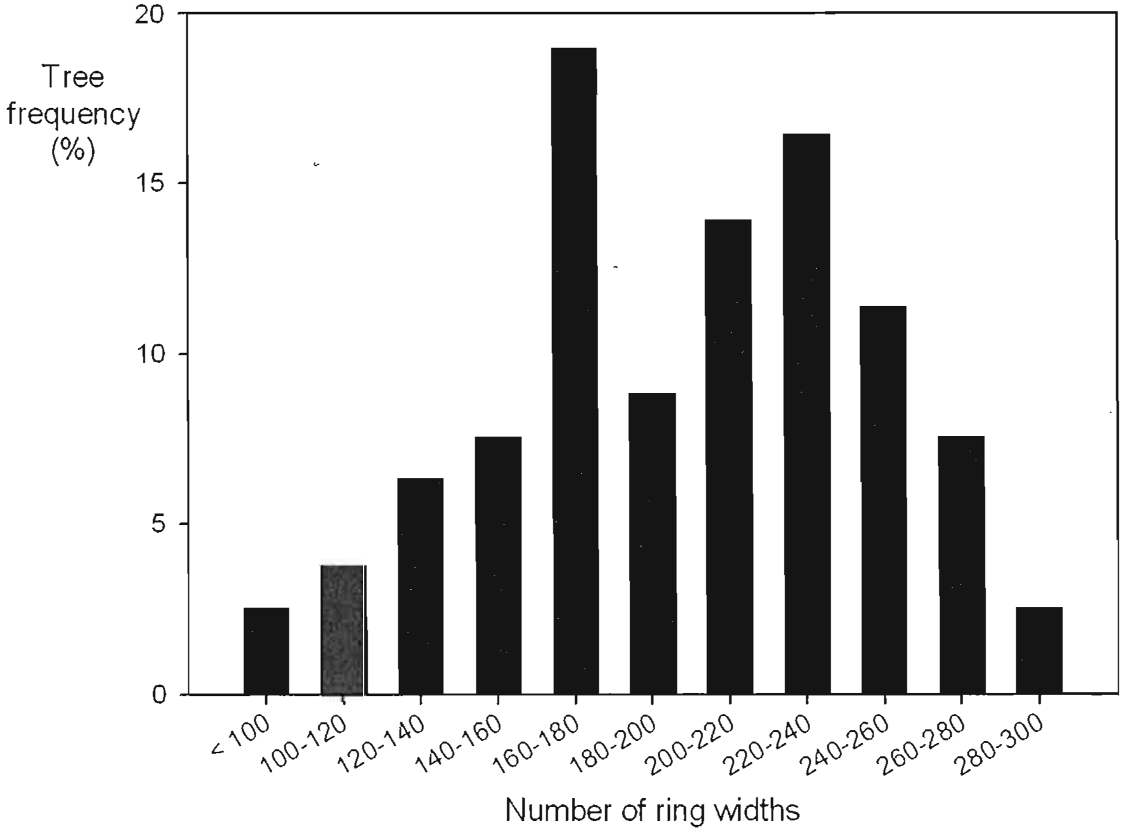


Figure 2.6: *Top graph*: Temporal distribution of moderate growth releases for all sampled gapmakers. *Bottom graph*: Number of sampled gap-makers that were alive during different time periods.

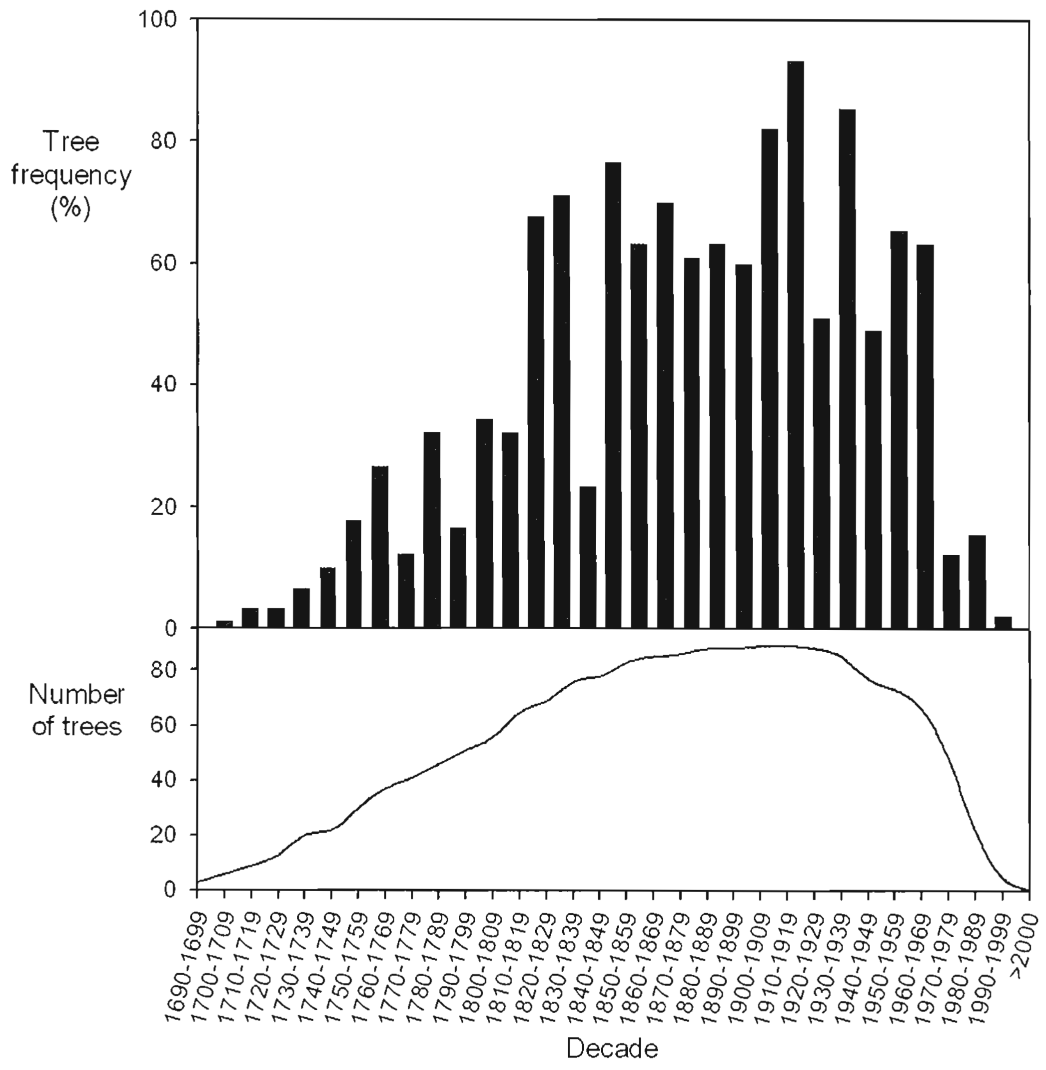


Figure 2.7 *Top graph*: Temporal distribution of major growth releases for all sampled gapmakers. *Bottom graph*: Number of the sampled gap-makers that were alive during the different time periods.

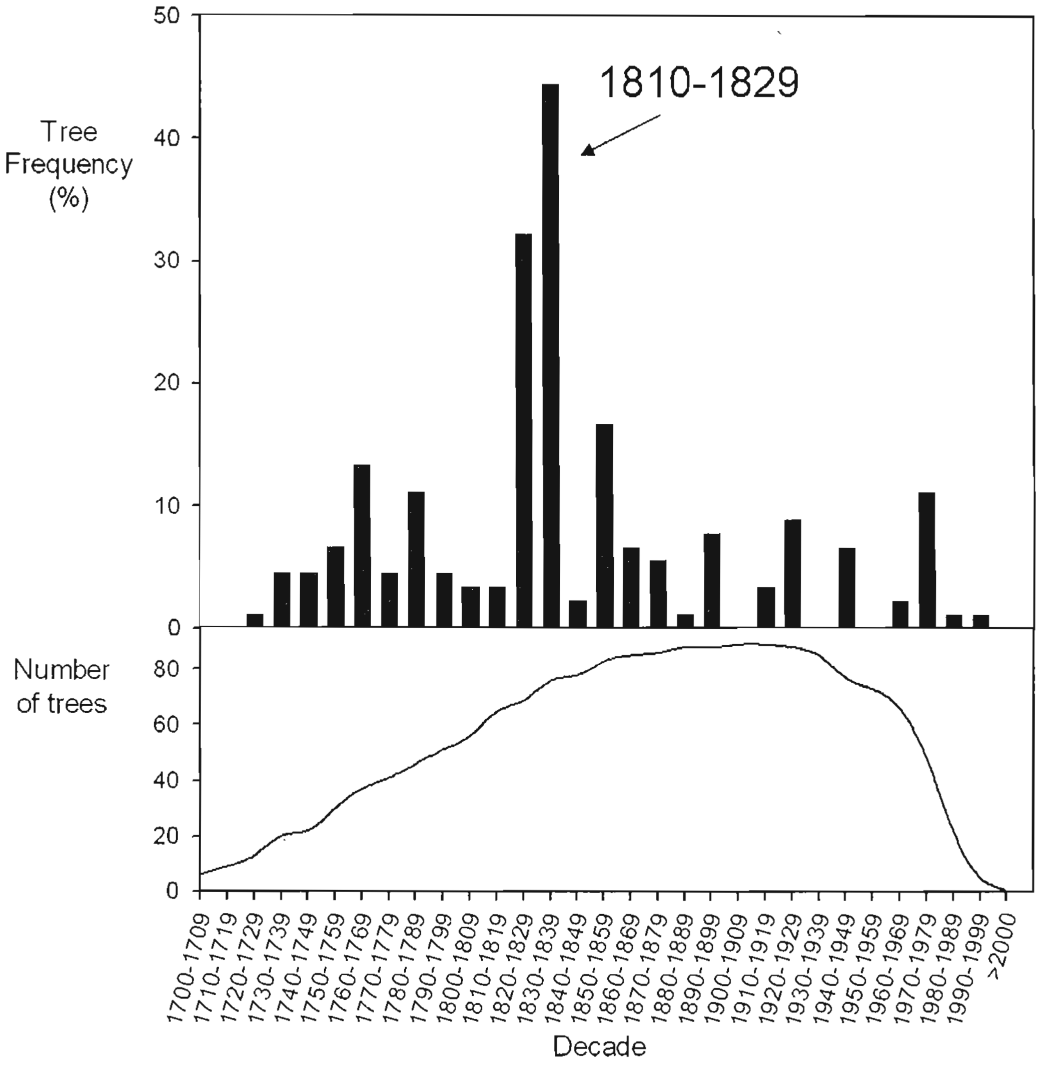


Figure 2.8 Temporal distribution of major growth releases of the sampled gapmakers in the six transects

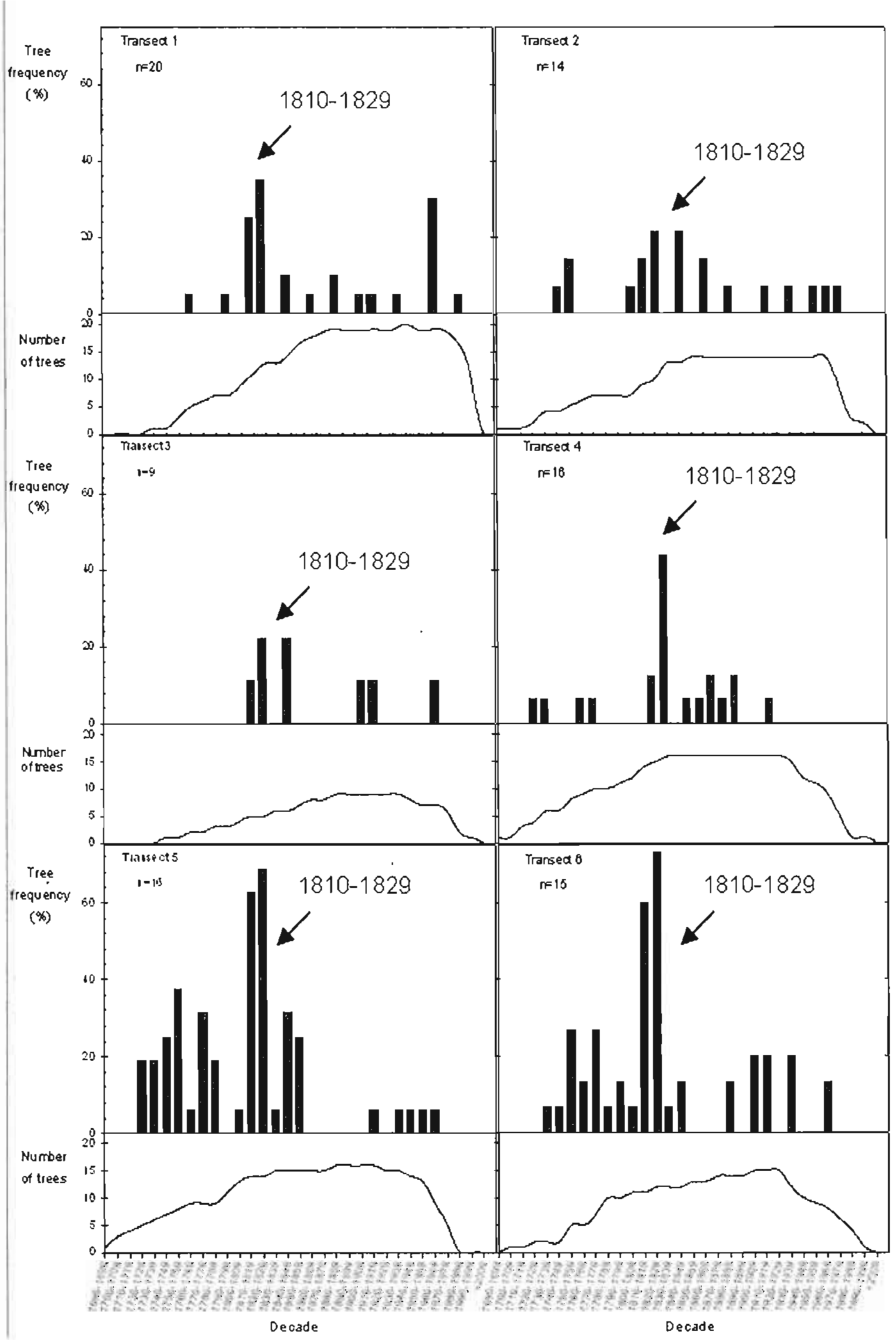
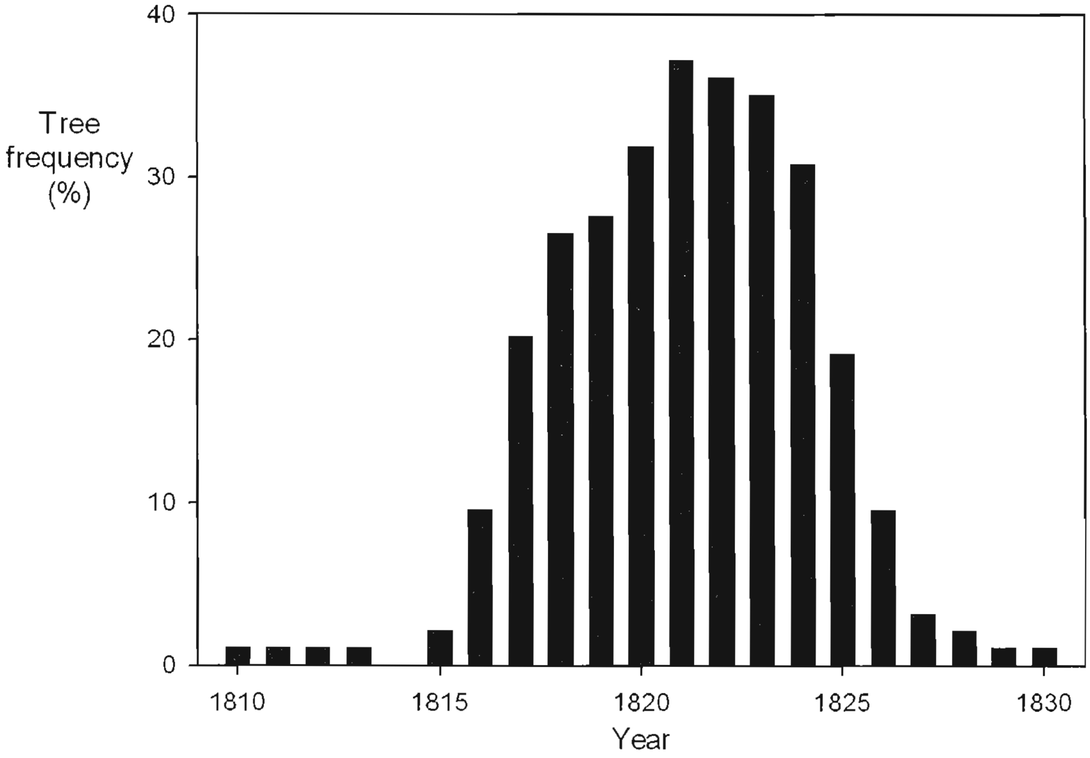


Figure 2.9 Temporal distribution of major growth releases of all sampled gapmakers for the period 1810-1830.



CONCLUSION GÉNÉRALE

Les attributs des trouées dans les peuplements de *Picea abies*

De façon général les attributs des trouées des peuplements de *P.abies* se distinguent des études faites jusqu'à ce jour à ce sujet en milieu boréale. Les différences reportées par cette étude ont apporté des précisions sur certains points déterminants de la dynamique de trouées. En autre, la localisation d'un peuplement semble être un facteur intrinsèque à la dynamique de trouées étant donnée que la localisation influence les composants d'un peuplement (ex. : la densité d'arbres, la productivité, la composition), et conséquemment cela détermine en partie le régime des perturbations. Dans notre cas, la localisation septentrionale de notre site d'étude a engendré la formation de grandes trouées bien que le nombre d'arbres créateurs de trouées par trouée respectait le seuil établi par Liu et Hytteborn (1991), c'est-à-dire de 1-10 individu(s). En fait, les sites nordiques sont caractérisés par une courte saison de croissance, de faible taux de croissances et un couvert de neige persistent qui font en sorte que les forêts sont faiblement peuplées (Lertzman *et al.* 1996). Cette plus faible densité entraîne une ouverture plus grande lors de la mort d'un arbre.

Les trouées sont engendrées par un nombre restreint d'individus et semblent se former selon une série d'événement de mortalité individuel étant donné les différents états de dégradation des arbres créateurs de trouées par trouées. Deux études canadiennes, Pham *et al.* (2004) et Lertzman et Krebs (1991) ont noté le même phénomène en forêt boréale au nord-ouest du Québec et en forêt subalpine en Colombie-Britannique, respectivement. La mortalité successive d'arbres au sein des trouées est consistante avec la littérature et suggère que les trouées s'agrandissent dans le temps en milieu boréale. De plus, la direction de chute des arbres créateurs sont influencé par la prédominance des vents sud-ouest. On peut supposer par conséquent que ces arbres étaient sénescent, voire déjà décédé, au moment de leur chute qu'une perturbation exogène, tel de fort vent, a engendré la chute des arbres.

Bien que la présence de régénération ait été notée dans la plupart des trouées, ceci ne supporte pas pour autant l'éventuelle fermeture des trouées. En effet, très peu de hautes régénérations ont été inventoriées. De plus, la présence de microsites ne semble pas être un facteur déterminant pour l'établissement de la régénération. La régénération devrait être étudiée plus finement afin de dégager les tendances du processus de recrutement des trouées de peuplement de *P. abies* à long terme.

La dynamique de trouées dans le temps dans les peuplements *Picea abies*

La caractérisation de la dynamique de trouées en forêt boréale demeure un sujet peu étudié jusqu'à ce jour. En utilisant la dendrochronologie, nous avons réussi à dresser un portrait sommaire de la temporalité de la dynamique de trouées dans les peuplements de *P.abies*. La distribution irrégulière des périodes de création de trouées et l'absence de pic distinct d'année créatrice de trouées supportent une occurrence continue de perturbation de petite envergure dont le temps de rotation est estimé à 250 années. Ces résultats s'opposent aux travaux de Périgon (2006) effectué dans des peuplements boréaux soumis à des perturbations de tordeuses des bourgeons de l'épinette où des pics de création de trouées ont suivi les années d'une épidémie, et où la rotation est beaucoup plus rapide. Conséquemment, l'agent principal de perturbation est un acteur important sur l'occurrence des trouées.

Bien qu'aucune perturbation de grande échelle connue n'ait pris cours sur le territoire, les patrons de croissances de plusieurs *P. abies* ont enregistré de forte reprise de croissance. La plus importante période de reprise de croissance eut lieu de 1810-1830, et culmina en 1821. Une perturbation intermédiaire est probablement tenue en cause.

En conclusion, nos résultats démontrent que la dynamique de trouées est continue dans le temps malgré son asynchronisme. Ces perturbations pour la plupart mineurs, sont toutefois suffisamment intenses pour engendrer des reprises de croissances majeures chez la plupart des arbres.

Implication dans l'aménagement

Selon nos résultats obtenus une foresterie durable dans les peuplements dominés par *P.abies* sous le développement et le maintien d'une dynamique de trouées requière à prime à bord un plan d'aménagement sur une longue rotation de l'ordre d'au moins 200 ans. La mortalité espacée dans le temps et l'espace supporte l'application de coupe sélective des arbres matures et surannés. Comme le bois mort fait partie intégrante de la structure, une quantité de bois mort debout et couché devrait demeurer lors des interventions sylvicoles. De plus, étant donné que la régénération semble s'établir difficilement à long termes, protéger la régénération s'avère nécessaire. Toutefois, une telle sylviculture serait peu viable économiquement, ainsi la conservation de ces forêts semblent être l'aménagement le plus sage à effectuer.

Dans le cadre de la restauration de forêt dégradée, le temps est la meilleure prescription afin de retour à l'état de vieux peuplement. Par contre, mettre en place des dispositifs qui accélérait l'établissement d'espèces de second cohorte peut réduire le temps nécessaire à l'atteint de cette état. Dans le cadre de notre étude, l'établissement de *P.abies* naturelle ou plantée peuvent accélérer un peu le processus de revitalisation.

Projets futurs

Cette étude a permis de décrire les principaux attributs de la dynamique de trouées dans les peuplements de *P.abies* du nord de la Finlande. Nous avons pu constater que même si la dynamique de trouées permet le maintien d'une structure irrégulière et inéquienne, les attributs des trouées ne sont pas nécessairement semblables d'un type de peuplement à un autre. Donc, il est important de bien caractériser les trouées selon le type de forêt avant d'élaborer des généralités. Toutefois, il reste encore des éclaircissements à faire sur le régime de perturbation des peuplements de *P.abies* du nord de la Finlande, mais aussi sur les régimes de perturbations d'autres régions boréales. Ainsi de futurs travaux de recherches pourraient porter en autres sur : 1) l'évaluation du temps de fermeture d'une trouées ; 2) l'identification des composantes des peuplements boréaux qui influencent principalement les attributs des trouées, tel que la densité d'arbres, les espèces, la classe diamétrale, le type sol; 3) le suivie à long terme du recrutement sur la compétition intra et extra-spécifique 4) une évaluation de la faisabilité de reproduire la dynamique de trouées, ou encore 5) l'identification des espèces fauniques et floristiques dont la survie est lié avec la dynamique de trouées. Ainsi, la dynamique de trouées engendre une foule de mécanisme écologique complexifiant la dynamique de peuplements.

APPENDICE A

Information relating to the study transects

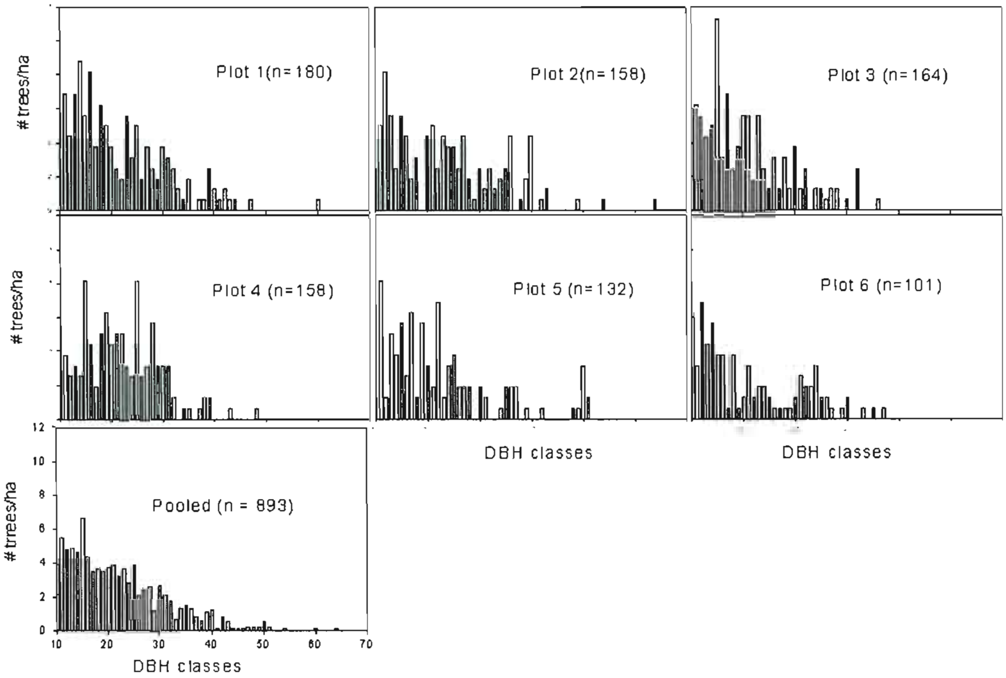
Table A1 Table about stand, gap and tree recruitment characteristics of the six study transects.

	TRANSECT					
	1	2	3	4	5	6
Stand level						
Living stem density (trees/ha)	516.9	472.5	490,0	446.25	365.6	450.6
Dead stem density (trees/ha)	112.5	98.8	102.5	98.8	82.5	69.8
Living basal area (m^2/ha)	15.5	14.9	13.9	12.9	19.4	16.6
Dead basal area (m^2/ha)	4.9	5.1	9	4	4	2.8
Living wood volume (m^3/ha)	101.9	104.2	90.8	84.6	125.5	119.3
Dead wood volume (m^3/ha)	14.7	18.5	15.6	15.1	12.2	12,0
Ratio livng/dead trees	0.22	0.21	0.21	0.22	0.22	0.15
Importance value						
Living spruce	68	68	69	60	84	79
Living birch	29	29	30	31	15	12
Living other species	3	3	1	9	0	9
Dead spruce	62	65	56	65	59	66
Dead birch	37	22	42	19	41	32
Dead other species	1	14	1	16	0	2
% area in canopy gaps	48.9	32.0	35.8	44.1	47.7	50.0
% area in expanded gap	abs	42.1	45.4	55.1	63.2	61.3
% area of developmental gap type	82.6	95,0	95.24	90.9	90.9	94.7
% area of other gap type	17.4	5,0	4.8	9.1	9.1	5.3
Number of intercepted gap	24	20	21	22	22	19
% gaps < 100m^2	39.1	20.0	19.1	9.1	13.6	5.3
% gaps < 300m^2	87.7	95.0	76.2	90.9	77.3	79.0
Gap level						
Mean gap size (m^2)	153.7	164.8	235.5	254.5	237.2	294.8
Median gap size (m^2)	113.3	162.2	170.2	202.2	203.6	249.5
Range gap size (m^2)	25-514	49-401	70-693	75-1599	55-855	91-1060
Total gapmakers	97	68	80	102	93	116
Average # of gapmakers/gap	4.3	3.4	3.8	4.7	4.2	6.1
Range of # of gapmaker/gap	1-13	1-8	2-7	0-8	0-12	1-20
% of spruce gapmakers	75.26	86.76	70,0	77.45	64.52	67.24
% of birch gapmakers	23.71	8.82	30,0	12.75	35.48	30.17
% of other gapmaker spp	1.03	4.41	0,0	9.8	0,0	2.59
Tree recruitment level						
Average recruitment trees/gap	18.6	12,0	15.3	14,0	53.5	30.3
Range of recruitment tree/gap	5-40	6-22	4-38	5-32	4-162	9-58
% spruce recruitment	97.3	91.7	98.4	89.3	91.6	97.8
% birch recruitment	2.7	8.3	1.6	7.1	4.7	0,0
% pine recruitment	0,0	0,0	0,0	3.5	0,0	1.1
% other species recruitment	0,0	0,0	0,0	0,0	3.7	1.1

Table A2 The location of the study transects. The coordinates are taken from the kkj national grid coordinate system of Finland. Kkj stands for Kartastokoordinaattijärjestelmä.

			Distance (m)			
	0		200		400	
Transect	**Latitude**	**Longitude**	**Latitude**	**Longitude**	**Latitude**	**Longitude**
1	7509929	2516348	7509736	2516357	7509540	2516362
2	7510122	2516366	7510092	2516560	7510061	2516759
3	7509636	2516302	7509660	2516108	7509697	2515916
4	7510226	2515606	7510240	2515410	7510239	2515209
5	7550108	2503200	7549997	2503368	7549880	2503529
6	7562007	2504231	7561821	2504316	7561632	2504367

Figure A3 The DBH distributions of living trees for each transect.



APPENDICE B

L'Évaluation de deux méthodologies pour déterminer la taille des trouées

B1 Introduction

L'estimation de la surface d'une trouées est fréquemment établie selon la formule de l'ellipse, soit la méthode établie par Runkle (1982, 1992) dans la forêt de feuillues du nord-est des États-Unis. Cette méthode consiste à mesurer la plus longue portion d'une trouée (A_{majeur}) avec sa plus longue perpendiculaire (A_{mineur}), et d'utiliser la formule de l'ellipse (aire d'une ellipse = π (A_{majeur} * A_{mineur}) / 4) pour déterminer la surface approximative de la trouée. Toutefois, l'ellipse peut ne pas convenir pour les trouées de forme irrégulière, c'est-à-dire non-elliptique (de Lima, 2005; Kneeshaw et Bergeron, 1998).

B2 Méthodologie

Afin de déterminer si la formule de l'ellipse convient, nous avons comparé la méthode de Runkle avec une méthode alternative dans un peuplement de *Picea abies* (L. Karst) du nord de la Finlande. La méthode alternative consistait à cartographier chaque arbre délimitant une trouée et de calculer l'aire de la surface à l'aide d'ARCVIEW. L'hypothèse était que la méthode de l'ellipse mal-estime la dimension réelle des trouées par rapport à la méthode cartographique. Avec la technique de l'ellipse, une trouée peut avoir des portions excédantes ou incluses dans la délimitation de l'ellipse (fig. B1). En cartographiant les arbres, il serait donc possible réduire l'erreur d'estimation de la surface d'une trouée.

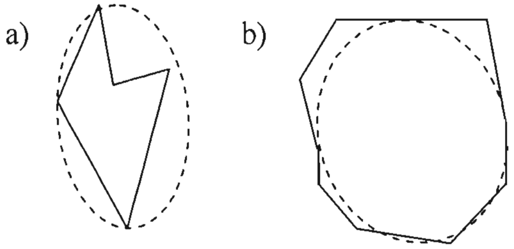


Figure B1 Schéma de deux situations d'évaluation de la surface d'une trouée. Les lignes noires continues délimitent les trouées et les lignes noires pointillées représentent la surface estimée selon l'utilisation de la méthode l'ellipse. La figure a) démontre une surestimation tandis qu'en b) l'ellipse sous-estime la trouée.

L'expérience fût effectué sur six transects linéaires comptant entre trois et quatre trouées chacun, pour un total de 22 trouées. La cartographie de ces arbres s'est effectué à l'aide d'un Vertex et d'un compas le long de six transects linéaires de 400 m selon une coordonnée X qui correspondait à la distance sur le transect et une coordonnée Y qui représentait la profondeur en relation avec le transect. Chaque coordonnée métrique (X, Y) a par la suite été géo-référencée par rapport à la coordonnée géographique du point de départ du transect mesuré avec un appareil GSP. Un test de 't' pairé (PROC MEANS, SAS 9.1) a été employé pour déterminer si la différence de surface obtenue par les deux méthodes étaient significativement différentes de zéro.

B3 Résultats et Discussion

Selon le test de 't', la différence entre la méthode de Runkle et la méthode cartographique est non-significative (t = -0,56; p = 0.5806) bien que les deux méthodes ont généré des valeurs différentes. Malgré l'absence de différence entre les méthodes, la distribution semble tendre vers l'obtention d'une valeur plus grande avec la méthode de Runkle. Une étude menée par de Lima (2005) en forêt tropical a aussi enregistré des valeurs plus grandes avec Runkle en comparaison avec la méthode des triangles et la méthode de Brokaw (1985). Il est donc possible que la méthode de l'ellipse donne une estimation plus élevée qui se fait ressentir plus fortement en forêt tropicale qu'en forêt boréale. Une étude exhaustive des différentes techniques dans des écosystèmes distincts pourraient éventuellement y trouver une relation. Pour le moment, Runkle semble entraîner une surestimation indépendamment de l'écosystème.

Toutefois, de par sa facilité d'utilisation sur le terrain et sa rapidité à être calculer, la méthode de Runkle est plus commode que la méthode de cartographie pour estimer la surface d'une trouée en forêt boréale.

B4 Références

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APPENDICE C

Tree spatial arrangement in old-growth *Picea abies* stands of northern Finland

C1 Introduction

Natural disturbances change forest tree spatial patterns. Even though, natural disturbances vary in time and space, they alter tree distribution into three possible arrangement patterns: cluster, regular or random Tree arrangement has a direct influence on both the vertical and horizontal stand structure. Consequently, quantifying and qualifying tree spatial arrangements become a tool in understanding the influence brought by disturbances on stand development (Koukoulas & Blackburn 2005). For instance, it was observed that tree spatial relationships and tree species associations in the boreal mixed-wood were changing depending on the time since the last fire (Park *et al.*2005).

As an explorative study, we evaluated tree spatial arrangement patterns of old-growth *Picea abies* stand of northern Finland which develops under gap dynamics disturbance. Using both univariate and bivariate Ripley's test, we analysed tree patterns based on tree states (living, dead), DBH-class (small, medium, large) and species. The general objective of this analysis was to evaluate whether tree spatial arrangement patterns are the legacy of past gap disturbances.

C2 Methods

C2.1 Study sites

The study took place in northern Finland in the National Park of Pallas-Ylläs Tunturi (67°30-67°44' N, 24°00-24°55'E), which extends over 1020 km^2 (Fig 3.1). The northern location of Pallas-Ylläs Tunturi National Park limits the growing season to 100-140 days. The mean annual temperature is around -0.8°C and the annual amount of precipitation is about 500 mm with 45% of it falling as snow (Varmola *et al.* 2004). The park counts many lakes and is surrounded by rocky mounts with the highest elevation being Pallas Tunturi which culminates at 807 m. Protected by the Finnish government since the mid 1930's, neither past nor recent forestry activities have taken place inside the park zone.

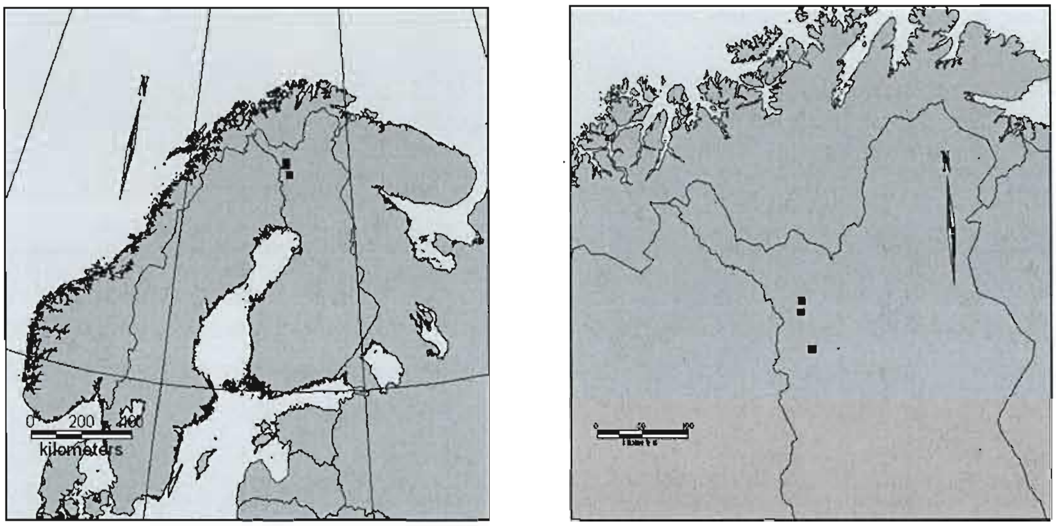

Figure C1 Location of Pallas-Ylläs Tunturi National Park in northern Fennoscandia.

Located in the northern Fennoscandian boreal vegetation zone (between N65° and N68°), Pallas-Ylläs Tunturi National Park is also part of the Peräpohjola vegetation subdivision (Ahti *et al.* 1968). Soil in this area originates from a glacial till and tends to podzolize easily, which promotes the accumulation of raw humus in the most mesic sites (Bonan & Shugart 1989); giving rise to the *Hylocomium-Myrtillus* type of forest (HMT) (Norokorpi 1979; Ahti *et al.* 1968). The high moisture of HMT forest favours the establishment of *Picea abies* (L. Karst), which is the dominant species (at about 70%) followed by *Betula pubescens* Ehrh (20 to 30%) and *Pinus sylvestris* L. (< 5%) (Essen *et al.* 1997; Norokorpi 1979). The shrub layer includes *Sorbus aucuparia* L. and *Salix caprea* L., while the dwarf-shrub layer is dominated by both *Vaccinium vitis-idaea* L. and *V. myrtillus* L. (Esseen *et al.* 1997).

C2.2 Measurements

A plot of 40 x 400 m (1.6 ha) was set at each site, for a total of 9.6 ha of forest inventoried. Both live and dead trees were mapped by using a metric tape, a VERTEX and a compass. The metric tape measured the X coordinate, and the VERTEX determined the Y coordinates. The compass ensured the perpendicularly between the metric tape and the tree. We identified and measured both the DBH (at the nearest 1 cm) and the height (at the nearest 0.1 m) of every mapped live and dead tree having a DBH over 9 cm. For dead trees, only the height of the standing portion was taken.

C2.3 Ripley's Univariate analysis

Univariate analyses were performed to evaluate dispersion pattern of one specific variable at the time. Ripley's K univariate function is based on a point pattern approach which describes the spatial pattern distribution of individual base on a two-dimensional distribution patterns (Haase 1995; Diggle 1983). The detected spatial patterns are random, aggregated or regular.

Basically, univariate analysis counts the number of neighbouring points present in a circular window for each individual point. The quantity of neighbours 'n' for a't' radius gives the tree density (λ) of an area 'A'. Tree density corresponds to λ=n/A. Ripley's K function evaluates the expected number of individuals for an arbitrary individual for a radius't'. This expected value becomes the comparison reference with the actual data. Under Complete Spatial Randomness (CSR), the K function = πt^2, the circle surface, which means that each tree location is completely independent from the others. Thus, CSR correspond to the null hypothesis according to the Poisson distribution. However, to simplify the K-function and facilitate the interpretation, the square root is extracted to linearise the equation, and then the radius't' is subtracted in order to have a reference point of 0. Using this transformation, the obtained equation becomes the L-function: L (t) = k½-t. Thus, L(t) equals 0 for a CSR, whereas clustering corresponds to a value greater than 0 and regularity is indicates by a value lower than 0.Monte Carlo techniques have been used to evaluate the confidence interval at 95%, where several iterations are done to best evaluate the interval of confidence.

In the study, Ripley's univariate analyses were performed on the living and dead trees, and the species spatial dispersion in a radius of 20m. Living trees were split into 3 DBH-classes: small, medium and large which correspond to [10-18[cm, [18-26[cm and [26 + cm, respectively. Dead trees were not subdivided into DBH classes.

C2.4 Ripley's Bivariate Analysis

Bivariate analysis is an extension of the univariate Ripley's K-function, which allows the analysis of the interaction between two populations (1 and 2) inside a plot. $K_{12}(t)$ calculates the number of individual of the population within an arbitrary radius 't' with the population 1. For ease of interpretation, $K_{12}(t)$ is transformed into $L_{12}(t)= (k/\pi)$ ½-t. As the univariate Ripley's K-function, the null hypothesis of the population independence is expected to be a circle, L_{12} (t) equals 0 for CSR, greater than 0 for segregation and lower than 0 for repulsion. Confidence is also calculated with the Monte Carlo technique at 95%.

Bivariate analyses were performed between the three DBH-classes and dead / living trees under the labelling classification, while species were evaluated under the independent events.

C3 Results and Discussion

C3.1 DBH-Classes

Clustering tree patterns are decreasing as trees get bigger (Table C1). The small DBH tree-class showed the strongest clustering patterns among the three DBH-classes, and this occurred over a wide range of radii, for instance from 1 m to 19 m. The medium DBH tree-class had a few clusters, and those were restricted to 1 m radius. Finally, the largest DBH class exhibited a random tree distribution in most cases, even though regular patterns have been detected at a few radii inside two plots.

Table 1C: Univariate Ripley analysis for the three DBH classes: small [10-18 [cm, medium [18-26 [cm and large [26 + cm. + cells indicate statistically significant cluster, - cells indicate over-dispersed, and empty cells indicate CSR.

Transect	DBH classes	n	Distance (m)																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Small																					
1		443	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
2		379	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	
3		474	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
4		415	+	+		+				+												
5		185	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
6		322	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
	Medium																					
1		264	+		+					-												
2		263	+																			
3		204	+																			
4		207	+																			
5		172	+	+	+		+			+		+	+	+	+	+	+	+	+	+	+	+
6		242																				
	Large																					
1		119																				
2		111																			+	+
3		106												-	-	-	-	-	-			
4		92							-													
5		227																				
6		156																				

Spatial association between DBH-classes becomes progressively repulsed as the difference between the DBH-class increases (Table 2C). For instance, small and medium DBH were attracted while small and large trees showed repulsion in most cases. The relationship between medium and large trees was mainly random with some scatter repulsion.

Table 2C: Bivariate analysis between the three DBH classes: small [10-18 [cm, medium [18-26 [cm and large [26 + cm. + cells indicate statistically significant attraction, - cells indicate repulsion, and empty cells indicate no-pattern.

Transect	DBH classes	n	Distance (m)																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	small vs med																					
1		707	+	+	+																	
2		642	+	+																		
3		678	+	+																		
4		622					-	-														
5		357	+	+	+	+																
6		564	+	+	+	+																
	small vs large																					
1		562	+				-			-	-	-	-	-	-	-	-	-	-	-	-	-
2		490			-	-	-	-	-	-		-			-			-	-	-	-	
3		580				-	-	-														
4		507																				
5		412						+	+													
6		478			-		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	medium vs large																					
1		383																				
2		374																				
3		310																				
4		299				-	-	-	-													
5		399																				
6		398					-	-														

The tree arrangement patterns based on the DBH size classes tend to support the gap filling process. For instance, once a gap is created many individuals get established inside it because of the new available resources which can be detected by the formation a cluster of small trees. But after time, competition takes place among gap fillings, and only a few trees get to the canopy level, which led to a decreasing of clustering as tree get larger. Furthermore, the repulsion between small and large trees support the gap filling process as smaller tree should be found in younger gap and the larger trees are more likely to be present in older gap which might have totally disappeared. Following the size spatial patterns over the years could provide a better comprehension of the gap filling process.

C3.2 Tree species

Both spruces and birches showed aggregation tree arrangement patterns and on a wide array of radius (Table C3). But, the two species together are attended to show repulsive interaction (Table C4).

Table C3: Univariate analysis about the spatial distribution of the spruces and the birches. + indicates statistically significant cluster, - over-dispersed, and empty cells indicate CSR.

Transect	Species	n	Distance (m)																			
			1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Spruce	545	+	+	+	+	+															+
2		480	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
3		502									+		+	+	+		+			+	+	+
4		407																				
5		464	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
6		560	+	+	+	+	+	+	+	+	+	+	+									
	Birch																					
1		275	+	+	+	+	+															
2		263	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
3		276	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
4		269	+	+	+	+			+												+	+
5		118	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+
6		114	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+	+

Table C4: Bivariate analysis about the spatial relationship between spruce and birches. + cells indicate statically significant attraction, - cells indicate repulsion, and empty cells indicate no-pattern.

Transect	Species	n	Distance (m)																			
	Spruce vs birch		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1		820							+					+	+	+						
2		743							-	-	-	-	-	-	-	-	-	-	-	-	-	-
3		778		-									+		+			+				
4		676			-																	
5		682						-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6		674	-	-	-	-	-	-	-		-											

Even though both species clustered on an individual basis, birch appeared to have a greater ability to grow into cluster. The inefficiency of spruces to asexually reproduce might be reflected by the lower occurrence of cluster patterns compare to birch which stem sprout easily. Besides the reproductive ability, birch aggregate on longer radius which might show the shade intolerance of this species compare to spruce.

The repulsion between the two species might reflect the reproductive ability behaviour of each species or some sort of allelophatic relationship between the two. However, the species spatial arrangement patterns do not supply any information about the influence of the gap dynamics of the species trees spatial distribution. A fire chronoséquence could may be have provide more information about the species spatial patterns such as Park *et al.* (2005) studied in mixed-wood boreal forest of western Quebec. Canada.

C3.3 Tree states

Aggregations of dead trees were seldom with no specific trend among the six transects (Table C5). This randomness of tree mortality distribution suggests that death is not contagious in space, which supports the fact that this region does not experience large scale disturbance. However, the restricted mortality in space does not allow to drawn any information about the timing of mortality. But from field observations base the variety of DBH and state of decay of dead trees encountered, we suppose that mortality is continuous in time.

Table C5: Univariate analysis about the standing dead trees. + indicates statically significant cluster, - over-dispersed, and empty cell indicate CSR.

Transect	Distance (m)																			
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	+	+	+	+										+	+			+	+	+
2				-																
3	+	+	+	+																
4	+	+																		
5	+	+		+		+	+	+	+	+										
6																				

Living and dead trees had an attractive relationship decreasing as the DBH of the living trees increased (Table C6). For instance, we recorded the highest number of dead and living tree associations with both small and medium trees (14 for each DBH class), while large living trees had a few associations with the dead trees. However, repulsion arrangement patterns between living and dead trees were seldom, only one transect recorded repulsion patterns.

Table C6: Bivariate analysis between dead trees against the three DBH classes of living trees. + indicates statically significant attraction, - repulsion, and empty cell indicate no-pattern. All analyses were performed with a confidence interval of 95%.

Transect	DBH classes	Distance (m)																			
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
	Small																				
1		+	+	+	+																
2		+	+																		
3		+	+	+																	
4		+	+																		
5		+	+	+																	
6																					
	Medium																				
1		+	+	+	+	+															
2		+	+	+															+	+	+
3		+			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4																					
5				+	+																
6																					
	Large																				
1						+															
2		+	+																		
3																					
4																					
5			+	+																	
6																					

Such trend of decreasing association patterns between dead and growing living trees were reported by in another study by Dovciak *et al.* (2001) in mixed-wood forest of the western Great Lakes region, USA. But rather than using DBH, the decrease of tree agglomeration patterns were detected from the increasing trees height (Dovciak *et al.* 2001). This relationship might be magnified by the decrease number of large living trees, but it also tells that trees get establish near a dead trees in a gap developing stand. Thus, the interaction between dead and living trees supports the presence of gap dynamics where dead trees represent an available growing space.

C4 Conclusion

Past gaps were possible to be redrawn with the use of spatial analysis of tree characteristics base on tree size and states. Species could not provide much information about past gaps. Thus, our results demonstrated that gap dynamics does influence the tree spatial distribution. The emulation of gap dynamics in HMT forest would require a single-tree selection system. Park *et al.* (2005) came to the same proposition following their study in the boreal-mixed forest at Lake Duparquet in northweastern Quebec. However, the single-tree selection cutting would also need to consider the gap regime.

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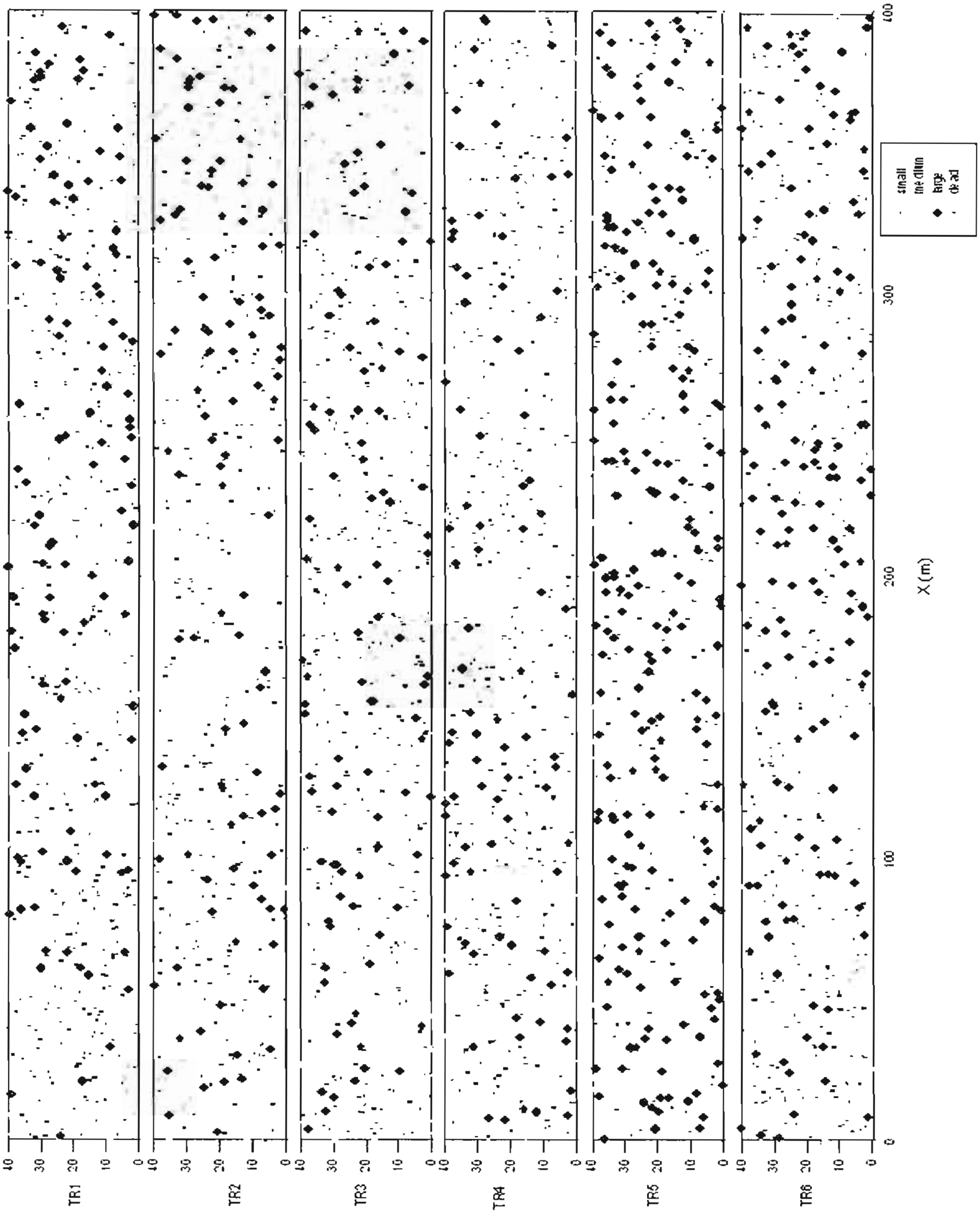
APPENDICE D

Graphical representation of the DBH-classes of living and dead trees



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