UNIVERSITÉ DU QUÉBEC À MONTRÉAL

EFFETS DES ÉPIDÉMIES DE LA TORDEUSE DES BOURGEONS DE L'ÉPINETTE SUR LA DYNAMIQUE DE LA RÉGÉNÉRATION DANS LA FORÊT BORÉALE DU NORD-OUEST DU QUÉBEC

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RÉSUMÉ

Les épidémies de la tordeuse de bourgeons de l'épinette (TBE) constituent la principale perturbation naturelle entre deux feux successifs dans les forêts boréales de l'est du Canada. Des intervalles plus longs entre les feux et l'utilisation de la régénération préétablie pour régénérer les forêts exploitées favorisent une augmentation de l'importance du sapin baumier l'hôte de la TBE. Un effet croissantdes épidémies de la TBE sur la dynamique de nos forêts est ainsi attendu.

Suite à la mortalité des arbres adultes, le recrutement des semis vers les strates supérieures assure la fermeture des trouées. La connaissance de la réponse de la régénération aux trouées permettrait donc une meilleure compréhension du rôle de la TBE dans le développement de la forêt. En Abitibi, le lieu de l'étude, dû au régime de feu, les forêts issuent des feux possèdent des peuplements d'âges et de compositions très variables, ce qui leur confèrent différents niveaux de vulnérabilité à la TBE. Il devient donc nécessaire de caractériser l'effet des épidémies de la TBE et la réponse de la régénération préétablie selon les différentes stades successionels.

Ainsi, le premier chapitre de cette thèse vise à déterminer les facteurs écologiques qui influencent l'abondance de la régénération préétablie selon les différents stades de développement de la forêt. Les résultats indiquent que les facteurs abiotiques sont faiblement corrélés à la densité des semis de la plupart des espèces. Par contre, les facteurs biotiques tels que la surface terrière des semenciers, le recouvrement arbustif et la présence des trouées sont liés à l'abondance de la régénération coniférienne. De plus, les semis de sapin baumier et d'épinette blanche sont plus abondants dans les peuplements mixtes d'âge intermédiaire que dans les vieux peuplements conifériens. La quantité de semis d'espèces intolérantes à l'ombre demeure quant à elle faible mais constante à travers les stades successionels. Seul l'abondance du thuya augmente avec la durée du temps après feu. Dans les vieux peuplements conifériens, les trouées causées par la TBE sont grandes, ce qui pourrait permettre le maintien du recrutement des espèces intolérantes à l'ombre.

Le deuxième chapitre a pour objet la caractérisation des régimes de perturbations par les trouées et son influence sur la succession. Un échantillonnage des trouées montre que l'abondance et la superficie de ces dernières sont proportionelles à l'abondance des adultes de sapin baumier ainsi qu'au temps écoulé depuis le dernier feu. Une importante régénération du sapin baumier est aussi associée à des trouées de petites dimension. La modélisation de la succession grâce à des matrices de transition suggère que le sapin remplacera le tremble dans les petites trouées de la forêt de feuillus, mais que dans les grandes trouées des vieilles forêts conifériennes, les feuillus réussiront à se maintenir et que le thuya deviendra plus abondant.

Une étude portant sur la réponse du sapin baumier à des trouées expérimentales est presentées dans le troisième chapitre. Une série de trouées expérimentales ont donc été créés

présentant différents degrés d'ouvertures de la canopée (témoin, annelage des conifères, coupe de conifères, et coupe totale) de 10m x 10m ont été répliqués dans quatre forêts d'âge et de composition différents. Aucun des traitements n'a eu un effet significatif sur le recrutement de nouveaux semis de sapin. Ceci suggère que l'impact des trouées se répercute surtout au niveau de la régénération préétablie. Même un an après les traitements «coupe conifère» et «coupe totale», les semis ont enregistré une hausse significative de leur accroissement en hauteur et une modification importante de leur architecture. En raison du délai entre le traitement « annelage » et la formation de la trouée, la réponse des semis était plus lente que celle suite aux coupes. La vitesse de la formation des trouées après une épidémie devrait donc aussi avoir un effet sur la réponse des semis.

Dans le chapitre quatre nous présentons les résultats d'une étude des patrons spatiaux et temporels de recrutement à l'intérieur de trouées formées durant la dernière épidémie de TBE dans la forêt la plus affectée. Les résultats montrent que les semis des espèces hôtes pour la TBE s'installent non seulement avant l'épidémie mais aussi durant et après celle-ci. Ce phénomène est probablement dû à la présence de quelques arbres qui survivent à l'attaque de la TBE. Le bouleau s'installe durant la formation de la trouée et le tremble surtout après une ouverture complète. Spatialement, la probabilité de trouver le tremble est plus élevée à la lumière directe au nord de la trouée, tandis que le sapin se retrouve dans l'ombre, au sud de la trouée. L'espèce compétitrice la plus importante, l'érable à épis, limite cependant l'abondance du sapin. En effet, le nombre de semis de sapin diminue avec la proportion d'érable à épis dont le recouvrement est plus important dans les grandes trouées.

L'ensemble des résultats suggère que les grandes trouées formées suite aux épidémies de la TBE sont importantes pour le maintien des espèces intolérantes à l'ombre dans les vieilles forêts. Ces espèces, en particulier le tremble, sont associées avec la région nord de la trouée, où la lumière directe se retrouve. Cependant, à cause du faible angle d'incidence de la lumière et de la formation lente des trouées causées par la TBE, les périodes et les zones de lumière directe sont limitées. C'est en partie pourquoi le sapin, dû à sa tolérance à l'ombre, demeure l'espèce la plus abondante. Seul le thuya semble être capable de déplacer le sapin. Ceci s'explique par sa tolérance à l'ombre mais aussi par sa longevité et par le fait que cette espèce n'est pas un hôte de la TBE. Nos résultats confirment que le thuya augmente en abondance et en proportion dans les vieux peuplements. L'interaction avec les arbustes, surtout l'érable à épis, affecte aussi l'abondance des différentes espèces.

INTRODUCTION GÉNÉRALE

Les perturbations à grande-échelle sont reconnues, depuis longtemps, comme facteur contrôlant la dynamique de la forêt boréale. Parmi ces perturbations, le feu est généralement celui qui influence le plus le développement de l'écosystème boréal (Rowe 1961, Rowe et Scotter 1973, Heinselman 1973, 1981, Bergeron 1991, Johnson 1992). Cependant, dans l'est du Canada, entre Terre-Neuve et l'ouest de l'Ontario, la tordeuse des bourgeons de l'épinette (TBE) apparaît comme un élément important de perturbation à grande échelle (Blais 1983, MacLean 1984, Baskerville 1975, Kettela 1983).

La dynamique des forêts suite à une épidémie devient plus complexe lorsqu'on quitte les sapinières relativement pures des maritimes pour atteindre les forêts comportant une diversité arborescente plus élevée en Ontario et dans l'ouest du Québec. D'une part, la variation en espèces est plus élevée et d'autre part, le régime de perturbations est davantage complexe en raison de l'importance des feux. À ce jour, l'interaction entre le temps depuis le feu et l'impact des épidémies sur la dynamique des peuplements n'a pas été étudié.

0.1 Impacts des épidémies de TBE

L'alimentation de la TBE, dans l'est de l'Amérique du Nord, est constituée, en ordre de préférence, du sapin, des épinettes blanche, rouge et noire. La défoliation occasionnée par la TBE peut entraîner la mortalité des arbres, une plus grande susceptibilité aux chablis ou aux pathogènes (par exemple au pourridié <*Armillaria* spp> ou au dendroctone de l'épinette <*Dendroctonus rufipennis*>), un ralentissement de la croissance en hauteur et en diamètre, une cassure de la cime, ainsi qu'une perte de productivité (Ostaff et MaClean 1989, Hudak 1991).

En ce qui concerne la mortalité, les arbres supprimés sont les premiers tués (Baskerville et MacLean 1979) et de façon générale, la mortalité s'avère plus élevée dans les peuplements mûrs que dans les peuplements jeunes. MacLean (1980) mentionne que la mortalité moyenne en volume est de 85% dans les vieilles sapinières et de 42% dans les jeunes, tandis qu'elle est de 36% dans les vieilles pessières et de 13% dans les jeunes. Au Québec, Bergeron et al. (1995) suggèrent que le sapin est moins vulnérable à la TBE dans les forêts comportant une importante proportion de feuillus.

Pour ce qui est de la régénération préétablie, elle est affectée par les épidémies les plus sévères puisque ces dernières sont associées à une importante déplacement des insectes à partir des arbres adultes (Ruel 1990, Spencer 1985). Quoique la flèche terminale des semis s'avère généralement l'unique portion affectée, en présence d'une défoliation sévère, seul des semis de moins de 50 cm ont survécus (Ruel et Huot 1993). Ghent et al. (1957) affirment que les effets secondaires des infestations, tels que la mortalité des arbres qui tombent sur les semis et l'augmentation du recouvrement d'arbustes, sont aussi responsables d'une réduction du nombre de semis. La TBE affecte aussi la période de recrutement des semis de sapin, car en plus du feuillage, les larves s'attaquent aux bourgeons des fleurs (Schooley 1978) limitant ainsi la production des graines.

La plupart des études sur l'impact de la TBE se rapportent aux dernières deux épidémies, bien que l'information sur les perturbations de la TBE ait été retracée pour les 300 dernières années (Blais 1965, 1981, Morin et Laprise 1990, Morin et al. 1993). Les reconstructions des épidémies du passé suggèrent que les épidémies de la TBE sont devenues plus fréquentes et plus sévères durant le siècle dernier (Blais 1983, Anderson et al. 1987). Suite à l'augmentation de la proportion des espèces-hôtes, il est probable que les épidémies auront un impact grandissant sur la forêt. En fait, une augmentation récente de l'intervalle entre les feux (Bergeron 1991, Bergeron et Archambault 1993), l'arrosage d'insecticide (incluant des insecticides biologiques tel le Bt), ainsi que des pratiques sylvicoles qui favorisent de plus en plus la régénération préétablie composée surtout du sapin baumier et de l'épinette noire (Doucet 1988, Harvey et Bergeron 1989), mènent à l'établissement d'une forêt dominée par les espèces-hôtes.

Bien qu'il existe plusieurs études sur la protection contre les attaques de la TBE, sur le cycle des épidémies, sur la vulnérabilité de la forêt, sur les modèles de prédiction de la mortalité des arbres et sur la planification des récoltes de récupération (Morris et al 1958, Hudak 1991, Royama 1984, Blum et MacLean 1985, Hardy et al. 1983) il y a relativement peu d'information quant aux effets des perturbations de la TBE sur la dynamique naturelle des peuplements. Pourtant, la connaissance des processus naturels régissant le développement des peuplements est essentielle à la compréhension de l'écologie d'un écosystème et à la réduction des risques associés aux opérations sylvicoles (Weetman 1991). Malgré ceci, actuellement, les opérations de récolte avec la protection de la régénération préétablie et du sols sont devenues la pratique la plus utilisée au Québec (Doucet 1992).

0.2 L'effet de la TBE sur la dynamique des peuplements

Plusieurs études de peuplements de l'est de l'Amérique montrent que le sapin est bien adapté aux épidémies de la TBE et que de telles infestations conduisent à des oscillations uniquement dans la distribution des classes d'âges de cette espèce (Blais 1983; Baskerville 1975). Cette oscillation subséquente est due au développement rapide de la régénération préétablie en sapin. Des études sur la régénération arborescente sous un couvert de sapin et d'épinette montrent que les semis sont abondants et majoritairement composés de sapin (Doucet 1988, Harvey et Bergeron 1989). D'ailleurs, Morin et Laprise (1990) et Morin (1994) ont montré que la plupart des peuplements se sont régénérés en peuplements de sapins, suite à une perturbation causée par la tordeuse.

A grande échelle, quelques modèles conceptuels suggèrent qu'à long terme, les forêts de sapin sont aussi maintenues en équilibre avec la TBE (Baskerville 1975, MacLean 1984, 1988). Bien que les épidémies puissent changer la composition de quelques peuplements il ne devrait pas y avoir de changement dans la composition des espèces sur une grande échelle (Blais 1954, 1985). En fait, l'histoire continue des épidémies est elle-même un témoignage de la stabilité des forêts de sapin (MacLean 1984).

Cependant, il existe de grandes différences régionales dans l'impact des épidémies et le modèle simple impliquant le retour rapide en sapin ne s'applique pas partout. Le modèle de Holling (1992) pourrait être intéressant pour comprendre l'effet de la TBE à travers sa distribution, sur la dynamique naturelle des peuplements forestiers. Ce modèle repose d'une part, sur les liens entre le climat et le début des épidémies et d'autre part, sur le fait que les épidémies se retrouvent où il y a des vastes étendues de forêt de sapin mature. Au sein de ce modèle, le sapin baumier est plus vulnérable aux attaques de la TBE que l'épinette et durant les périodes non-épidémique, sa croissance est meilleure. De cette façon, l'épinette peut profiter d'une épidémie pour accéder aux positions de dominance tant que la compétition avec le sapin est réduite mais lorsque l'infestation est terminée, la régénération préétablie peut encore assurer un couvert de sapin. Le modèle prédit la distribution et la proportion relative du sapin et de l'épinette à travers tout l'est du Canada. Il montre par exemple que la proportion de ces deux espèces d'arbres est bien corrélée avec l'intensité de l'épidémie, donc plus l'infestation sera intense, plus la proportion d'épinette dans la forêt subséquente sera forte. Les résultats du modèle sont supportés par les données empiriques de Gordon (1985), malgré le fait que ce modèle ne considère pas les interactions avec le feu et la composition forestière avant les infestations.

Ailleurs, Ghent et al (1957) n'ont pas trouvé une relation entre l'intensité de l'épidémie et la proportion relative des espèces mais ils ont observé que la composition des peuplements suite à une épidémie de la TBE varie d'une région à une autre. Bien que la proportion relative des espèces soit maintenue à grande échelle on observe le remplacement d'espèces à l'échelle des peuplements. Ainsi, Baskerville (1975) suggère que les épidémies favorisent un retour du bouleau. À l'île du Cape Breton les feuillus comptent pour 2% à 53% dans les peuplements affectés par la TBE (MacLean 1988). Plus à l'ouest, Frelich et Reich (1995) suggèrent que le cèdre, une espèce non-hôte, augmente en abondance dans les peuplements non-brûlés depuis très longtemps.

Malgré les différences entre ces études, quelques facteurs communs ressortent: la régénération préétablie est importante pour la composition du prochain peuplement (Ghent et al. 1957, Fye et Thomas 1963, Morin 1994, Morin et Laprise 1990, Morin et Laprise sous-presse, Baskerville 1975, Osawa 1994), la mortalité des sapins est plus élevée que celles des épinettes (MacLean 1980, MacLean et Ostaff 1989) et les dommages sont fonction de l'intensité de l'épidémie (Ostaff et MacLean 1989). Au niveau des forêts de diversité arborescente plus élevée, le développement des peuplements, suite à une infestation, pourrait être associé à la proportion initiale d'épinette, de sapin et d'autres espèces, à l'intensité de l'épidémie, ainsi qu'au degré d'ouverture du couvert forestier. Par exemple, Ruel (1990) a trouvé que la densité des feuillus intolérants était plus forte dans les peuplements ayant subi une défoliation sévère et que les espèces conifériennes dominaient les peuplements avec une faible défoliation.

0.3 L'utilisation des trouées

Ainsi, la caractérisation de l'ouverture du couvert forestier (trouées) s'avère essentielle à la compréhension de l'effet de la TBE sur la dynamique des peuplements, au sein de la forêt boréale. De façon intéressante, l'utilisation de la trouée s'apparente à un design semi-expérimental où la comparaison de l'état d'un peuplement, avant et après la perturbation est permise, grâce à la présence des arbres morts.

La dynamique des trouées dans la forêt boréale de l'Amérique du nord ne fut que très peu étudiée. Les recherches sur les trouées, dans plusieurs autres écosystèmes (dont la forêt boréale en scandinavie), concernent le taux de formation de celles-ci, la proportion de la forêt composée de trouées, la détermination des arbres y ayant eu une reprise de croissance ainsi que le processus de remplacement des espèces au sein des trouées (Lertzman 1992, Spies et Franklin 1988, Lorimer et al. 1988, Runkle 1981, 1982, 1985, Whitmore 1989, Battles et al. 1995, Qinghong et Hytteborn 1991). La dynamique de formation des trouées dans les forêts non-boréales est aléatoire tandis que les trouées créées par la TBE sont contagieuses dans l'espace et le temps et sont surtout liés à la mortalité du sapin.

L'étude de la dynamique des trouées dans les forêts d'épinettes et de sapins fut limitée aux forêts appalachiennes sous-alpines (Foster et Reiners 1986, White et al. 1985, Worral et Harrington 1988, Perkins et al. 1992). Bien que la structure de ces forêts, comparativement à celle des forêts de la côte ouest ou à celle des forêts de feuillus tempérés, soit plus semblable à la forêt boréale, leur régime de perturbations diffère de celui de la forêt boréale puisque les feux et les épidémies de la TBE y sont peu importants. Ainsi, la taille des ouvertures et l'intensité de perturbation de l'ouverture dans les trouées (par exemple, le feu peut brûler la matière organique du sol et tuer toute la régénération préétablie) soit plus élevées en forêt boréale. Malgré ceci, le taux de renouvellement (dû aux trouées) de la forêt appalachienne, varie de 0.6% à 0.9% est comparable à celui de la forêt boréale (entre 0.5% et 2.0% du territoire est brûlé chaque année en moyenne) (White et al. 1985).

Le régime de feux permet le maintien des espèces intolérantes à l'ombre et il est suggéré que le régime de trouées, à cause de la présence des trouées de différentes grandeurs, peut aussi maintenir l'ensemble des espèces (Brokaw 1985, Whitmore 1989, Putz 1983). Dû au faible angle du soleil dans la forêt boréale, on peut s'attendre également que la position dans la trouée aura une influence sur l'abondance et la croissance des semis de différentes espèces (Canham *et al* 1993, Ban *et al* soumis). Les semis intolérants à l'ombre seraient trouvés au nord de la trouée et les tolérants au sud.

L'étude de la forêt appalachienne indique qu'il y a une mortalité spécifique des espèces dans les trouées et que le sapin est habituellement l'espèce formant la trouée (bien que le dépérissement de l'épinette est dominant à quelques endroits). Certains auteurs suggèrent que la création des trouées dans la forêt appalachienne engendre un équilibre stable dans la composition des espèces, de sorte que la forêt serait toujours dominée par le sapin avec une faible proportion de bouleau et d'épinette (White et al. 1985, Perkins et al 1992). Ces résultats concordent avec les théories de Baskerville (1975) et de MacLean (1984) sur l'effet des épidémies de la TBE sur les sapinières boréales.

La région de l'Abitibi, site de l'étude, est très riche en espèces arborescentes, pour un écosystème boréal. Une grande variation d'âges et de composition de peuplements pourraient donc être associée à un éventail de formes et de tailles des trouées. Dans la majorité des études sur les trouées, la réponse des espèces à une perturbation a été examinée en fonction de la taille des trouées (Runkle 1982, Brokaw 1985, Lertzman 1992). Quoique la taille des trouées ne fut pas directement mesurée dans la forêt boréale, la régénération des espèces arborescentes, suite à une épidémie de la TBE, varie avec le taux de mortalité des arbres. Par exemple au Maine, le sapin, l'épinette et le bouleau sont bien régénérés lorsque la mortalité est modérée tandis que le framboisier (*Rubus idaeus*) et le cerisier (*Prunus pennsylvanica*) sont plus abondants lorsque la mortalité est élevée (Osawa 1994). Au Minnesota, les arbustes seraient plus abondants dans les peuplements ayant subi une forte mortalité (Batzer et Popp 1985). La réponse des semis à une ouverture peut être aussi en fonction des changements dans leurs croissance et architecture (MacLean 1988, Hatcher 1964, Ghent 1958, Sundkvist 1994, Oliver et Dolph 1992).

0.4 Objectif général

Bien que l'on reconnaisse que les incendies forestiers de grande superficie contrôlent la dynamique de la forêt boréale, il existe peu d'information quant aux effets des perturbations de la TBE qui constituent la perturbation majeure entre les feux et qui est plus important que le feu à certains endroits. Ainsi cette thèse a pour objectif de clarifier l'influence de la tordeuse des bourgeons de l'épinette sur la dynamique de la régénération dans la forêt boréale de l'Amérique du nord.

0.5 Objectifs spécifiques

Puisque la régénération préétablie, suite à une perturbation de la TBE, déterminerait de façon importante la composition et la structure du prochain peuplement et que la régénération préétablie peut être influencée par des facteurs biotiques et abiotiques, l'impact des facteurs abiotiques et biotiques sur l'abondance de la régénération préétablie, sera évalué dans les forêts de différents stades successionels.

La caractérisation de l'ouverture du couvert forestier s'avère essentielle à la compréhension de l'effet de la TBE. Malgré l'importance des caractéristiques des trouées pour la régénération, leur importance, au sein des différents stades successionels, ne fut jamais étudiée. Ainsi, le régime de perturbation des trouées sera caractérisé afin de comprendre son influence sur la régénération préétablie.

Puisque les trouées ont une influence sur le recrutement, la croissance et l'architecture des semis de sapin (l'espèce de semis la plus abondante dans l'aire d'étude) l'effet d'ouvertures d'intensité différente sur ces paramètres sera évalué à l'aide de trouées expérimentales dans chacun des stades successionels.

La recherche dans d'autres écosystèmes suggère que la position au sein de la trouée ainsi que la position relative des espèces compétitrices influencent la régénération des différentes espèces. De plus, la tolérance à l'ombre et la susceptibilité à la TBE pourraient affecter le moment de recrutement de l'espèce. Pour toutes ces raisons, l'influence des patrons spatiaux et temporels, sur le recrutement des semis des différentes espèces des trouées naturelles, sera évaluée.

CHAPITRE 1

ECOLOGICAL FACTORS AFFECTING THE ABUNDANCE OF ADVANCED REGENERATION IN QUÉBEC'S SOUTHWESTERN BOREAL FOREST

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1.1 Abstract

Boreal forest disturbance regimes are changing, in turn changing regeneration and stand dynamics of these forests. This is occurring at the same time that the forest industry is emphasizing operations that take advantage of pre-established natural regeneration. This study has therefore investigated the effect of various ecological factors on the abundance of *Abies balsamea, Picea glauca, Picea mariana, Thuja occidentalis, Betula papyrifera* and *Populus tremuloides* natural regeneration in some boreal stands in the Abitibi region of Quebec. Abiotic ecological site classification variables were found to be poorly correlated to seedling densities for most species. Parent trees, as a seed source, and stand type, for its influence on the quality of the seed bed, were strongly correlated with abundant conifer regeneration. As expected, time since fire was positively correlated to seedling abundance, for late succesional species, whereas it was not related to the abundance of early successional species. Post-fire disturbances, such as those due to spruce budworm outbreaks (*Choristoneura fumiferans* (Clem.)), accounted for the variations in seedling densities observed with respect to stand age. The presence of budworm caused gaps was positively correlated to regeneration abundance whereas shrub competition, which was greatest in large gaps, was negatively correlated with advanced regeneration density. Forest management based on abundance of pre-established regeneration should focus mainly on mixed stands because seedling density is very low in hardwood stands and because of the strong competition in large gaps of coniferous forests. The low number of seedlings observed, especially in coniferous stands, may limit the effectiveness of operations that take advantage of advanced regeneration. The large variability in seedling densities limits the operational use of stand or site conditions in predicting seedling densities.

1.2 Résumé

Les régimes de perturbations en forêt boréale ont changé au cours du siècle dernier entraînant des changements dans la dynamique de la régénération. Parallèlement, l'industrie forestière a augmenté la pratique de la coupe avec protection de la régénération préétablie. Cette étude évalue l'effet des variables écologiques sur l'abondance des semis de *Abies balsamea, Picea glauca, Picea mariana, Thuja occidentalis, Betula papyrifera* et *Populus tremuloides* dans la région de l'Abitibi au Québec. Les données abiotiques servant à la classification écologique sont faiblement corrélées avec la densité des semis de la plupart des espèces. Par contre, les semenciers et le type de peuplement, probablement dû à son influence sur le lit de germination, sont liés à une forte abondance de la régénération coniférienne. Alors que l'abondance de la régénération des espèces associées aux stades successionels avancés augmente avec le temps après un feu, la régénération des espèces pionnières demeure basse mais constante tel que prévu. Les perturbations après feu comme les épidémies de la tordeuse des bourgeons de l'épinette (*Choristoneura fumiferana* (Clem.)), expliquaient les variations dans la densité des semis qui étaient fonction de l'âge du peuplement. Les trouées causées par la tordeuse sont positivement corrélées à l'abondance de la régénération tandis que la compétition arbustive, qui est la plus élevée dans les grandes trouées, est négativement corrélée à la densité des semis. L'aménagement des forêts basé sur l'abondance de la régénération préétablie devrait se concentrer essentiellement sur les peuplements mixtes dû à la faible abondance des semis en peuplements feuillus et à la forte compétition trouvée dans les grandes trouées de peuplements conifériens. La faible densité des semis trouvée, particulèrement dans les peuplements conifériens, peut limiter l'efficacité des opérations qui comptent sur la régénération préétablie. Leur grande variabilité limite aussi l'utilisation opérationelle des données abiotiques ou du type de peuplement pour prédire la densité des semis.

1.3 Introduction

The establishment of new stands following disturbance is dependent on natural regeneration, and where disturbance events primarily affect individuals in the canopy layer advance regeneration will play a crucial role in determining the composition and structure of the next stand. In boreal forests, fire has been so long recognized as the primary disturbance agent (Rowe and Scotter 1973, Heinselman 1973, 1981) that intermediary disturbances have only rarely been considered (Ghent et al. 1957, Fye and Thomas 1963, Batzer and Popp 1985). While such an approach may be valid where fire cycles are so short that smaller disturbances have a negligible effect, it is inadequate where these secondary disturbances modify or even begin to control stand dynamics.

In Québec's boreal forest, changes in disturbance regimes are increasing the importance of secondary disturbances in stand development. Fire frequency has been reported to have decreased since the end of the Little Ice Age (Bergeron and Archambault 1992). On the other hand, during the last century spruce budworm epidemics have become more frequent and more severe (Morin *et al.* 1993, Blais 1983). Their influence on stand dynamics, for example, may be responsible for a greater proportion of fir in a region dominated by black spruce (Morin 1994). Harvesting operations that protect advance regeneration are also becoming more common (Doucet 1992) leading to a greater importance of late successional species in post-harvest stands.

In traditional polyclimax theories of succession, species assemblages within a region are governed not only by climate but by distinctive soils, drainage, topography or disturbance regime. Although this view operates at a coarse spatial scale, ecosystem classification studies have shown that plant community distributions can be explained by such factors as moisture gradients and surface deposits (Bergeron *et al.* 1985). It has therefore been suggested that, in the province of Quebec, such factors may be used to predict which sites will have high seedling densities (Levac 1991). However, stand composition and species silvics have also been recognized for their influence on successional processes (Horn 1975, Noble and Slayter 1977, Franklin 1982). A growing body of research has also emphasized the importance of gap-phase dynamics in both deciduous and coniferous forests (Runkle 1991, Lertzman 1992, Qinghong and Hytteborn 1991, Foster and Reiners 1986). In field studies, forest age, stand composition, seedbed type, canopy openings and shrub competition have also been identified as controlling seedling abundance (Ruel 1989, Coté and Bélanger 1991). This paper thus attempts to assess the relative importance of these various factors on seedling establishment in a small region of Québec's southern boreal forest, which will lead to a better understanding of interfire stand dynamics.

From a pratical point of view, understanding such ecological changes will be equally important in any harvesting strategy proposing to use available advance regeneration. Silvicultural systems in which advance regeneration is protected have become the dominant harvesting prescription in Québec, and it has been reported that the new forest strategy calls for their use on 54% of the logged public lands (Doucet 1992) . Their importance is also growing in neighbouring provinces, as forest managers seek alternatives to high cost cut-and-plant operations. This strategy of using existing seedlings is obviously most effective where advanced regeneration is abundant and hence, the need for tools to predict where seedlings are most abundant is a key part of this strategy. The second objective of this paper is, therefore, to determine which site and stand variables can be used to predict the abundance of advance regeneration for use in forest management planning.

1.4 Study Area

The study area is part of the northern clay belt, a large physiographic region in Québec and Ontario, created by lacustrine deposits left after the maximum post-Wisconsin extension of the proglacial lakes Barlow and Ojibway (Vincent and Hardy 1977). In this region hills with partially reworked or eroded morainal deposits are interspersed in lowlands covered by clays from the proglacial lakes (Bergeron *et al.* 1983). The study sites are located around Lake Duparquet, in the Abitibi region of northwestern Québec (Figure 1). All the forests involved in this study are located along the shores of this lake with the exception of the youngest forest which is found 10 km northwest of the lake.

Lake Duparquet is located at the southern limit of the boreal forest in Rowe's (1972) Missinaibi-Cabonga section and Grandtner's (1966) *Abies balsamea-Betula papyrifera* climatic climax domain. In our study area balsam fir *(Abies balsamea* (L.) Mill.), black spruce (*Picea mariana* (Mill.) BSP), paper birch (*Betula papyrifera* Marsh.), white spruce (*Picea glauca* (Moench) Voss), and trembling aspen (*Populus tremuloides* Michx.) dominate. Jack pine (*Pinus banksiana* Lamb.) may also be present on some sites and where fire has not occurred for long periods eastern white cedar (*Thuja occidentalis* L.) may dominate (Bergeron and Dubuc 1989).

The closest meteorological station is at LaSarre, 35 km north of Lake Duparquet, which has a mean annual temperature of 0.6^{0}C, a mean annual precipitation of 820mm and an annual frost-free period of 64 days. However, freezing temperatures may occur through out the year (Anonymous 1982).

The fire history of stands in the Lake Duparquet area has been reconstructed using dendroecological techniques (Bergeron 1991, Dansereau and Bergeron 1993). The eight most important stand initiating fires, representing the successional gradient of forests in the area from hardwood to fir dominated stands, were used for this study: 1964, 1944, 1916, 1870, 1847, 1823, 1797 and 1760. The fire cycle has changed from an estimated 63 years for the period before 1870 to greater than 99 years after 1870. Spruce budworm epidemics have been reconstructed by Morin *et al.* (1993) with the 1970 to 1987 outbreak resulting in the death of most of the balsam fir trees (Bergeron *et al.* In Press). Defoliation due to a 1950's forest tent caterpillar outbreak in the region has also been documented as causing a significant hardwood growth decrease (Bergeron and Charron 1994). Forest harvesting did not become important until large-scale clear-cuts were initiated in the western part of the region in 1978.

1.5 Field Methods

In each of the different fire origin forests, four to six kilometres of transects were established (each one averaging about 1 km in length). At each 50 m, along all transects, 16m x 16m quadrats were established, for a total of 624 quadrats to be used in the anaylses. In each quadrat the diameter of all trees greater than 5cm DBH was measured and the species and state of the stem (live or dead) were noted. In one quarter of each quadrat ($64m^2$) the number and species of all saplings > 1m in height and < 5cm DBH were counted. Seedlings (stems < 1m in height) were counted by species in twelve $1m^2$ quadrats. Along the central 16m axis of the quadrat, perpendicular to the transect, the percent cover of the understory species was evaluated using the line-intercept method (Mueller-Dombois and Ellenberg 1974).

In each of these quadrats the type of surface deposit: till, clay or rock (Gerardin and Ducruc 1987), texture of lacustrine deposits (Jones *et al.* 1983), drainage: six classes from poorly to well-drained (Brais and Camiré 1991), topograhic position, percent slope, and percent of soil aggregates were evaluated. As well, a soil sample from the B horizon was taken from all quadrats on tills for fine particle analysis.

1.6 Data Analysis

Time since fire is correlated with other variables such as species composition and thus could not be included in the regression analysis. The effect of time since fire on regeneration abundance has therefore been investigated through descriptive techniques and by using an analysis of covariance in conjunction with a combined moisture regime and surface deposit type.

The variables used to explain patterns of species regeneration abundance have been divided into three parts. The first set of variables are abiotic site variables that would be of greatest use to forest managers in predicting the presence of natural regeneration due to their relative long-term stability. The use of abiotic site variables is increasingly important in Quebec because of the recent arrival of ecological forest maps which are being used as the basis for planning forestry operations. Forest operations planners therefore would like to use these site variables to directly predict the presence of advance regeneration. Thus, dividing the variables into three parts, and directly testing the effect of abiotic variables will allow for a clear assessment of their potential value. These variables include soil texture, drainage, type of deposit, stoniness, depth of the organic matter layer, slope, topographic position and percent insolation. Percent insolation for each quadrat was derived from its aspect and its slope (Urban 1990). Non-ordered variables were decomposed into dummy variables (one for each category) for the multiple regression analysis. Surface deposit and moisture regime were combined to produce six dummy variables representing rock deposits, glacio-lacustrine deposits on well-drained and poorly-drained sites, tills and shallow tills (which were all well drained) and organic soils. Organic soils were not compared in the analysis of covariance due to an insufficient number of samples on these sites. Percent variables were normalized using the arcsine of the square root of the value (Sokal and Rolf 1981).

The second set of variables was associated with stand composition. For this study we used the basal area per quadrat of all stems greater than 5 cm DBH. The following species were used in the multiple regression analysis: balsam fir, white spruce, eastern white cedar, trembling aspen, paper birch, balsam poplar (*Populus balsamifera* L.), black spruce and jack pine. Although these variables change with time, for the practical purpose of predicting advance regeneration they could be easily obtained from forest stand inventories or forest cover maps.

The third set of variables described both availability of, and competition for, resources (primarily light). These variables include the abundance of *Corylus cornuta, Taxus canadensis, Rubus* spp. and *Acer spicatum* individually, and the abundance of all shrub species combined, the density of adult trees (in terms of total basal area), and the density of dead stems (both for fir alone because of its vulnerability to the spruce budworm and for all species combined). As the degree of canopy opening was not assessed directly, to evaluate its effect we used the ratio of basal area in dead stems to the total basal area per quadrat to express gap openings. This was done both for spruce budworm caused gaps by considering fir alone and for all gaps combined by considering the mortality of all species in the quadrat. This meaure was then normalised using the arcsine square-root transformation. This last set of variables offers additional insight into the factors controlling regeneration abundance although their predictive utility is low because of the difficulty in obtaining this information and the relatively quick rates at which these variables change, especially with respect to the time scales of change associated with the first two sets of variables.

The statistical analyses were performed using the natural log transformation for seedling density data. These data included all stems less than 1cm DBH (approximately 2m in height). Seedling data were used instead of sapling data to understand which factors control the abundance of understory regeneration without also evaluating the factors responsible for recruitment to the sapling size class.. It is noted however, that conifer sapling densities were generally quite low compared to seedling totals (average 865 stems/ha, std.dev. 570). Since six species (balsam fir, white spruce, eastern white cedar, trembling aspen, paper birch, black spruce and jack pine) accounted for 95% of all regeneration in this region they were the ones used for the regression analysis. The choice of variables to be included in each model was determined using SAS's *stepwise* regression procedure with correlated variables eliminated by the collinearity test in the *reg* regression procedure (SAS Institute Inc. version 6.04, 1987). The first set of variables were the initial ones entered into the *stepwise* procedure as their predictive ability was considered to be the most important for forest managers in Quebec, who are to use the new ecological forest maps for forest planning operations. These variables were then kept in all subsequent models by forcing their entry before subsequent stepwise procedures. Similarly, the second set of variables was forced into the model for the final regression analysis. These equations were then compared with regressions in which variables were not forced into the equations.

To separate the effects of time since fire from stand composition, stand types were determined for each quadrat using the relative proportion of conifer and hardwood species basal area per plot. Conifer stands are defined as those stands with greater than 76% conifer basal area, mixed conifer stands as greater than 51% and less than 75% conifer basal area, mixed hardwood stands as greater than 51% and less than 75% hardwood basal area and hardwood stands as having greater than 76% hardwood basal area. More detailed stand composition information is presented in Table 1. Hardwood stand types were then further subdivided into those dominated by paper birch and those dominated by trembling aspen based on the relative proportion of these two species in the quadrat. Differences in regeneration abundances between stands were then compared by an analysis of variance of the normalised data. Again a possible interaction between stand type and surface deposit and moisture regime was tested by an analysis of covariance.

1.7 Results

1.7.1 Time Since Fire

A number of patterns can be observed in the distribution of seedlings in stands established following fire over a two hundred year period (Figure 2). The conifer species have very few seedlings in the 28 year old stand. In the stands not burned for long periods, however, conifer seedling recruitment (with the possible exception of white spruce) is generally high, especially for the climax species, eastern white cedar and balsam fir. The pattern is strongest for eastern white cedar as its abundance seems to increase with time since fire whereas for balsam fir, seedling densities are greater in the four oldest stands than in the four most recently established stands. The relationship is, however, not linear but rather shows that balsam fir regeneration, as well as that of white spruce, is greatest in the middle aged stands.

The two hardwood species show different responses to time since fire. Trembling aspen has fairly constant recruitment across all forest ages, except for the two oldest stands, where seedling densities are lower. Paper birch, on the other hand, has a pattern that is remarkably similar (although at a smaller scale) to balsam fir and white spruce, with seedling densities being lower in the younger versus the older stands; it also has a regeneration peak in the 145 year old stand and declines towards the 232 year old stand.

1.7.2 Effects of Site Variables

Abiotic variables, used in ecological site classification, generally explained alone only a small proportion of the variation in seedling distribution (Table 2). The abiotic regression models for black spruce (R^2 =0.28) and for balsam fir(R^2 = 0.14) are the best for the species studied. The most important factors in the equation for balsam fir are positive relationships to the slope followed by soil texture. For black spruce the most important factor explaining its seedling distribution is its restriction to rock deposits (partial R^2 = 0.24). Regression equations for all other species based on abiotic factors explain less that 6% of the variation. Despite the weak correlations, seedling densities of the three most abundant conifer species are positively correlated to fine soil texture.

An analysis of covariance using the combination of surface deposit type and drainage class against time since stand initiation was used to evaluate whether a relationship of seedling abundance to these site variables was obscured by a confounding relationship with stand age (Table 3). None of the models were found to be significant suggesting that these ecological variables have little influence on regeneration abundance in these forests and that their use as derived from Quebec ecological forest maps would be of little value in forest planning. However, it should be noted that stand age (yr) was significant for all species except black spruce and trembling aspen. For black spruce, deposit and the interaction between year and deposit were instead significant, reflecting again the strong influence of the rocky deposits.

1.7.3 Stand Composition

Stand composition variables greatly improved the regression equations for the conifer species (Table 2). Softwood regeneration, as would be expected, is strongly correlated with the presence of adult trees of the same species, however, for the hardwood species there does not appear to be such a relationship. An analysis of variance comparison of seedling abundance by stand type shows that seedling densities were lowest for all species, except trembling aspen under hardwood canopies (Table 4). For trembling aspen, seedling densities were lowest under conifer and birch canopies, stand types in which trembling aspen adults are also poorly represented. Paper birch recruitment was lowest under trembling aspen canopies and in contrast to trembling aspen, seedling densities were high under conifer canopies.

Black spruce and eastern white cedar seedling densities were highest in stands dominated by conifers (Table 4). The situation is more complex for balsam fir and white spruce. Seedling densities of these species were not greatest in conifer stands but rather were most abundant in mixed stands. For balsam fir, regeneration abundance is clearly greatest in mixed conifer stands and statistical analysis shows that it is significantly highest for white spruce under mixed hardwood stands. In both cases seedling densities are lower in conifer dominated stands than under mixed stands. It should also be noted that variations in seedling abundance were high under all stand types.

Once again a significant interaction between stand type and site variables surface deposit and moisture regime could not be found for most species (Table 5). Significant interactions were found only for black spruce and trembling aspen, the two species whose abundance was influenced solely by these variables.

1.7.4 Canopy gaps and competition

The final set of models in the regression analyses (Table 2) demonstrates the importance of canopy gaps and competition from shrub species. In the case of balsam fir, white spruce and paper birch, advance regeneration was negatively correlated with the abundance of competing shrub species. Individual species often recognized as important competitors (e.g. ***Rubus*** spp. (Ruel 1992), ***Corylus cornuta*** (Buckman 1964, Zelazny and Hayter 1991)), although entered into the analyses were not included in any of the models. Gaps caused by the spruce budworm (as represented by the proportion of dead fir basal area to the total basal area per quadrat) were found to have an important positive influence on seedling densities for all conifers except black spruce. They were not found to be significantly correlated to the hardwood species.

The models containing the three sets of variables explained from 22 to 43% of the variation in seedling densities for the coniferous species but were very poor with respect to the hardwood species. A comparison with unconstrained regression analyses in which all variables were introduced at the same time emphasizes these same patterns. Equations for black spruce and trembling aspen were unchanged. For the other species, abiotic variables with small partial correlation coefficients and secondary tree species also with small partial correlation coefficients dropped out of the final equations while parent trees, competion from shrubs and the presence of gaps continued to explain most of the variation in seedling densities.

1.8 Discussion

1.8.1 Seedling density and time since fire

Patterns in seedling abundance related to time since fire have, as expected, been identified which demonstrates the lasting influence of fire events. The greater abundance of balsam fir and eastern white cedar seedlings in stands undisturbed by fire for long periods is explained by their status, for this region, as late succesional species. These species are not well adapted to fire and must seed in from outside the burned zone. This process may be long due to relatively short seed dispersal. Researchers in Ontario have found, for example, a maximum seed dispersal of 160 m for balsam fir with most seed falling below the parent trees (Sims *et al.* 1990). This may explain low balsam fir seedling densities in young stands with subsequent increases related to the recruitment of parent trees. The decreases in seedling densities of balsam fir, white spruce and paper birch found in the oldest stands and the relatively constant seedling recruitment of trembling aspen, an early successional species, however, suggest that processes other than time since fire should also be considered, as will be discussed later.

1.8.2 Abiotic factors

Generally, the relationship between site variables and local seedling abundance was poor with the exception of black spruce and possibly balsam fir. Béland and Bergeron (1993) working in the same region, but focusing on jack pine stands, also found that, of all species, regeneration densities of balsam fir and black spruce were most stongly correlated to the abiotic variables (20% and 32% respectively). Our results were lower for these, and all other species investigated, perhaps due to their use of sapling sized individuals and to the more extreme site conditions found in their jack pine stands. However, it can be noted that in both studies the seedling species most strongly correlated to abiotic variables was black spruce (possibly because of its restriction by inter-specific competition to the poorer sites) with balsam fir being moderately correlated and white spruce, eastern white cedar and the hardwood species poorly correlated to these site variables.

The ability of hardwood species regeneration to vegetatively reproduce may explain their weak relationship to abiotic variables. Especially in the case of trembling aspen, which reproduces almost exclusively by root suckers, regeneration is highly dependent on the presence of adult trees. In the second set of regression analyses, however, parent trees were not found to be correlated to trembling aspen regeneration. This may be due in part to the small quadrat size relative to the large distance root suckers can be found from the parents (Lavertu *et al.* 1994). Seasonal differences also occur in abundance, because of sprouting in the spring followed by mortality due to reduced light as the canopy closes or due to browsing. Data collection, which was not restricted to a particular period but which rather occured over the entire growing season may thus also be largely responsible for the low correlation of trembling aspen to site variables.

Factors that were identified as being correlated to high seedling abundances, for the conifer species, include organic matter, slope and fine textured soils. These variables may all reflect to some degree a qualitative assessment of surface moisture and seed bed requirements neccessary for seedling establishment. However, the relatively low correlations seem to pre-empt their use as predictive tools, suggesting that other factors need to be considered. Even when accounting for the confounding effect of (1) studying stands recruited at different intervals following fire and (2) different species compositions on the correlation between drainage and surface deposit type (Table 3, Table 5), a significant relationship could not be identified. Abiotic factors may, however, act at coarser spatial scales or stages other than seedling establishment.

1.8.3 Stand composition

The species composition of the canopy is not only an important factor because of the presence of parent trees but also due to its effect on seedbed characteristics. Bélanger *et al.* (1993) and Place (1955) have found that tree regeneration is more problematic on hardwood leaf litter than on conifer needle or moss seedbeds. Our results clearly demonstrate that regeneration is weakest under hardwood stands. Bergeron and Charron (1994) also suggest that cedar regeneration may be limited by the absence of adequate seedbeds in younger stands and Doucet (1988) notes that stand type is the greatest factor controlling balsam fir regeneration. In our study, balsam fir was by far most abundant in the mixed conifer stand type.

The question of whether time since fire or stand composition has a greater influence on the abundance of advanced regeneration is clouded by the correlation between these two factors. Succession in these forests generally results in a shift from hardwood- to conifer-dominated stands (Bergeron and Dubuc 1989, Cogbill 1985, Carleton and Maycock 1978). Although time since fire is important to the development of moss and decaying wood seedbeds, the type of leaf litter is determined by stand composition. For species such as eastern white cedar that regenerate preferentially on decaying woody substrates (for example, Johnston (1990) states that more than 70% of eastern white cedar seedlings in undisturbed forests are found on these substrates), time since fire would seem particularly important for the accumulation of coarse woody debris and thus germination beds. However, the presence of parent trees, as shown by the regression analysis is an equally important factor. The slight peak in eastern white cedar regeneration in the 76 year old stand may be due to a nearby area with many potential parent trees. Distance to seed source may thus be an important factor accounting for some of the unexplained variation for all species regenerating primarily by seed.

It is also true that for these forests, time since fire is not neccessarily directly linked to stand age. Stands more recently burned by fire are dominated by even-aged cohorts of individuals recruited directly after the fire. Those sites which have not been burned for much longer periods become dominated, as trembling aspen dies out, by relatively even-aged cohorts of balsam fir released following spruce budworm epidemics. These stands have either been recruited following an outbreak in the 1920s or a later outbreak in the 1940s and 1950s. These adult firs are thus all greater than 30 years release age and would have all been producing seed on a regular basis.

1.8.4 Shrub competition and canopy gaps

It has also been noted that in stands dominated by conifers, balsam fir seedling abundance is not at its peak but has declined from higher densities in mixed species stands. This apparent contradiction in logic to the parent tree hypothesis is partially explained by the third set of regression models in which shrub competition is negatively correlated with the presence of balsam fir, white spruce and paper birch regeneration. Some competitors such as *T.canadensis* are late successional species appearing primarily on sites that have not burned for long periods (DeGrandpré *et al.* 1993) while others such as *C.cornuta* were observed to increase where canopy openings were most abundant. In the oldest stands, mortality of adult firs due to the 1970-80s spruce budworm outbreak created such openings.

Although budworm gaps are positively correlated to the abundance of balsam fir and white spruce regeneration, there is probably a tradeoff between an initial increase in resource availability and subsequent competition from invading shrubby competitors. Gap size may be an important factor influencing the abundance of shade intolerant shrubs, however, due to the fixed size of our quadrats this could not be evaluated within the context of this present study. It seems logical, however, to presume that gaps would be larger in the balsam fir dominated forests than in the more recently established mixed or hardwood forests. Smaller sized gaps, less suitable to hardwood shrubs, may help to explain the better recruitment of balsam fir and white spruce in mixed forest stands. In these mixed-stands early season incident light before hardwood leaves have developed may also benefit the evergreen coniferous species by permiting greater establishment and recruitment on these sites.

Vincent (1956), Ruel (1990) and Ruel and Huot (1993) also found that in cases where spruce budworm outbreaks were most severe, such as in our fir dominated stands, the larger balsam fir advanced regeneration (> 50 cm) may also suffer mortality directly due to the spruce budworm. Severe infestations, presumably resulting in larger gaps, have also been reported as leading to increases in hardwood, especially paper birch, recruitment (Osawa 1986, Ruel 1989, Harvey and Bergeron 1991, Ruel and Huot 1993). In our study paper birch seedling densities were highest in stand types most affected by the budworm outbreak (those with a high conifer proportion). The lack of correlation to budworm gaps in the regression analysis may, again, be a function of the inability to evaluate gap size. It should be noted, however, that paper birch was strongly correlated to the presence of adult balsam fir trees, suggesting that in stands where balsam fir is most abundant, gaps may be larger and more suited to paper birch regeneration. Conifer regeneration is, however, generally more abundant than hardwood regeneration and our results do not indicate that trembling aspen and paper birch will out compete conifer seedlings even in the larger gaps.

Finally, despite the recognition of the importance of disturbance in controlling regeneration dynamics (Pickett and White 1985) the impact of secondary disturbances such as spruce budworm outbreaks is, with few exceptions (Ghent et al. 1957), rarely considered in fire dominated boreal regions. However, the importance of these infestations with respect to the presence of advanced regeneration has been demonstrated in this study. As in the case following fire, the influence is two sided, leading both to increases in resources but also to increased competition. Attempts to evaluate the abundance of tree seedlings and subsequent stand development will therefore need to consider stand composition and small-scale stand disturbances.

1.8.5 Implications for Forest Management

From a forest management perspective, balsam fir seedlings, as in other fir dominated regions of Quebec, account for the majority of all advance regeneration (Doucet 1988, Harvey and Bergeron 1989, Coté and Bélanger 1991, Béland and Bergeron 1993). In fact, seedling density of all species is highly variable, and only on certain sites (e.g. in mixed conifer stands) does total seedling density exceed the 30 000 seedlings per hectare that Zelasny and Hayter (1991) suggested was neccessary to achieve adequate stocking (>60%) following harvesting operations. This low regeneration may be partly explained by reduced recruitment following the last spruce budworm outbreak. The regeneration density in adjacent conifer stands was estimated to be 65 000 seedlings per hectare in the early 1980s, before maximum balsam fir mortality peaked (Harvey and Bergeron 1989).

The low abundance of regeneration, particularly in pure conifer stands, may reduce the effectiveness of management strategies based on advanced natural regeneration. It appears that the greatest opportunity for the use of silvicultural operations based on advanced growth would be in mixed stands. Overall, seedling densities are clearly far greater in mixed stands than in any other stand type.

The predictive capabilities of both biotic and abiotic variables, however, leave much variation in seedling densities unaccounted for and preclude their use on a large-scale basis. This is especially true for the operationally more useful permanent site variables. As a consequence, any attempt to predict local advance regeneration from stand or site classifications is very limited and preharvest field estimations are required.

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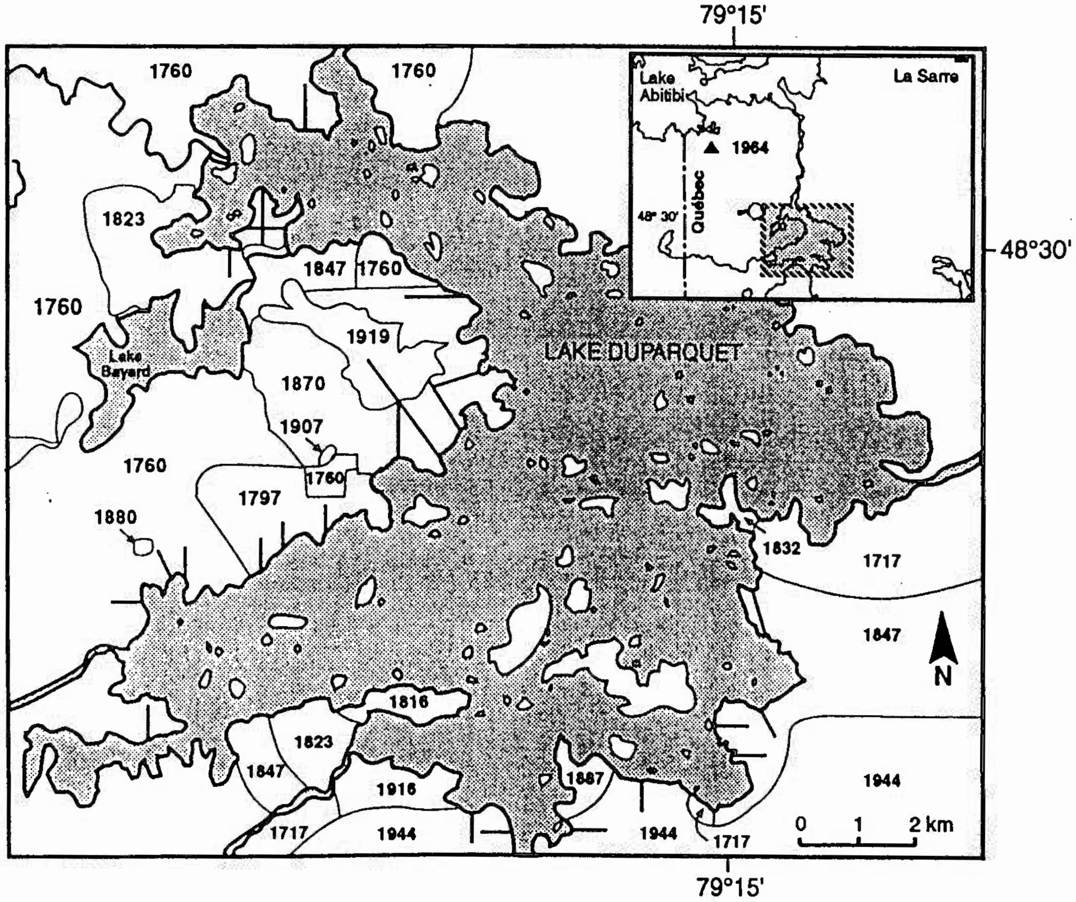

Figure 1.1 Location of the study site with year of stand origin and transects marked.

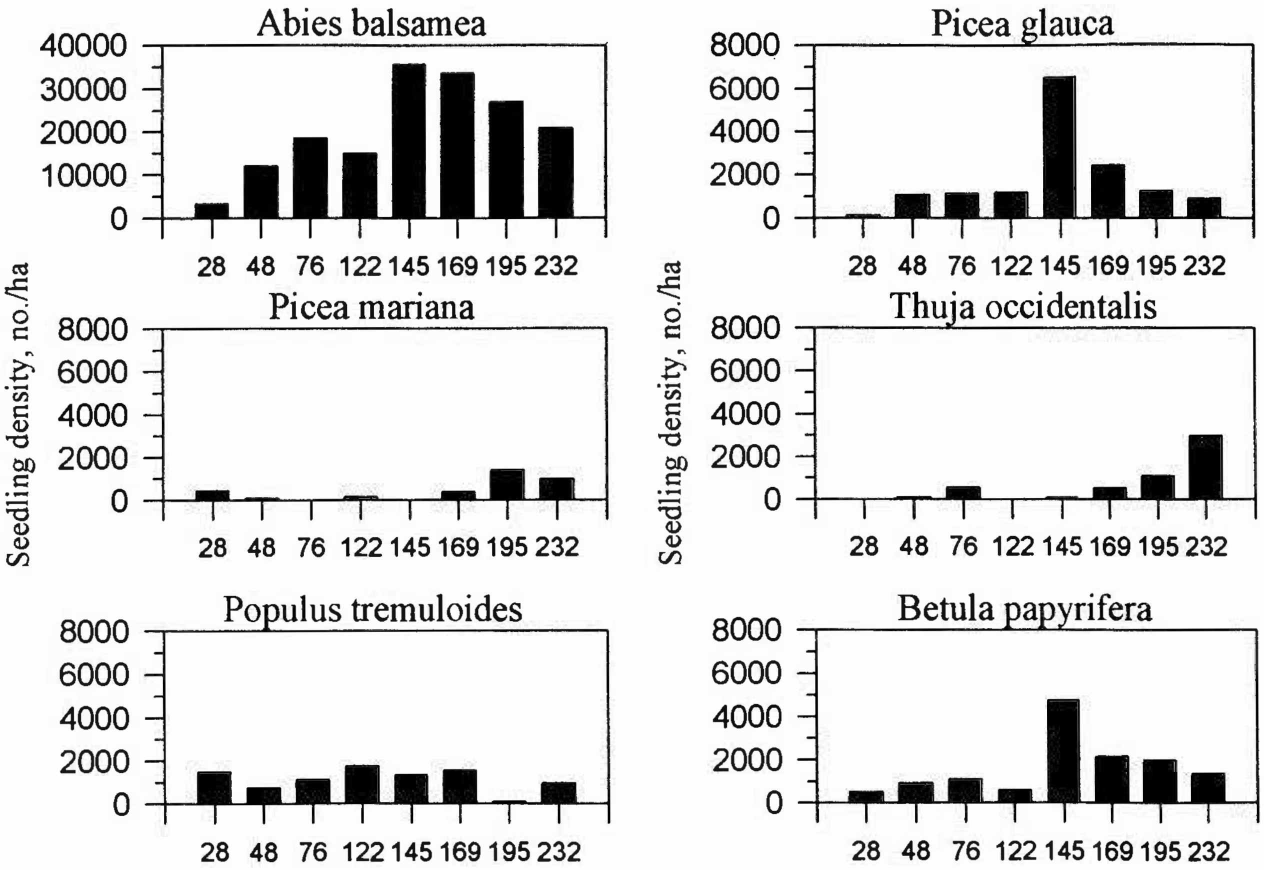

Figure 1.2 Seedling densities of the studied species by years since fire

Table 1.1 Stand composition in terms of basal area (m^2/ha) for each of the stand types.

	Hardwood	Mixed Hardwood	Mixed Conifer	Conifer
Abies balsamea	2.9 ±2.8	9.4 ± 4.9	13.1 ± 7.0	10.9 ± 9.8
Picea glauca	0.5 ± 1.1	2.7 ± 3.2	4.0 ± 5.2	2.3 ± 3.7
Thuja occidentalis	0.3 ± 0.8	0.5 ± 0.9	0.7 ± 1.1	0.7 ± 1.0
Picea mariana	0.2 ± 0.9	0.7 ± 2.2	1.0 ± 2.6	4.6 ± 6.9
Betula papyrifera	7.4 ± 6.9	9.2 ± 7.0	6.9 ± 4.4	2.3 ± 2.5
Populus tremuloides	20.5 ± 15.7	13.0 ± 11.2	5.0 ± 6.2	0.7 ± 1.6
Total	31.7 ± 15.5	35.6 ± 13.7	31.1 ± 12.6	23.0 ± 12.0
Total Live	21.9 ± 9.6	20.4 ± 9.9	17.8 ± 9.6	14.5 ± 8.7
Total Dead	10.2 ± 15.7	15.2 ± 13.3	13.2 ± 13.8	8.5 ± 11.3

Table 1.2 Selected multiple linear regressions to predict the abundance of advanced regeneration.

Species and regression equation	R^2
Abies balsamea	
6.7 +.04OM +.04SLOPE +.02CLAY +.02SILT -1.3(R7)	0.14
5.3 +.04OM +.04SLOPE +.001CLAY +.008SILT -.7(R7) +.006ABA +.003PGL +.001PTR +.002BPA	0.32
4.95 +.03OM +.02SLOPE +.001CLAY +.008SILT -1.0(R7) +.003ABA +.001PGL +.0001PTR +.0001BPA -.004COMP +.002TOTBA +7.7ABAGAP -.001ABADEAD	0.43
Picea glauca	
2.4 +.02CLAY +.03SILT	0.035
1.5 -.01CLAY +.02SILT +.007PGL +.006ABA +.001PTR	0.15
1.8 +.15CLAY +.02SILT +.005PGL +.003ABA -.001TOC +.001PTR -.001COMP +6.3ABAGAP	0.22
Thuja occidentalis	
-0.4 +.03CLAY +.04SLOPE	0.06
-0.4 +.007CLAY +.03SLOPE +.01TOC +.001ABA	0.32
-0.4 +.006CLAY +.03SLOPE +.01TOC -.001ABA + 2.2ABAGAP	0.34
Picea mariana	
-0.5 +.04OM +.03SLOPE +3.1(R7)	0.28
-0.5 +.04OM +.03SLOPE +1.3(R7) +.001PMA +.007PBA -.001BPA	0.48
Populus tremuloides	
0.8 +2.5(4BL(1-3)) +1.5(4BL(4-6))	0.045
0.9 +3.0(4BL(1-3)) +1.7(4BL(4-6)) -.0002TOC -.0002BPA	0.06
Betula papyrifera	
3.3 -.02SAND +.01INSOL	0.02
2.0 -.02SAND +.01INSOL +.006ABA -.003TOC +.009PBA	0.10
2.0 -.02SAND +.01INSOL +.006ABA -.002TOC +.006PBA -.001COMP	0.16

Note: The three models for each species are based on 1) ecological site indicators, 2) stand composition and 3) competition/canopy opening variables. Where only two models exist, no significant competition/canopy opening variables were found. All regressions are significant at $a \leq 0.05$ and N = 624. (OM = depth of organic matter, SLOPE = % slope, CLAY, SILT and SAND = soil texture, R7 = rock deposits, 4BL(1-3) = well drained clays, 4BL(4-6) = poorly drained clays, INSOL = % Insolation; adult composition - ABA = *Abies balsamea*, PGL = *Picea glauca*, TOC = *Thuja occidentalis*, PMA = *Picea mariana*, PBA = *Pinus banksiana*, PTR = *Populus tremuloides*, BPA = *Betula papyrifera*; COMP = % shrub competition, TOTBA = total basal area of all species area in the quadrat; ABAGAP = % of the quadrat in budworm caused gaps, ABADEAD = basal area of dead *Abies*

Table 1.3 Analysis of covariance for species seedling abundance by type of deposit and drainage (D.D.) and site age (year).

	Level	S.S.	M.S.	F	Prob.	
Abies	Dep/Dr	16.6	4.2	0.7	0.5956	
balsamea	Year	139.2	139.2	23.0	0.001	*
	D.D. x Yr	17.4	4.4	0.7	.5791	
Picea	Dep/Dr	121.5	30.4	2.1	.0756	
glauca	Year	203.4	203.4	14.3	0.0002	*
	D.D. x Yr	123.2	30.8	2.2	0.0721	
Thuja	Dep/Dr	66.8	16.7	2.1	0.0815	
occidentalis	Year	81.0	81.0	10.1	0.0016	*
	D.D. x Yr	638.8	15.9	2.0	0.0945	
Picea	Dep/Dr	474.6	118.6	34.6	0.0001	*
mariana	Year	1.8	1.8	0.5	0.4669	*
	D.D. x Yr	436.6	109.1	31.8	0.0001	*
Populus	Dep/Dr	121.3	30.3	2.3	0.0580	
tremuloides	Year	19.5	19.5	1.5	0.2247	
	D.D. x Yr	117.8	29.4	2.2	0.0647	
Betula	Dep/Dr	35.4	8.9	0.6	0.6600	
papyrifera	Year	128.9	128.9	8.8	0.0032	*
	D.D. x Yr	33.6	8.4	0.6	0.6830	

Significant relationships marked with an asterisk, $p = 0.05$.

Table 1.4 Mean density (±SD) of advanced regeneration by stand type.

	Conifer	Mixed Conifer	Mixed Hardwood	*Populus tremuloides*	*Betula papyrifera*
Abies balsamea	19760 a ± 27110	34760 b ± 32480	19080 c ± 22990	9495 a ± 11820	6345a ± 7865
Picea glauca	1915 a ± 5905	2545 a ± 4840	2170 b ± 4840	730 a ± 1765	185 a ± 385
Thuja occidentalis	1575 a ± 3645	690 b ± 1950	485 bc ± 3010	270 bc ± 1200	75 c ± 340
Picea mariana	1615 a ± 3740	195 b ± 995	150b ± 905	80 b ± 470	18 b ± 120
Populus tremuloides	475 a ± 1240	1220 b ± 2740	1200 b ± 2305	1540 b ± 4140	1455 ab ± 2725
Betula papyrifera	2230 a ± 6170	2405 a ± 4895	1570 a ± 3205	540 b ± 1665	715 ab ± 1665

Values followed by the same letter are not statistically different, p=0.05.

Table 1.5 Analysis of covariance for species seedling abundance by type of deposit and drainage (D.D.) and stand composition (comp.) as ranked by proportion of conifer basal area to total basal area.

	Level	S.S.	M.S.	F	Prob.	
Abies	D.D.	17.7	4.4	0.7	0.5923	
balsamea	Comp.	111.9	111.9	17.7	0.001	*
	D.D. x Comp	77.9	19.5	3.1	0.0160	
Picea	D.D.	127.3	31.8	2.2	0.0644	
glauca	Comp.	241.3	241.3	16.9	0.001	*
	D.D. x Comp	131.2	32.8	2.3	0.0576	
Thuja	D.D.	11.1	2.8	0.3	0.8551	
occidentalis	Comp.	97.6	97.6	11.7	0.0007	*
	D.D. x Comp	48.1	12.3	1.4	0.2170	
Picea	D.D.	54.7	13.7	3.9	0.0042	*
mariana	Comp.	83.0	83.0	23.4	0.0001	*
	D.D. x Comp	319.1	79.8	22.4	0.0001	*
Populus	D.D.	88.1	22.0	1.7	0.1510	
tremuloides	Comp.	72.7	72.7	5.6	0.0185	
	D.D. x Comp	191.9	48.0	3.7	0.0057	*
Betula	D.D.	25.2	6.3	0.4	0.7878	
papyrifera	Comp.	41.1	41.1	2.8	0.0948	
	D.D. x Comp	19.5	4.9	0.3	0.8568	

Significant relationships marked with an asterisk, $p= 0.05$.

CHAPITRE II

CANOPY GAP CHARACTERISTICS AND TREE REPLACEMENT IN THE SOUTHEASTERN BOREAL FOREST

Daniel D. Kneeshaw and Yves Bergeron

Article sous presse dans Ecology

2.1 Abstract

This study identifies patterns in the gap distubance regime along a successional gradient in the southern boreal forest and uses this information to investigate canopy composition changes. Gaps were characterized in hardwood, mixed forest and conifer stands surrounding Lake Duparquet in northwestern Quebec. From 39 to 80 gaps were evaluated along transects established in each of these stands. The abundance of gap-makers, gap-fillers and total regeneration was evaluated by species as well as the size of each gap encountered along the transects. The percentage of the forest in canopy gap was calculated directly from the proportion of the transect in gap and by using gap-area and line-intercept techniques. Changes in composition were evaluated from gap-maker and gap-filler distributions and by using transition matrices based on species mortality and regeneration in canopy gaps. The percentage of the forest in canopy gap ranges from 7.1 % in a 50 year old forest dominated primarily by aspen to 40.4% in a 234 year old fir- dominated forest. Gap events are due to individual or small-group tree mortality in the early successional forest but become species-specific events controlled by spruce budworm outbreaks in the later stages of succession. Due to the high latitude, direct light reaches the forest floor in only the very largest gaps found in the conifer-dominated stands. However, these gaps form slowly as budworm caused mortality occurs over a number of years, whereas in aspen-dominated stands gaps are formed quickly by the snapping of tree stems. Balsam fir is the most abundant gap-filling species; however, its abundance is negatively correlated to gap size in all stand types. Markovian transition matrices suggest that in the young aspen-dominated forests small gaps lead to species replacement by more shade-tolerant conifers but that in the oldest forests the larger gaps will result in maintenance of the intolerant species and an increase in the abundance of cedar.

Key words: boreal forest, canopy gaps, balsam fir, cedar, chronosequence, species replacement, tree mortality, gap-makers, gap-fillers, regeneration, trembling aspen, spruce budworm

Key Phrases: boreal forest disturbance regimes, gap characteristics along a chronosequence, gap size distributions, compositional change and forest turnover time, spruce budworm caused gaps, and changes in canopy composition

2.2 Résumé

Cette étude vise à identifier les patrons de perturbations associés aux trouées selon un gradient successionel dans le sud de la forêt boréale et à évaluer comment ceux-ci sont reliés aux changements dans la composition des forêts. Les trouées ont été caractérisées dans des peuplements feuillus, mixtes et conifériens autour du lac Duparquet, nord-ouest du Québec. De 39 à 80 trouées ont été répertoriées le long de transects établis dans chacun des peuplements. La superficie de chaque trouée a été mesurée de même que l'abondance des espèces à l'origine des trouées et recolonisant les trouées. L'abondance de la régénération fut aussi évaluée. Le pourcentage du milieu forestier occupé par les trouées a été calculé en utilisant la proportion de trouées le long des transects et en couplant ces résultats avec des relations de la surface de chaque trouée. Les changements dans la composition de la forêt ont été évalués en utilisant la distribution des arbres à l'origine et recolonisant les trouées de même que de matrices de transition. La proportion des trouées varie de 7.1% pour une jeune forêt de 50 ans dominée par le tremble à 40.4% pour une forêt de 234 ans dominée par le sapin. Dans les forêts de début de succession, la formation des trouées est surtout attribuée à la mortalité d'un ou de quelques arbres tandis que dans les forêts de fin de succession, les trouées sont surtout monospécifiques et associées à la présence de la tordeuse des bourgeons de l'épinette (TBE). Dans nos sites, situés à une latitude élevée, la lumière directe n'atteint le sol forestier que dans les trouées de grandes dimensions retrouvées dans les peuplements conifériens. La formation de ces trouées est toutefois un processus lent à cause de la période requise pour la mort des arbres attaqués par la TBE. À l'opposé, les trouées se forment rapidement dans les peuplements de tremble car elles sont associées aux bris des tiges par le vent. Le sapin est l'espèce la plus abondante qui recolonise les trouées. Cependant, on observe une diminution de l'abondance du sapin dans les trouées plus grandes et cela peu importe le stade successionel. Les matrices de transition suggèrent que dans les petites trouées des jeunes forêts le tremble sera remplacé par les conifères. Alors que dans les grandes trouées des forêts âgées, les feuillus se maintiennent tandis que le cèdre devient plus abondant.

2.3 INTRODUCTION

In forests where large-scale disturbances are rare, stand dynamics are controlled by the creation of gaps due to single or multiple overstory tree mortality. It is within these openings that newly established seedlings or advance regeneration will be recruited to the canopy. Gap dynamics have been described for tropical forests (Denslow 1987, Brokaw 1985, 1987, Lawton and Putz 1988, Whitmore 1978), temperate hardwood forests (Runkle 1981, 1982, 1990, Runkle and Yetter 1987, Barden 1981, Krasny and Whitmore 1992), temperate coniferous forests of western North America (Spies *et al.* 1990, Stewart 1986) and coniferous montane or subalpine forests (Lertzman and Krebs 1991, Lertzman 1992, Foster and Reiners 1986, Worral and Harrington 1988, Yamamoto 1993, Battles *et al.* 1995, Battles and Fahey1996). Although some research has been conducted on boreal forests in Europe (Qinghong and Hytteborn 1991, Leemans 1991, Kuuluvainen 1994), in North American boreal forests the influence of gaps has usually been ignored due to the pervasive nature of large scale disturbances such as fire (Bergeron 1991, Heinselman 1981, Johnson 1992).

Numerous studies have demonstrated examples of species replacement within different regions of the boreal forest (Bergeron and Dubuc 1989, Carleton and Maycock 1978). Although the replacement of overstory pioneer species by understory trees has thus been acknowledged it has rarely been studied. In young boreal forest stands, intolerant species such as trembling aspen (*Populus tremuloides* Michx.) dominate. Over time since fire these stands develop into mixed stands as more shade-tolerant conifers replace the pioneers. If succession is allowed to continue the resulting forests will be dominated primarily by these more shade tolerant conifers. This successional model has been developed from observations of stand chronosequences (Dansereau and Bergeron 1993). Recent work has, however, shown that a second rotation of aspen occurs before stand conversion to conifers (Paré and Bergeron 1995), suggesting the importance of gap openings with a light environment sufficient to permit recruitment of the intolerant aspen.

Nonetheless, stand conversion to conifers occurs gradually if the inter-fire period is sufficiently long. With recent research suggesting that the fire return interval is being extended (Bergeron 1991, Bergeron and Archambault 1993, Johnson 1992), an increasingly large proportion of the forest (if not cut) will attain old growth status. At this stage individual or group-tree mortality will dominate and gap-phase processes will be responsible for maintaining the forest canopy (Oliver 1981, Oliver and Larson 1990, Runkle 1991). In the eastern part of the southern boreal forest these mature and old stands are dominated by balsam fir (*Abies balsamea* (L.) Mill.), a species that is highly vulnerable to spruce budworm outbreaks. The abundance of balsam fir has increased this century due to decreased fire frequency and changes in timber harvesting methods. Retrospective studies suggest that budworm outbreaks are now having a greater impact on the forest than in the earlier part of the century (Morin *et al.* 1993, Blais 1983).

Research from eastern fir forests suggests that spruce budworm outbreaks lead to a cycling of balsam fir forests (Baskerville 1975, Maclean 1984, 1988), thus maintaining the climax forest. However, in more species rich forests of western Quebec and eastern Ontario, Ghent *et al.* (1957) noted that openings caused by the budworm favoured balsam fir in some regions and white spruce (*Picea glauca* (Moench) A. Voss) in others. In Minnesota, spruce was found to recruit in low but consistent numbers with fir regeneration dependent on the presence of non-host trees and the proportion of overstory fir mortality or gap intensity (Batzer and Popp 1985). However, in none of these cases is the explicit effect of gap size on tree recruitment investigated.

Gap size has not only been positively correlated with resource availability (Canham and Marks 1985), but gradients of gap size have also been proposed as important elements in determining the composition of gap-filling species in tropical forests (Brokaw 1985, 1987, Whitmore 1989). Indeed such theories have been invoked to at least partially explain the maintenance of tropical forest tree species diversity (Denslow 1987). Gaps of differing size may also explain different successional patterns found with time since fire in boreal forest stands. However, to date the only part of the North American boreal forest gap regime that has been adequately studied is the periodicity of spruce budworm caused mortality (25 to 30 years in our study area (Morin *et al.* 1993)).

To better understand inter-fire stand dynamics it is important to evaluate gap characteristics as they change from random mortality as trees senesce to budworm caused mortality. This study therefore attempts to evaluate differences in the gap size class distribution, as well as mortality and recruitment patterns in gaps in a section of the southern boreal forest. We conducted the study along a chronosequence in an attempt to explain and predict forest compositional change.

2.4 STUDY AREA

Our study was conducted in northwestern Quebec, in the forests surrounding Lake Duparquet, at a latitude between 48° 15` and 48° 30` North and a longitude of 79^{0} 15` and $79^{0}$ 30` West. This region, known as Quebec and Ontario's northern clay belt, is characterized by clay deposits from the post-glacial lakes Barlow and Ojibway (Vincent and Hardy 1977). The study region is dominated by a rolling clay lowland interspersed by small rocky hills up to 550 m in height overlain with reworked till deposits (Bergeron *et al.* 1983). The climate can be classified as cold and continental with an annual average temperature of 0.8^{0}C and with an average annual precipitation of 857 mm (Anonymous 1993). The average number of frost free days is 64, although frost can occur at any time during the growing season (Anonymous 1993).

Lake Duparquet is located at the southern limit of the boreal forest in the balsam fir-white birch climax region (Thibault and Hotte 1985) or in Rowe's (1972) Missinaibi-Cabonga section where an association of balsam fir, black spruce (*Picea mariana* (Mill.) BSP.) and white spruce with paper birch (*Betula papyrifera* Marsh.) and trembling aspen dominates. Jack pine (*Pinus banksiana* Lamb.) may also be present on some sites, and where fire has not occurred for long periods white cedar (*Thuja occidentalis* L.) may be abundant (Bergeron and Dubuc 1989).

The fire history of stands in the Lake Duparquet area has been reconstructed using dendroecological techniques (Bergeron 1991, Dansereau and Bergeron 1993). Four of the fire years, 1760, 1847, 1870 and 1916, representing conifer, mixed-conifer, mixed hardwood and hardwood stands, respectively, were retained for use in this study: Gap sampling was also conducted in stands dating from fires in 1944, 1823 and 1797. The fire cycle has changed from an estimated 63 years for the pre 1870 period to greater than 99 years in the current period. Spruce budworm epidemics have been reconstructed by Morin *et al.* (1993), with the 1972 to 1987 outbreak resulting in the death of most of the fir trees (Bergeron *et al.*1995). Defoliation due to a 1950's forest tent caterpillar outbreak has also been documented as causing a significant hardwood growth decrease (Bergeron and Charron 1994). Forest harvesting was unimportant until large-scale clear-cuts began in the western part of the region in 1978.

2.5 METHODS

Canopy openness was evaluated along 3-8 transects each located in forests that originated following fires in 1760, 1797, 1823, 1847, 1870, 1916 and 1944. References to stand age are to the time since fire as calculated from fire scars. At each metre along these transects the canopy was evaluated as forest crown (covered) or open (due to the mortality of an adult tree). From 2.5 to 8.4 km of transects were established in each stand to calculate canopy gap percentages. Stand composition was evaluated by measuring the basal area and density of trees in 256 m^2 quadrats placed at fixed intervals along the transects and is displayed in Table 1.

In forests that originated following the 1760, 1847, 1870 and 1916 fires, more detailed sampling of gaps (n=80, 46, 46 and 39 respectively) along three to five transects was used to evaluate gap size, expanded gap size, species of border trees, tree mortality, and recruitment. Gaps were defined as the vertical projection of a canopy opening, caused by the mortality of one or more trees, onto the ground (as verified using a clinometer to ensure vertical sightings) and expanded gaps as the area circumscribed by the stem of those trees whose crowns define the gap (Runkle 1982). In the data presented in this paper, expanded gap areas and proportions include gap area. Gap area was evaluated using the formula for an elipse for small, regularly shaped gaps and by a modified method of subtending extra width measurements from the central long axis as necessary to capture the form of larger and/or irregularly shaped gaps.

For each of these gaps, the species and number of all bordering trees were noted. The number, species and relative size class of all dead trees both standing and fallen were also recorded. Regeneration was completely censused by species in the smaller gaps (<100 m^2) and was sampled in a two metre wide band along the gap axes for the larger (>100 m^2) gaps. The regeneration was divided into two classes: seedling regeneration and gap fillers. Seedling regeneration was defined as stems < 1m in height, and is an objective evaluation comparable to other regeneration studies. The gap-filler category is an attempt, similar to that of Lertzman (1992), to assess those individuals that due to their height, growth rates and good form will have a better probability of making it to the canopy. Gap-fillers were defined as (modified from criteria used for B.C. Ministry of Forest regeneration and free-to-grow surveys) seedlings or saplings of good form, > 1m in height and < 5cm dbh, free of competition and at least 50cm from the nearest similar individual of the same species.

Percentage of the forest in canopy opening was calculated following Runkle (1985, 1992) as the proportion of the total distance of the transect in canopy opening divided by the length of the transect. For transects where size of the canopy gap was measured, these calculations can be compared with the gap percentage calculated using the line intercept method (DeVries 1974 as cited in Runkle 1992), in which

$$e(X) = \frac{1}{L}\sum_{j=1}^{n}\frac{X_j}{d_j}$$

where,

e (X) = estimate of the proportion of the forest in canopy gap

L = the length of the transect
X_j = area of the *j*th gap
d_j = the diameter of the the *j*th gap.

This method can also be modified to calculate the density of gaps per hectare within different size classes as

$$Density\,/\,ha = 10000 * \frac{1}{L} * \sum_{j=1}^{n} \frac{1}{d_j}$$

for j = 1..n gaps of a given size class.

Gap size class distributions and gap diameter to tree height distributions were compared using Kolmogorov-Smirnoff tests. The gap-filler and all other regeneration data for most species could not be normalised using ecologically meaningful transformations and thus relationships between advance regeneration and gap size by species and by stand age were tested using a Spearman correlation test.

To evaluate the potential effect of gaps on succession, Markovian transition probabilities were used with individual gaps as the entity of evaluation rather than individual trees. This approach does not presuppose tree mortality and subsequent tree replacement but bases transitions on currently observed replacement processes. Replacement probabilities were calculated for the youngest hardwood stand, the combined (147 and 170 yr) mixed stands (since the distributions of the proportion of forest in canopy gap by gap size class were not statistically different, Kolmogorov-Smirnoff test $p > 0.05$) and the oldest 234 year old conifer dominated stand. It has been demonstrated that stationary Markovian models do not provide accurate predictions throughout succession due to changing transition probabilities (Bellefleur 1981, Binkley 1980). Thus, only one iteration for each model was performed on current composition. Replacement probabilities for each species were calculated based on the proportions, by species, of gap-fillers to gap-makers in each gap. These individual gap probabilities were then pooled by gap size class. The same procedure was then followed to calculate seedling regeneration to gap-maker proportions. The proportion of forest area in each gap size-class was then used to weight the proportions before summing them to get the overall transition probabilities.

Successional change in the tree layer is a function of both compositional changes in gaps and canopy turnover times. These turnover times can be calculated by dividing the time taken to fill a gap (T_{fill}) by the proportion of the forest in gap. These calculations were made using the assumption that gaps were filled when gap fillers reach a height of 7 metres and stem analysis data from the region (Y. Bergeron, unpublished data). These data show that fill times vary with stand age. In the younger forests T_{fill} approaches thirty years whereas in the older forests T_{fill} is about fifteen years.

2.6 RESULTS

2.6.1 Gap characteristics

The percentage of the forest in canopy gap ranged from 7.1% in the 50 year old stand to 40.4% in the stand that burned 234 years ago (Table 2). The proportion of the forest in expanded gap was eight to thirteen percent higher. In relative terms the proportion of forest in expanded gap was greater in the younger forests due to the larger sized crowns of the overstory aspen. The largest gaps were found in the oldest conifer-dominated forests, although gap boundaries for gaps larger than 1000 m^2 in these forests were somewhat arbitrary due to the large size of the gaps, and the heterogeneous open nature of these older forests. Residual trees were also occasionly found within the larger gaps.

Gap size distributions show that, in the all but the oldest forest, the majority of gaps are found in the smallest size classes (Figure 1). In the oldest forest gaps are more evenly and continuously distributed throughout the size classes. Gap distributions for each of the four studied forests were significantly different (Kolmogorov-Smirnoff tests, $p< 0.01$).

It has often been suggested that simple measures of gap area do not provide an accurate portrayal of the potential impact of various sized openings because of differences in tree heights between stands within the same study and also when comparing studies. In this study, aspen dominated stands had much taller canopies than fir dominated stands, as aspen individuals can easily attain heights of 30 metres while balsam fir canopies may be 6 to 12 metres lower (Paré and Bergeron 1995). To account for this difference, gap distributions for each aged forest are also presented on the basis of the ratio of gap diameter to canopy height (Figure 2). The gap diameter to canopy height ratios were not significantly different between the two mid-succession stands (120 and 147 years old) (Kolmogorov-Smirnoff tests, $p>0.05$).

The smallest shadow length (i.e. on the summer solstice) for our study area is 1.1224 times the canopy height. Therefore at this latitude, gap ratios must be greater than this to receive full direct sunlight within the projected outline of the gap. Thus very few gaps except the largest ones in the old-growth forest receive direct sunlight at the forest floor.

2.6.2 Mortality and recruitment

In all but the youngest forest, gaps are created primarily by the mortality of balsam fir trees (Figure 3). Fir trees make up 36% of the gap-makers in the 78 year old forest, increase to 83% of the gap-makers in the mid-successional, 124 to 147 year old, forests and approach 90% of the gap-makers in the oldest (234 year old) forest. In the 78 year old stand, gaps are caused primarily by the death of aspen. As the aspen are generally much larger than the fir trees it requires a smaller number of deaths to create similar sized openings. Despite the smaller stature of fir, gaps created by fir mortality attain large sizes due to the severity of the last spruce budworm outbreak. This outbreak effectively killed most overstory fir trees in the area (Bergeron *et al.* 1995). It is also interesting to note that even in the 78 year old aspen-dominated stand, gaps are not due to individual tree deaths but rather are usually the result of multiple gap-maker mortality (Figure 3).

In all four of the intensively studied stands balsam fir is the most abundant species, both in terms of gap-fillers (Figure 4) and all regeneration combined (not shown). The trend in the number of gap fillers per gap (all species combined) is unusual in that it does not increase with gap size as would be expected. Instead there appears to be a plateau, except perhaps in the youngest stand, that occurs at gap sizes between 150 and 200 m^2 beyond which the total number of gap-fillers declines (Figure 4). In fact, there is a negative correlation between the density of both balsam fir seedlings and balsam fir gap-fillers and gap size in all forests (Table 3). Birch and white spruce have positive relationships to gap size in the mixed and conifer dominated forests.

Gap regeneration (relative to the number of gap makers) was most abundant in the youngest stand (Table 4). Mortality of fir adults exceeds recruitment from gap-fillers in all but the youngest stand , suggesting that if gap-fillers are a reasonable prediction of the future stand, fir densities will be lower than in the original forest (although fir may still be the most abundant species in the forest), or that recruitment processes are slower in these older forests.

Transition probabilities for the different species suggest that fir will be the most successful species in recruiting to the canopy in all stages of forest development, although its greatest abundance occurs in the transition from mixed to old conifer-dominated stands (Table 5). The model based on gap-fillers does not, however, show fir to be as successful as the model based on all regeneration. Aspen's lowest projected abundance, based on both the gap-filler and regeneration based models, is in the transition from our oldest stands into an even older state not observed in our study area. Spruce and birch fluctuate between models but seem to maintain themselves as important secondary components of the forest. Cedar's relative abundance, on the other hand, increases as a result of recruitment in the 234 year old forest.

As a result of the increase in gap area, canopy turnover time decreases with stand age (Figure 5). The time to reach 7m in height (the fill time), derived from stem analysis data, also decreases in the older forests, leading to even larger changes in turnover time with stand age. Thus the rate of transition from one state to another (as estimated by transition probabilities) accelerates from the youngest towards the oldest stands. The concept of a static turnover time is therefore highly unrealistic, especially in the early stages of succession where it decreases rapidly.

2.7 DISCUSSION

2.7.1 Gap characteristics

The picture that emerges from our study is of small randomly generated gaps in the initial stage of forest succession (dominated by the intolerant hardwoods, primarily aspen). The percentage of the 78-yr old forest in gaps (11%, Table 2) compares well to those reported for temperate hardwood forests to the south (Runkle 1982, 1985, Krasny and Whitmore 1992).

With an increase in balsam fir abundance, spruce budworm mediated gaps dominate the landscape and the percentage of forest in gap and average gap size increase dramatically. However, the percentage of our mixed-wood forest in canopy gaps (18.7 and 24.4% respectively) still falls within the range (3.2 to 24.2 %) reported by Runkle (1982) and the 5 to 31% suggested by Yamamoto (1992) for temperate forests. Gap area in our coniferous forests is also comparable to other coniferous forests in which gap area varied from 15 to 63% but on general averaged 30-40% of the total area (Spies et al. 1990, Lertzman and Krebs 1991, Battles and Fahey 1996, Worrall and Harrington 1988, Qinghong and Hytteborn 1991, and Perkins *et al.* 1992).

In our study, the small range of gap sizes (Figure 1) in the hardwood forest is due to the random nature of gap events throughout the forest as individual or groups of overstory trees senesce and die. The greater range of gap sizes in the older conifer forests at Lake Duparquet is due to the the mortality of all individuals in different sized patches of fir due to outbreaks of the spruce budworm. Large gap events are usually caused by exogenous factors (Kuuluvainen 1994). While spruce budworm is the causal agent in fir dominated regions of eastern North America, severe wind storms have been cited as the source of large gaps in other coniferous forests (Qinghong and Hytteborn 1991).

Despite the large size of these openings direct light only reaches ground level in the very largest gaps (Figure 2) due to the low sun angle at these northern latitudes. As shown by Canham *et al* (1990), increases in light at ground level will be displaced to the north of the gap edge. The deep crowns of the three conifer species and the abundance of mountain maple (*Acer spicatum*) in hardwood stands and in large gaps will effectively reduce the amount of direct light penetration into the understory north of the gaps. Seedlings growing in the area north of the gaps will also experience declining light levels as they grow in height, whereas seedlings located within gaps will grow into a zone of higher light levels. In the boreal forests of northeastern China, Ban *et al* (submitted) found that increased light levels in obliquely projected gaps (e.g. to the north of the gap) resulted in increased seedling survival but that vertically projected gaps were necessary for seedling recruitment to the canopy. Gap expansion to the north of the original gap area may therefore be an important element in gap-filler recruitment to the canopy in hardwood and mixed forests. In our conifer forests, gap formation is essentially a periodic phenomenon due to spruce budworm caused mortality (90% of mortality in the oldest stands is composed of fir). Gap expansion may, therefore, account for only a small proportion of the area in gaps in these old forests.

2.7.2 Mortality and Recruitment

There is a definite progression in the species of gap-maker with time since fire that parallels the shade tolerance of the species in these forests. However, despite the greater number of fir gap-makers in the 123 year old stand, hardwood mortality continues to be important due to the greater size of adult birch and aspen compared to fir. The expanded gap measures are proportionately much greater under the large crowned aspen canopies than under the narrow conical fir canopies. Such a difference implies that the death of a single aspen adult will have a greater effect than that of a fir on gap size. Similarly, the rate of gap formation, which influences the rate at which resources become available, varies between the aspen and fir dominated forests. Aspen death was almost always the result of a snapped bole (the usual mode of death) or uprooting. Balsam fir, on the other hand, usually died standing due to defoliation by the spruce budworm. Seven years after the end of the last epidemic and twelve years after the mortality of many of the adults (Bergeron *et al.* 1995), more than 80% of the boles are still standing (although the branches have long since fallen). Thus gaps in conifer-dominated stands are slowly created over a period of years, whereas hardwood gaps are usually sudden events. Gradual gaps have also been noted as being important in forests where diseases, notably beech bark disease, are a major cause of overstory mortality (Krasny and Whitmore 1992).

The high number of gap-makers per gap observed in this study exceeds those reported for all other studies, in which the number of gap-makers rarely exceeds twenty (Lertzman and Krebs 1991, Qinghong and Hytteborn 1991, Spies *et al.* 1990). This is natural considering that the agent of death - the spruce budworm - causes large patches of mortality in epidemic years. However, even the youngest hardwood stand in our study is dominated by multiple gap-maker gaps. This may be a reflection of the stand age (78 years) which is close to the average lifespan of aspen in the area. For stands of this age and older, synchronous mortality may become more and more frequent. We also speculate that such group death may be linked to the clonal establishment of aspen.

The fact that balsam fir is the most abundant gap-filler and seedling species in these forests is not surprising due to its prolific seeding and its status as a late successional species. However, the fact that the numbers of seedlings does not increase with gap size is. Kneeshaw and Bergeron (1996) suggest that in these large canopy gaps there is a trade-off between increased resource availability and increased competition from shrubby species. Such competition may be responsible for the fact that the number of gap-fillers is not at this present time sufficient to replace the number of gap-makers (Table 4a). This reduced or delayed recruitment may also lead to an increase in canopy turnover times. Earlier studies from western Quebec, eastern Ontario and Minnesota all note that competition from shrub species such as hazel (*Corylus cornuta*), raspberry (*Rubus idaeus*) and mountain maple (*Acer spicatum*) is greatest when overstory mortality is high (Batzer and Popp 1985, Ghent *et al.* 1957). Personal observations for our study area suggest that raspberry is an unimportant competitor in these forests and that the strongest competition comes from mountain maple, followed by hazel.

Balsam fir's projected dominance in filling gaps in the 78 year old forest is primarily a reflection of its high stem density. The composition of existing 147 and 161 yr old forests shows that fir is indeed the most abundant species (Table 1b). However, in terms of basal area these forests are not yet dominated by balsam fir (Table 1a). Earlier research from our study area showed a slow progression towards mixed stands due to a second generation of aspen (Paré and Bergeron 1995, Bergeron unpublished data). Aspen's more rapid growth and its greater height at maturity result in two-tiered stands dominated by aspen with a subcanopy of shorter balsam fir (Paré and Bergeron 1995).

The second set of probabilities, derived from the mid-aged forests, predicts that succession in these gaps will lead to a more heavily conifer-dominated forest. This prediction agrees with similar observations from chronosequences in the area, in which the oldest stands are dominated primarily by conifers, in particular by balsam fir (Table 1). Transitions from spruce budworm caused gaps in the oldest forests to the hypothetical next generation do not suggest the continued maintenance of the current canopy composition. Rather, the importance of fir decreases in these large gaps. This contrasts with work from pure fir forests in eastern Canada in which it has been suggested that spruce budworm created openings would lead to a maintained cycling of fir forests (Baskerville 1975, Maclean 1984, Morin and Laprise 1989, Morin 1994).

Hardwood species are maintained via gap recruitment but they do not increase in abundance. Although large gaps would at first seem suitable to the recruitment of fast growing intolerant species, the nature of gap creation by the spruce budworm does not result in an immediate increase in resources. Instead, trees die slowly over a number of years with maximum mortality usually occurring six to seven years after the onset of an outbreak (Baskerville and MacLean 1979). These large, slow forming gaps are generally dominated by shrubs.

The tree species that is projected to increase the most in the generation following our oldest stand (i.e. in the last transition series) is eastern white cedar. Considering the long lifespan of species such as cedar (and white spruce), which live 3-4 or more times longer than fir (Burns and Honkala 1990), the actual increase in abundance may be greater than suggested by the transition models. Cedar is considered to be extremely shade tolerant, poorly adapted to fire and a non-host tree for the budworm. It has also been suggested that the presence of decomposing logs (as seedbeds) may be necessary before this species can become abundant. An evaluation of cedar regeneration in the area demonstrates a large increase in the oldest present day stands (Kneeshaw and Bergeron 1996). Frelich and Reich (1995), on the basis of their transition probabilities, suggest that spruce budworm outbreaks will limit fir's ability to increase in dominance but find no similar constraint for cedar in the absence of fire. Paleoecological reconstructions also suggest that cedar was most abundant when fire cycles were thought to be longest (Richard 1993, Liu 1990). The projected increase in cedar does not seem therefore to be related to large budworm-caused gaps but rather to length of time since fire.

In conclusion, small gaps found early in succession in these boreal forests generally promote a gradual transition towards a more fir-dominated forest. As the forest becomes increasingly dominated by fir, gap dynamics are controlled more and more by outbreaks of the spruce budworm. The resulting gaps are aggregated in fir-dominated patches. These larger gaps not only allow for the maintenance of intolerant hardwoods but also promote competition between tree regeneration and shrubby species and may eventually lead to an increase in the proportion of cedar. Our results show that these stands have not entered a state of relative compositional equilibrium, and therefore do not follow the cyclical model of continued fir maintenance after spruce budworm outbreaks proposed for eastern fir forests.

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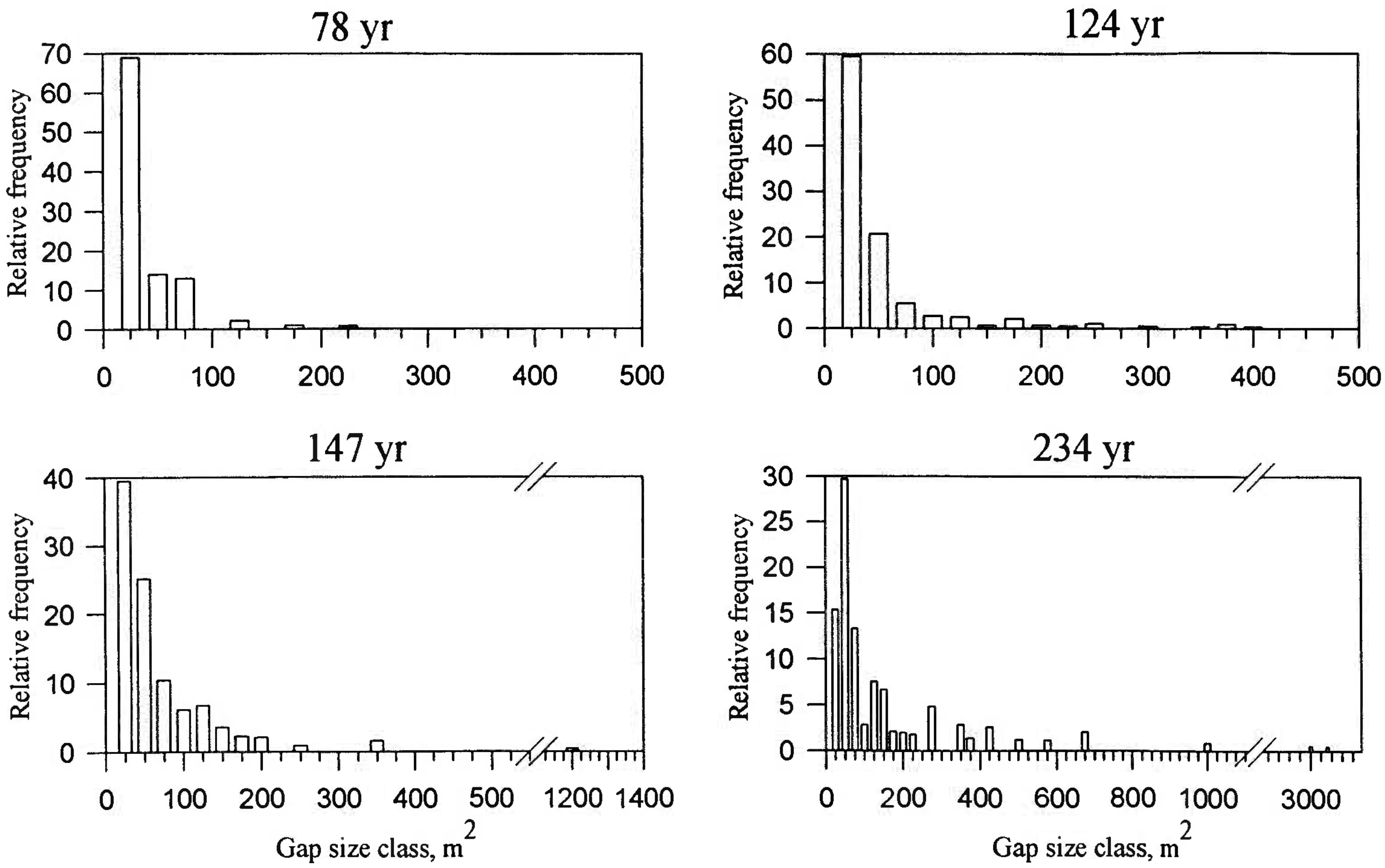

Figure 2.1 Relative frequency of gap size distributions for forests that haven't burned for 78, 120, 147 and 234 years

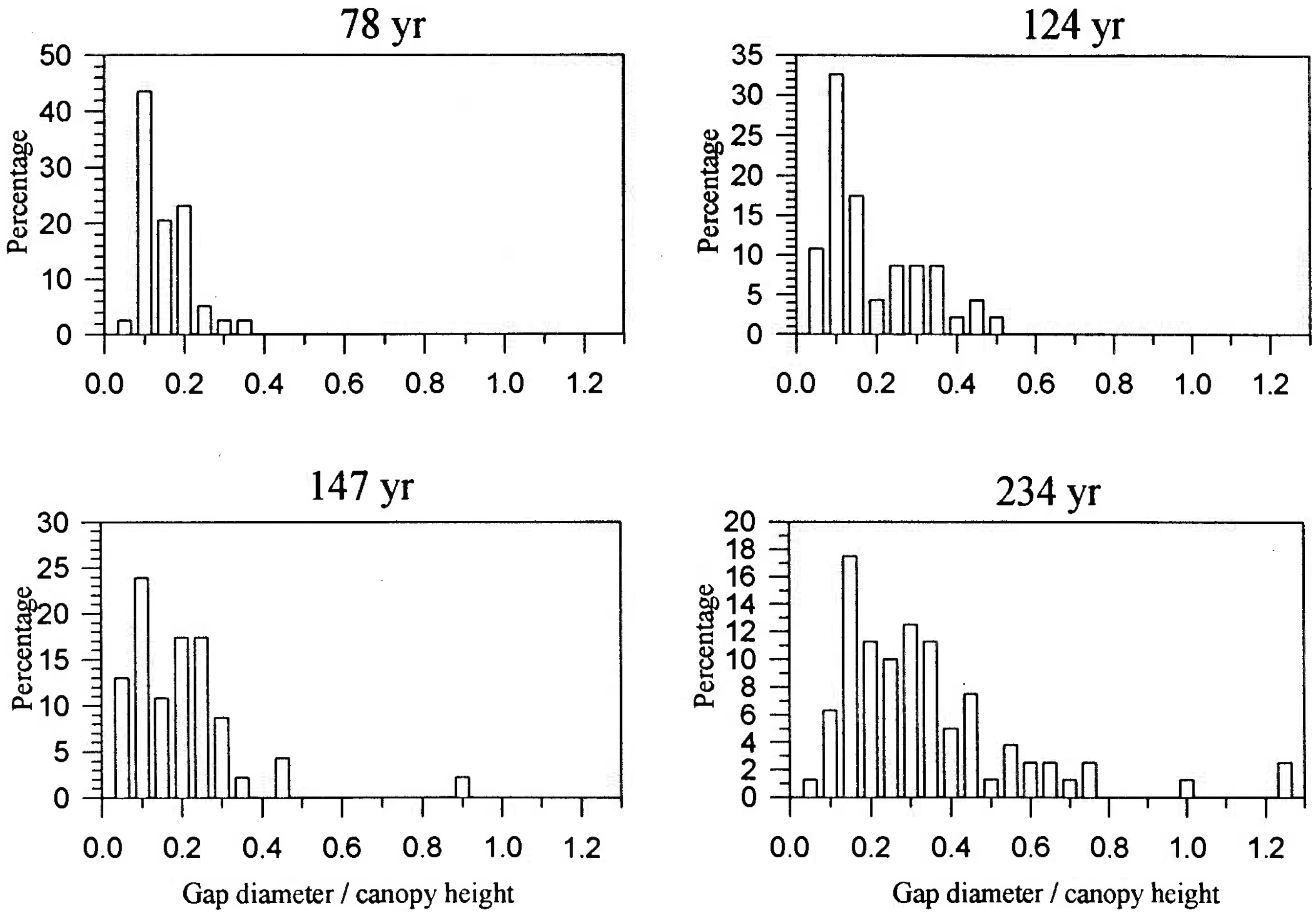

Figure 2.2 The percentage of gaps versus the ratio of gap diameter to canopy height for four different aged forests

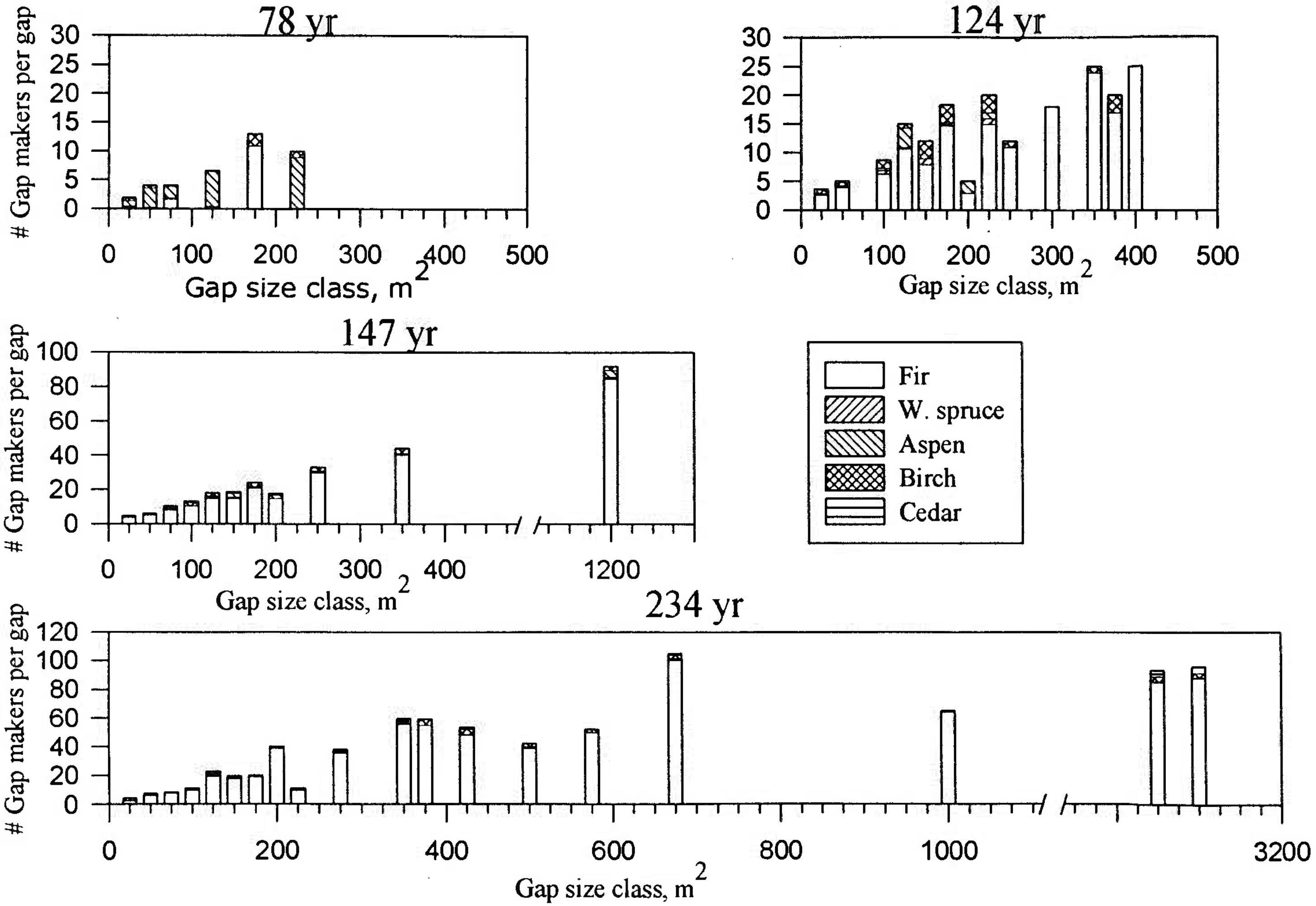

Figure 2.3 The number of gap-makers of each species per gap in each gap-size class

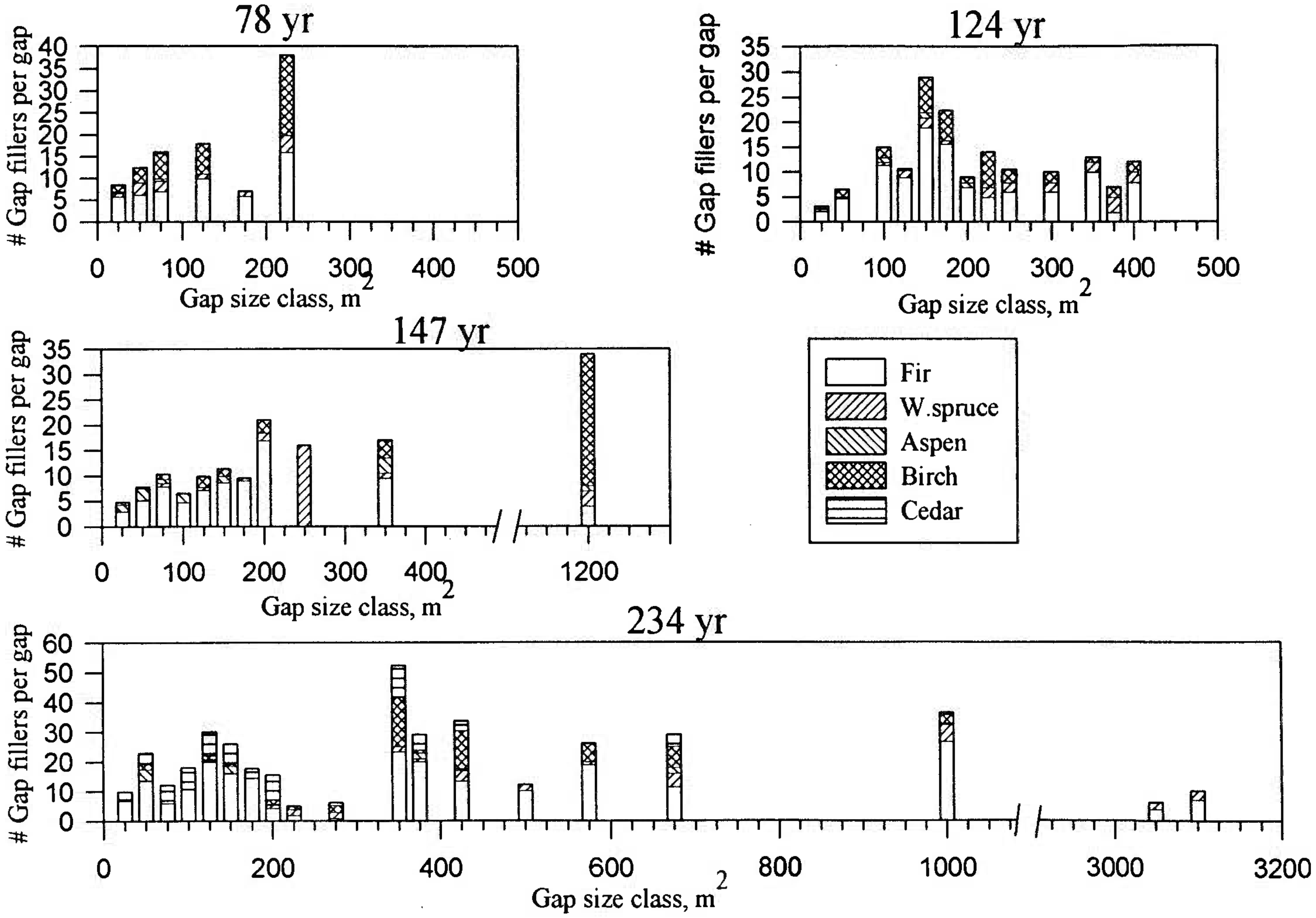

Figure 2.4 The number of gap-fillers by species found in each gap-size class

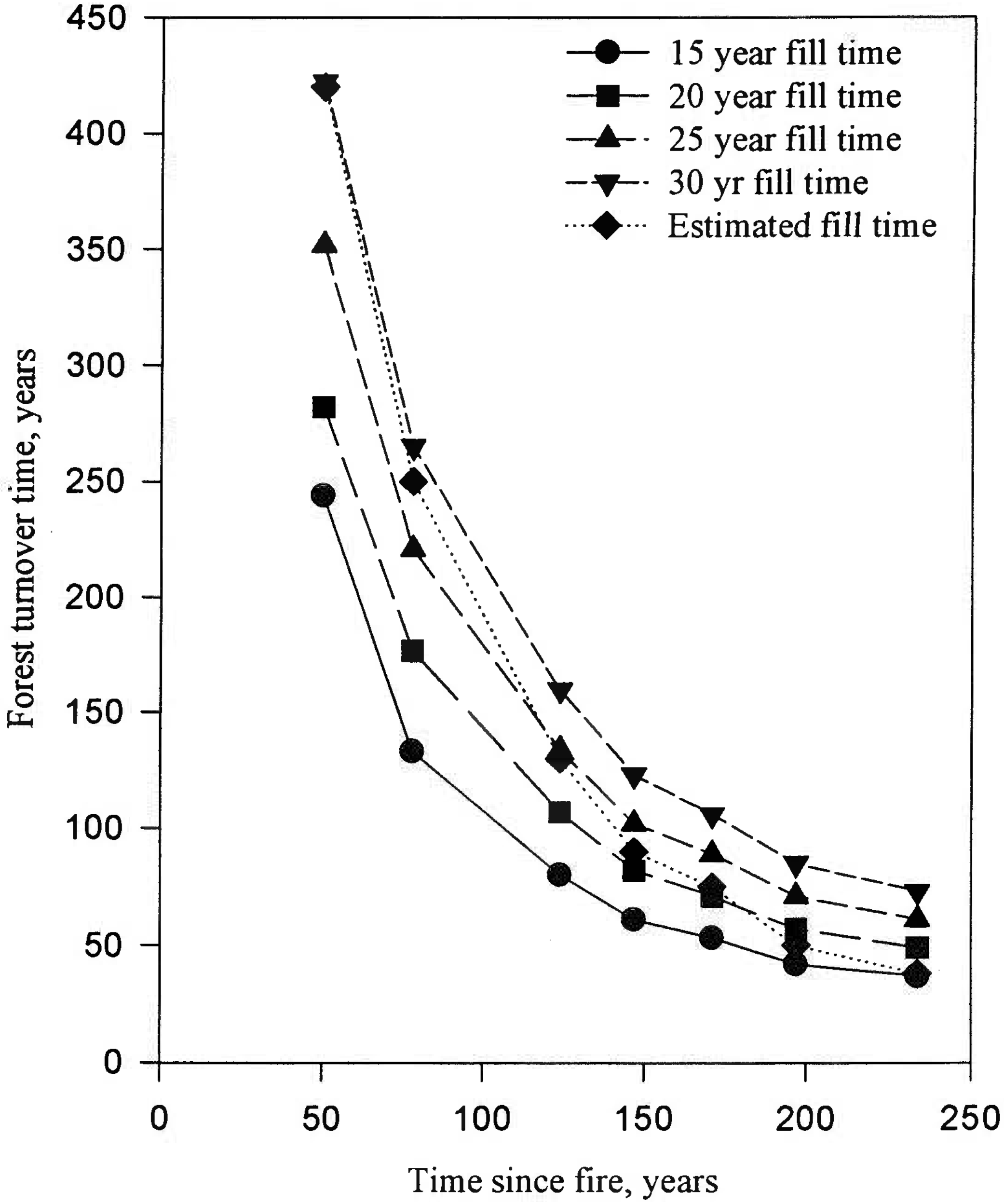

Figure 2.5 Changes in canopy turnover time with time since fire for various gap fill times (gap fill times are the time taken for the regeneration in a gap to close the gap opening). The changing fill time is the best estimate of the actual fill timesfor forests having initiated at different times following fire.

Table 2.1 a) Average basal area and standard deviation (m^2/ha) and b) density and standard deviation (#/ha) of the different species of canopy trees by time since the forest last burned.

a)

Time since fire, yrs	Balsam fir	White spruce	Aspen	Birch	Cedar
50	4.2 ± 5.1	0.6 ± 1.6	13.7 ± 16.1	9.4 ± 7.0	0.3 ± 0.8
78	5.9 ± 4.2	1.7 ± 3.6	17.3 ± 15.8	8.4 ± 6.7	0.8 ± 1.1
124	7.5 ± 4.7	4.5 ± 4.5	14.9 ± 12.8	7.8 ± 5.6	0.0 ± 0.2
147	15.5 ± 5.5	5.6 ± 5.4	16.7 ± 11.8	5.4 ± 4.2	0.2 ± 0.6
171	12.8 ± 5.8	2.4 ± 3.3	12.1 ± 11.1	4.7 ± 3.5	0.4 ± 0.8
197	10.6 ± 8.3	2.0 ± 2.6	0.8 ± 2.7	9.4 ± 8.1	0.9 ± 1.0
234	13.4 ± 7.4	2.3 ± 3.3	3.4 ± 7.3	6.9 ± 6.6	1.5 ± 1.3

b)

Time since fire, yrs	Balsam fir	White spruce	Aspen	Birch	Cedar
50	514 ± 520	42 ± 86	447 ± 621	874 ± 598	7 ± 31
78	746 ± 527	132 ± 152	397 ± 469	683 ± 492	33 ± 86
124	730 ± 434	158 ± 113	617 ± 566	295 ± 180	3 ± 23
147	2055 ± 754	148 ± 129	386 ± 324	191 ± 176	32 ± 117
161	1200 ± 523	86 ± 90	399 ± 516	215 ± 223	32 ± 40
197	1266 ± 725	106 ± 130	14 ± 55	360 ± 395	132 ± 145
234	1190 ± 555	66 ± 76	69 ± 156	244 ± 367	338 ± 352

Table 2.2 Gap and expanded gap (EG) size characteristics for different aged forests.

		Total area	Range of gap area, m^2		Total area	Range of EG area, m^2	
Age, yrs	Forest type	in gaps, %	Minimum	Maximum	in EG's, %	Min	Max
50	Hardwood	7.1	NA	NA	NA	NA	NA
78	↓	11.3	4.1	214	19	19.5	434
124	↓	18.7	6.3	390	26.1	34.4	577
147	Mixed	24.4	4.4	1200	32	11.6	1450
171	↓	28.2	NA	NA	NA	NA	NA
197	↓	35.3	NA	NA	NA	NA	NA
234	Conifer	40.9	10.2	3090	53.9	35.8	3480

NA = not available

Table 2.3 Spearman correlation between gap fillers (GF) and seedling (Sdlg) abundance by species, and gap size for three forest age classes

	78 yr old stand		124 & 147 yr combined		234 yr old stand	
	R	α	**R**	α	**R**	α
GF Fir	-0.581	0.001	-0.505	0.0001	-0.453	0.0001
GF Spruce	n.s.		n.s.		0.405	0.0002
GF Aspen	n.s.		n.s.		n.s.	
GF Birch	n.s.		0.237	0.0349	0.400	0.0002
GF Cedar	n.s.		n.s.		-0.250	0.0300
Sdlg Fir	-0.383	0.0160	- 0.260	0.0207	n.s.	
Sdlg Spruce	n.s.		-0.266	0.0690	0.350	0.0014
Sdlg Aspen	n.s.		n.s.		0.220	0.0446
Sdlg Birch	n.s.		n.s.		0.374	0.0006
Sdlg Cedar	n.s.		n.s.		n.s.	

n.s. = not significant

Table 2.4 Ratio of the number of a) gap-fillers and b) seedlings to the number of gap-makers by forest type.

a) Gap-fillers

Forest	Fir	W.Spruce	Aspen	Birch	Cedar	Total
78 yr	3.3	126.8	0.1	1.3	3.5	1.9
124&147 yr	0.5	5.3	1.3	0.7	1.4	0.6
234 yr	0.6	1.7	18	3.2	1.4	0.8

b) Seedlings

Forest	Fir	W.Spruce	Aspen	Birch	Cedar	Total
78 yr	18.3	651.6	2.1	1.4	9.4	9.1
124&147 yr	6.5	39.7	5.1	8.5	863.2	7.5
234 yr	7.4	10.5	18.3	10.7	17.7	8.3

Table 2.5 Proportional future composition based on transition probabilities from tree mortality and (a) gap-fillers, and (b) regeneration in forests of different ages.

(a)

Species	78 year aspen forest	124-147 year mixed forest	234 year conifer forest
Balsam fir	61.5	72.7	54.0
White spruce	14.8	9.9	8.0
Trembling aspen	4.9	7.2	3.5
Paper birch	16.5	9.8	8.5
Eastern white cedar	2.3	0.4	26.0

(b)

Species	78 year aspen forest	124-147 year mixed forest	234 year conifer forest
Balsam fir	71.0	78.5	68.1
White spruce	11.1	6.2	2.0
Trembling aspen	12.8	5.8	6.1
Paper birch	4.5	8.7	6.3
Eastern white cedar	0.6	0.8	17.6

CHAPITRE III

EARLY SEEDLING RESPONSE OF *ABIES BALSAMEA* TO ARTIFICIALLY CREATED OPENINGS

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Article soumis au Journal of Vegetation Science

Note: Louis DeGrandpré a été un étudiant de doctorat qui a effectué les différents dispositifs

3.1 ABSTRACT

Small scale canopy openings are being increasingly recognized for their importance in boreal forest stand development yet more work is necessary to understand their effects on seedling growth. This study investigated the effect of different degrees of canopy opening (all trees cut, conifers cut, conifers girdled and control quadrats) in different stand types on *Abies balsamea* seedling recruitment, growth and architecture. In each of the treatments the relative height increment, the ratio of leader to lateral branches as well as the number of branches produced per whorl were measured in each of the three years of this study. Seedling establishment by species and year of recruitment were also noted. The lack of a treatment effect on seedling establishment suggests that gaps primarily affect advance regeneration. In the first year after treatment the advance growth seedlings in the cut blocks (both conifer cut and all trees cut) responded with an increase in height growth. Changes in the leader to lateral branch ratio were also significant. Continued architectural change in terms of number of branches produced did not occur until after two years had passed. Although not significantly different than the control increases can be observed in all measurements for the girdled treatment. It is therefore concluded that the growth response of advance regeneration is more important following canopy opening than new seedling recruitment and that seedling performance is greatest where degree of opening is greatest.

Keywords: canopy gaps, boreal forest, *Abies balsamea*, experimental openings, seedling recruitment, seedling growth, seedling architecture

Abbreviations: RHI - relative height increment, LB ratio - leader to branch ratio, PAR - photosynthetically active radiation, DBH - diameter at breast height, H -hardwood stand, MH - mixed hardwood stand, MC - mixed conifer stand, C - conifer stand

Nomenclature: Nomenclature follows Burns, R.H. and Honkala, B.H. Silvics of North America. USDA Agricultural Handbook 654. Washington, D.C.

3.2 RÉSUMÉ

Les petites ouvertures du couvert forestier sont de plus en plus reconnues pour leur rôle dans le développement des peuplements de la forêt boréale, bien que davantage de travaux de recherche soient requis afin de comprendre l'influence des petites trouées sur la croissance des semis. Cette recherche a pour objet d'étudier l'effet des ouvertures d'intensités différentes sur le recrutement, la croissance en hauteur et l'architecture des semis de sapin baumier dans des peuplements de composition différente. L'effet de quatre traitements (témoin, annelage des conifères, coupe des conifères et coupe totale) est comparé. Dans chacun des traitements, la croissance relative en hauteur, le rapport longueur de la flèche/ longueur des branches latérales ainsi que le nombre de branches produites ont été mesurés durant les trois ans de cette étude. Le recrutement des semis fut aussi évalué. L'absence d'un effet significatif des traitements sur l'établissement des semis de sapin suggère que l'impact des trouées se situe surtout au niveau de la régénération préétablie. Un an après les traitements coupe des conifères et coupe totale, les semis ont enregistré une hausse significative de leur accroissement en hauteur et du rapport longueur de la flèche/ longueur des branches latérales. Une augmentation du nombre de branches et par conséquent une modification de l'architecture furent aussi enregistrées à partir de la seconde année suivant les traitements. Le traitement annelage n'a pas eu d'effet significatif. Cependant, la valeur des indices calculés était plus élevée que pour le traitement témoin. Nous pouvons donc conclure que suite à la création d'une ouverture, la réponse du sapin se fait surtout par une modification de la croissance et de l'architecture des semis déjà en place que par le recrutement de nouveaux semis. De plus, les semis sont plus vigoureux et de meilleure forme dans les trouées dont le degré d'ouverture est supérieur.

3.3 INTRODUCTION

Traditionally research on disturbance dynamics in the boreal forest has focused on the impacts of fire. Recently, a growing number of researchers have started to study the impacts of smaller-scale canopy openings (Hytteborn *et al.* 1987, Leemans 1991, Paré *et al.* 1993, Bergeron and Charron 1994, Kuuluvainen 1994, Kneeshaw and Bergeron in press). In terms of stand dynamics, tree response to these openings will be either from existing advance regeneration or due to the recruitment of new individuals.

Following stand destroying fires, seedling establishment is primarily from seed (or from root suckering for such species as trembling aspen *Populus tremuloides*). On the other hand, despite some mortality (Spencer 1985, Ruel & Huot 1993), advance regeneration is usually abundant following gap formation caused by spruce budworm outbreaks or windthrow (MacLean 1984, 1988; Morin 1990). The creation of gaps may also result in favourable conditions for germination and seedling establishment (Batzer & Popp 1985).

For advance regeneration it has been demonstrated that those individuals growing in an open environment will have a different architecture than those growing in a shaded environment (Sakai 1987, O'Connell & Kelty 1994, Parent & Messier 1995). In shaded environments apical control is reduced. This results in greater lateral branch than leader growth which will lead to seedlings and saplings developing a sympodial or umbrella shaped form (Sakai 1987, O'Connell & Kelty 1994, Parent & Messier 1995). In open environments the opposite is true and seedlings develop a conical form. Increases in height increment have also been reported following canopy openings created due to both budworm outbreaks and timber harvesting (Ghent 1958, Hatcher 1964, MacLean 1988, Sundkvist 1994).

Understanding the growth response in trees whose environment has changed from a closed canopy environment with little PAR to a more open environment with higher PAR is essential towards explaining and predicting stand development. Such information will also be crucial in supporting all silvicultural decisions that use the release of pre-established individuals. With increasing pressure for sustainable forestry practices that recognize and protect biodiversity and visual aesthetics, alternative silvicultural techniques that use smaller openings and that take advantage of advance regeneration are being increasingly favoured by the public. In Quebec's boreal region, harvesting with the protection of advance regeneration is already the dominant silvicultural system.

In Quebec's boreal fir forests, balsam fir (*Abies balsamea*) is the dominant late successional species. It accounts for more than 80% of all advance regeneration in the region's forests (Kneeshaw & Bergeron 1996). It therefore constitutes the majority of the softwood component in second growth stands of this region. In naturally regenerated stands it recruits, following fire, beneath a hardwood canopy dominated by trembling aspen (***Populus tremuloides***) and gradually attains dominance through a series of gap events (Bergeron submitted, Bergeron & Charron 1994). This species is also highly vulnerable to the spruce budworm; more than half of all fir adults were killed during the last outbreak (Bergeron *et al.* 1995). A cyclical successional pattern has been suggested for pure fir forests in the maritimes due to high overstory mortality and abundant regeneration in the understory (Baskerville 1975, MacLean 1984). Balsam fir is thus exposed to gaps of different size and degree of canopy opening which may influence its success in recruiting to the overstory (Kneeshaw & Bergeron in press). The objectives of this study are therefore to investigate the effect of different degrees of gap opening in different stand types on balsam fir seedling recruitment, growth and change in architecture through a series of experimentally created openings in order to understand better natural stand development and response to cutting.

Study Area

The study sites are located in Quebec's southwestern boreal forest in the area surrounding Lake Duparquet (latitude 48° 15` to 48° 30` North, longitude 79° 15` to 79° 30` West). This region, characterized by clay deposits from the post-glacial lakes Barlow and Ojibway (Vincent and Hardy 1977) , is known as Quebec and Ontario's northern clay belt. The study region is dominated by a rolling clay lowland interspersed by small rocky hills up to 550 m in height overlain with reworked till deposits (Bergeron *et al.* 1983). The climate can be classified as cold and continental with an average annual temperature of 0.8°C and with an average annual precipitation of 857 mm (Anonymous 1993). The average number of frost free days is 64, although frost can occur at any time during the growing season (Anonymous 1993).

Lake Duparquet is located at the southern limit of the boreal forest in Thibault & Hotte's (1985) fir to white birch climax region or in Rowe's (1972) Missinaibi- Cabonga section where an association of balsam fir, black (*Picea mariana*) and white spruce (*Picea glauca*) with paper birch (*Betula papyrifera*) and trembling aspen dominates. Jack pine (*Pinus banksiana*) may also be present on some sites, and where fire has not occurred for long periods white cedar (*Thuja occidentalis*) may be abundant (Bergeron & Dubuc 1989).

The fire history of stands in the Lake Duparquet area has been reconstructed using dendroecological techniques (Bergeron 1991, Dansereau & Bergeron 1993). The fire cycle estimated to be 63 years for the pre 1870 period has since decreased and no major fires have been recorded since 1964. Spruce budworm epidemics have been reconstructed by Morin *et al.* (1993) with the 1972 to 1987 outbreak resulting in the death of most of the *Abies* trees (Bergeron *et al.*1995). Defoliation due to a 1950's forest tent caterpillar outbreak has also been documented as causing a significant hardwood growth decrease (Bergeron & Charron 1994). Forest harvesting was unimportant until large-scale clear-cuts began in the western part of the region in 1978.

METHODS

Field Sampling

Four stand types, hardwood (H), mixed hardwood (MH), mixed conifer (MC), and conifer (C), were chosen to represent the successional changes found in the region. The youngest of these stands, burned in 1944, is dominated by hardwoods, and the oldest stand, burned in 1760, is dominated by conifers (Table 1). The intermediate aged stands represent different proportions of hardwood to conifer mixes. All sites chosen for cutting within these forests were located on mesic, clay soils.

Three replicates of each of four treatments, in a Randomized Block Design using 10m x 10m quadrats, were located within the different stands for a total of 48 quadrats. This chosen gap size is consistent with naturally occuring gaps in these forests (Kneeshaw and Bergeron In-Press). These treatments, by removing different proportions of the tree layer, represent different degrees of openings possible within the forest. The first treatment, in which all trees greater than 1 cm DBH were cut and removed from the site, removed the most basal area and therefore resulted in the greatest degree of canopy opening (Table 1). The second and third treatments were attempts to imitate the effect of spruce budworm outbreaks. In the second treatment all balsam fir and white spruce (>1cm DBH) were cut and removed from the site. In the third treatment all balsam fir and white spruce trees were girdled by cutting through the cambium to the sapwood in two rings that completely encircled the tree. This treatment leads to the slow death (1-2yrs) of these trees. The final treatment was the control (no cutting).

Within each of these treatments two 1m wide transects were established perpendicular to each other on north-south and east-west axes. All conifer seedlings within these transects were identified to species and tagged for further analysis. Due to low numbers of seedlings in the transects of some quadrats, sampling area within the quadrat was increased until a minimum of 15 balsam fir seedlings per block were located or until the maximum quadrat size (100 m^2) was attained. Even so, balsam fir was limited to less than 15 seedlings in six quadrats. In total, 939 seedlings greater than 10 cm in height (to ensure the possibility of branch production) were measured in the 48 quadrats. Poor form, loss of leaders due to browsing or breakage in transport reduced the number of seedlings used in the analysis to 764 in the analyses for branch production, 732 for RHI and 684 for LB ratio. The latter two ratios required more measurements and were thus limited to a greater degree by breakage.

Although the different treatments were established before the beginning of the 1992 growing season their effects on seedling growth were not observable until the following season. This is due to the determinate nature of balsam fir and white spruce growth, in which the current season's growth is pre-determined in the previous growing season. At the end of the 1994 growing season, tagged seedlings were harvested and taken back to the laboratory for analysis. All seedlings were aged and total height as well as height growth was measured for the previous four years. Similarly the length of all lateral branches to their first node was measured for each of these years. The number of branches produced in each year was also noted. Seedling recruitment, i.e. the establishement of new individuals, by species was also counted in each quadrat at the end of the 1992, 1993 and 1994 growing seasons

The creation of canopy gaps leads to changes in resource levels available to seedlings growing within the newly opened area. Although much research has focused on the effects of light on seedling growth and architecture (Reed *et al* 1983, Canham 1988, Cline 1991, Aarsen 1995) changes in nutrient and moisture availability may also be important (Canham & Marks 1985, Denslow 1980, 1987). Abiotic and biotic factors were therefore measured in order to evaluate their effect on changes in seedling growth and architecture. Percent cover of all herb and shrub species was evaluated in the transects. Species were then stratified into different groups: ground herbs (herbs growing along the ground e.g *Linnaea borealis*), low growing herbs (> 5cm and < 50 cm height), tall herbs (> 50 cm), low shrubs (<50 cm) and tall shrubs (>50cm height).

Soil temperature, at a depth of 15 cm, was measured at intervals throughout the first two growing seasons. Percent moisture of the organic horizons was also evaluated throughout the first two growing seasons as was the rate of nitrogen mineralization. Nitrogen mineralization was evaluated using plastic tubes inserted into the soil and then withdrawn at different dates (at least 30 days apart) to determine the differences in the quantity of nitrates and ammonium (DeGrandpré 1997). Light measurements made in ten micro-quadrats randomly located in the transects were made at heights of 5cm, 1m above the forest floor, and above the shrub layer. Light was measured on cloudy days, using the thechniques described by Parent & Messier 1996 and Messier & Puttonen 1995. Average light levels per strata (as well as for all other variables) were retained for further analysis as the object of the study was to evaluate the effect of each treatment on overall seedling performance.

Data Analysis

To evaluate seedling response a number of indices were used. The first, the leader to lateral branch (LB) ratio, reflects changes in architecture. This ratio is calculated as $L/(\text{average}[B_i..B_n])$, where L is the leader length and $B_{i..n}$ are the lengths of the lateral branches produced from the same node as the leader. Individuals growing in high light environments produce longer leaders relative to the lateral branches than do individuals growing in low light environments (Chen *et al.* 1996). Ratios greater than one occur when leaders are longer than the average of the lateral branch lengths. Therefore any increase in the ratio from one year to the next reflects a change in architecture towards a more monopodial form adapted to height growth. This ratio has been highly positively correlated to percent light received (Parent & Messier 1995, Klinka *et al.* 1992) To evaluate whether treatments had an effect on leader to lateral branch architecture, ratio differences were calculated : 1) from before treatment to one year after, 2) before to two years after and 3) from the first year to second year after treatment. These year to year variations were tested in order to identify the period of time required before a significant response occured.

The second index used was the relative height increment (RHI). Since earlier studies have shown the effect of initial size on height increment response following openings (Hatcher 1964, Ghent 1958) the traditional technique of using ratios of leader growth to seedling height would lead to biased comparison. Instead we used the method proposed by Brand (1986) to permit comparisons in height growth between individuals of different initial size. In this method RHI is defined as the ratio of the height increment in year *n* to the height increment of year *n* plus year *n-1*. The formulation of the RHI in this manner, also results in it being more sensitive to changes in relative height than ratios based on leader length to total seedling height. Again statistical analyses were performed on differences from pre-treatment RHI's to one year and two years after treatment as well as the difference between the first and second year RHI.

The final index used was the total number of branches per node, again compared using year to year differences. The number of branches produced has also been found to increase in environments with higher irradiance for a number of species including balsam fir (O'Connell & Kelty 1994, Parent & Messier 1995).

Treatment effects on changes in these indices were analysed in SYSTAT (version 6.0) using a two-way analysis of variance. Pre-treatment values of these indices are presented in Table 2. A two-way ANOVA was also used to test for differences in seedling recruitment and seedling mortality. To investigate the impact of abiotic variables and competing plant cover on seedling growth response, a step-by-step multiple linear regression was used. Variables that were inter-correlated were identified using SYSTAT's 'Tolerance' values and were subsequently eliminated. Transformations were performed on a number of variables in order to respect assumptions of normality and homogeneity of variances. Density of seedling recruitment and mortality as well as light measurements were log transformed, and soil moisture was arcsine transformed.

RESULTS

Seedling recruitment

None of the treatments had a significant impact on seedling recruitment or mortality (Table 3). Seedling recruitment was, however, affected by the stand type. Much greater seedling recruitment occurred in the hardwood and conifer stands than in the mixed stands (Figure 1a). A comparison of new seedling recruitment to the abundance of seedlings >10 cm in height shows that although there is still no treatment effect (Table 3), only in the hardwood stand type is the number of new recruits more important than the number of advance seedlings (Figure 1b).

Seedling growth response

The all cut, and in some cases the conifer cut, treatment caused significant increases in all the indices of seedling growth and architecture (Figure 2). The greatest significant increases were found in the pre-treatment to post treatment measurements and in all but one case the changes from the first to second year after treatment were not significantly different from the control (Figure 2). This trend was particularly noticeable for the RHI.

After the 1st year the number of branches produced was similar following all treatments. Two years after treatment a greater number of branches were produced in the all cut quadrats than in either the girdled or control quadrats (Figure 2). The response of seedlings in terms of branch production, in contrast to the RHI, is not immediate but rather occurs after a short delay.

The girdling treatment did not result in significant increases in any of the indices when compared to the control. However, after two years its effects were also similar to the conifer cut treatment. The conifer cut treatment did cause significant increases in the LB ratio and the RHI when compared to the control

Changes in RHI and the LB ratio are not affected by stand type (Table 3). However, both stand-type and the interaction term caused significant changes in the number of branches produced: the number of branches produced being greater in the C and MC stand types than in the MH stand type (Figure 2). Significant interactions between treatments and stand type were linked to the greater proportion of conifers cut in the oldest stand.

The observed increases in the RHI were primarily due to increases in the maximum light available in the quadrat (Table 4). Changes in the LB ratio were not, however directly related to light. Instead this ratio was positively correlated to summer soil temperatures and moisture content. It was also correlated to changes in percent cover of other understory plants. Characteristics found to be important by Carter & Klinka (1992), Lorimer (1983) and Sundkvist (1994). The relationship of the LB ratio to moisture, temperature and understory vegetation cover suggests that this indice is sensitive to many variations in the environment and thus provides a good reflection of changes in canopy opening on seedling growth. Branch production was also positively correlated to soil moisture and plant cover, as well as to maximum light levels in the year of greatest branch production (yr1 to yr2).

Discussion

Seedling recruitment

Natural gap formation in similar mixed-wood forests may due to mortality cause by the spruce budworm, to individual tree senesence and mortality or to windthrow: in our study area, the majority of gaps are caused by the spruce budworm (Kneeshaw and Bergeron In-Press). Advance regeneration is abundant on many sites in our study area but seedling establishment following canopy openings may be important on sites where advance regeneration is considered inadequate (Kneeshaw and Bergeron 1996). Batzer & Popp (1985), for example, found that 45% of their budworm attacked stands contained only post-outbreak seedlings. Kneeshaw & Bergeron (in review) also show seedling establishment to be important following budworm outbreaks. The lack of a treatment effect on seedling recruitment may be due in part to the short period of time that seedling recruitment was followed after the treatment. In eastern Canada, newly established seedlings accounted for less than 2% of the regeneration immediately following the last spruce budworm outbreak (MacLean 1988). The presence of parent trees, the production of seed crops in the years following disturbance, and the distance to seed trees all affect fir seedling establishment (Place 1955, Frank 1990, Sims *et al.* 1992, Galipeau *et al.* 1997).

The poor recruitment in the mixed stands may be a result of fewer available quality microsites as conifer and total advance regeneration is most abundant in the mixed forests of this region (Kneeshaw and Bergeron 1996). The abundance of seedling recruitment in the conifer stand may be explained by the abundant fir seed source. This stand was one of the few conifer dominated stands not devastated by the the spruce budworm during the last outbreak. This stand had not only high seedling establishment but also a high density of advance regeneration. In the hardwood stand the recent recruitment of balsam fir may due to trees that survived the last budworm outbreak (Bergeron *et al* 1995) and are only now reaching sexual maturity. This is supported by the young age of this forest, having burned in 1944, the relatively small stature of the trees (Table 1) and the fact that recent seedling establishment accounts for a large proportion of the total regeneration (Figure 2b).

An argument that poorer seedling survival following establishment may explain the higher seedling establishment to total regeneration ratio in hardwood stands does not appear to be valid as greater seedling mortality was not observed in these stands. Longer term observations would distinguish any real patterns in seedling recruitment among stands from short-term temporal variations. However, the lack of any treatment effect or interaction (due to the variation between stand types) and the relatively low ratios of new regeneration to advance regeneration suggest that the initial effect of canopy openings in these forests is on advance regeneration.

Response of advance regeneration

In our study, as in similar research on Scots pine (Sundkvist 1994), the greatest response in all indices was to the all cut treatment. Studies of understory regeneration also show that biomass of the understory vegetation increased most where overstory removal was greatest (Stone & Wolfe 1996, DeGrandpré 1997). The response, in terms of height increment and branch production as also demonstrated by Parent & Messier (1995), Williams (1996) and O'Connell & Kelty (1994), was primarily related to maximum light levels in the different quadrats (Table 4).

In large openings or on drier sites a period of acclimatation may be required for plants to adapt to new growing conditions. In fact, Sundkvist (1994) and Gordon (1973) did not find, as we did, a first year response in height growth to canopy openings but rather they observed a delay or a relative decrease in seedling height growth.

In natural forest dynamics in the claybelt region of the boreal forest, sudden small-sized canopy openings are due primarily to the snapping of aspen stems. Our results suggest that the ensuing conditions would be favourable to an immediate growth response from advance fir regeneration. However this form of gap opening is minor compared with those created by the spruce budworm (>80% of tree mortality in all but the youngest hardwood dominated stands is due to the budworm, Kneeshaw & Bergeron in press).

During spruce budworm outbreaks trees die slowly over a number of years with maximum mortality usually occurring a number of years after the onset of an outbreak (Baskerville & MacLean 1979). The girdled quadrats were the ones designed to most closely mimic this disturbance. Although the girdling treatment was not significantly different from the control it resulted, for all indices, in increased values when compared to the control. Since this treatment does not result in an immediate increase in light, but rather in a gradual increase in light as needles fall off and the tree dies, it is not surprising that significant results are not apparent after two years. The implications are, thus, that in gaps created due to spruce budworm outbreaks advance regeneration is released gradually. In natural systems, height growth has been found, with time, to increase up to five times pre-outbreak levels (Ghent 1958, see also Batzer & Popp 1985).

Silviculturally, it has been suggested that a minimum opening should result in irradiance great enough to permit height growth to equal or to be greater than lateral growth (Klinka et al. 1992). In fir forests in the same area, height growth equalled lateral growth at 25% full light (Parent & Messier 1995). Our study shows that LB ratios greater than one can be achieved with 100 m^2 openings in which all trees are cut.

Conclusion

In fir dominated boreal forests, small openings in which all trees are removed do not affect balsam fir seedling establishment (at least in the short term) but rather influence tree growth and architecture. Silvicultural decisions should therefore focus on concentrating operations where there is sufficient advance regeneration. Stand development in even small cuts of 100 m^2 will be faster than in naturally created spruce budworm gaps due to greater seedling height growth and greater investments in the structure needed to maximize growth.

The results of the girdling treatment suggest that responses of seedlings to budworm outbreaks will be delayed or reduced due to the slow mortality of the overstory trees. Our three year study does not, obviously, provide conclusive results on long-term changes following gap creation but it does suggest that a long-term response to a prolonged increase in light would include not only increased height growth and an increase in the leader to lateral branches ratio, but also an overall increase in the number of branches produced that is proportional to the degree and rapidity of canopy opening.

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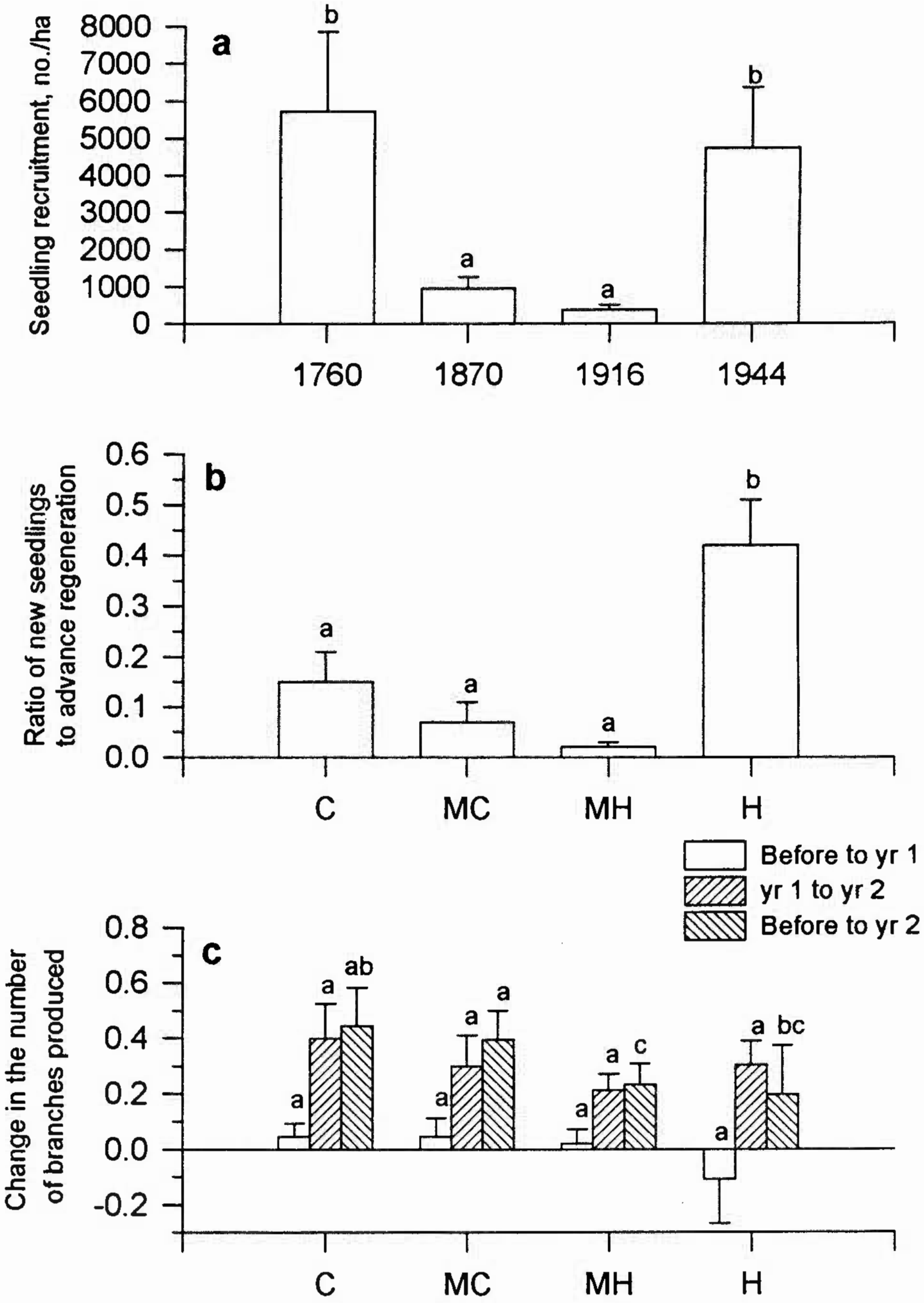

Figure 3.1 Seedling response to the different stand types in terms of a) seedling recruitment, b) the ratio of seedling recruitment to total regeneration and c) changes in branch production. Significant differences ($p < 0.05$) between stand types are noted by different letters.

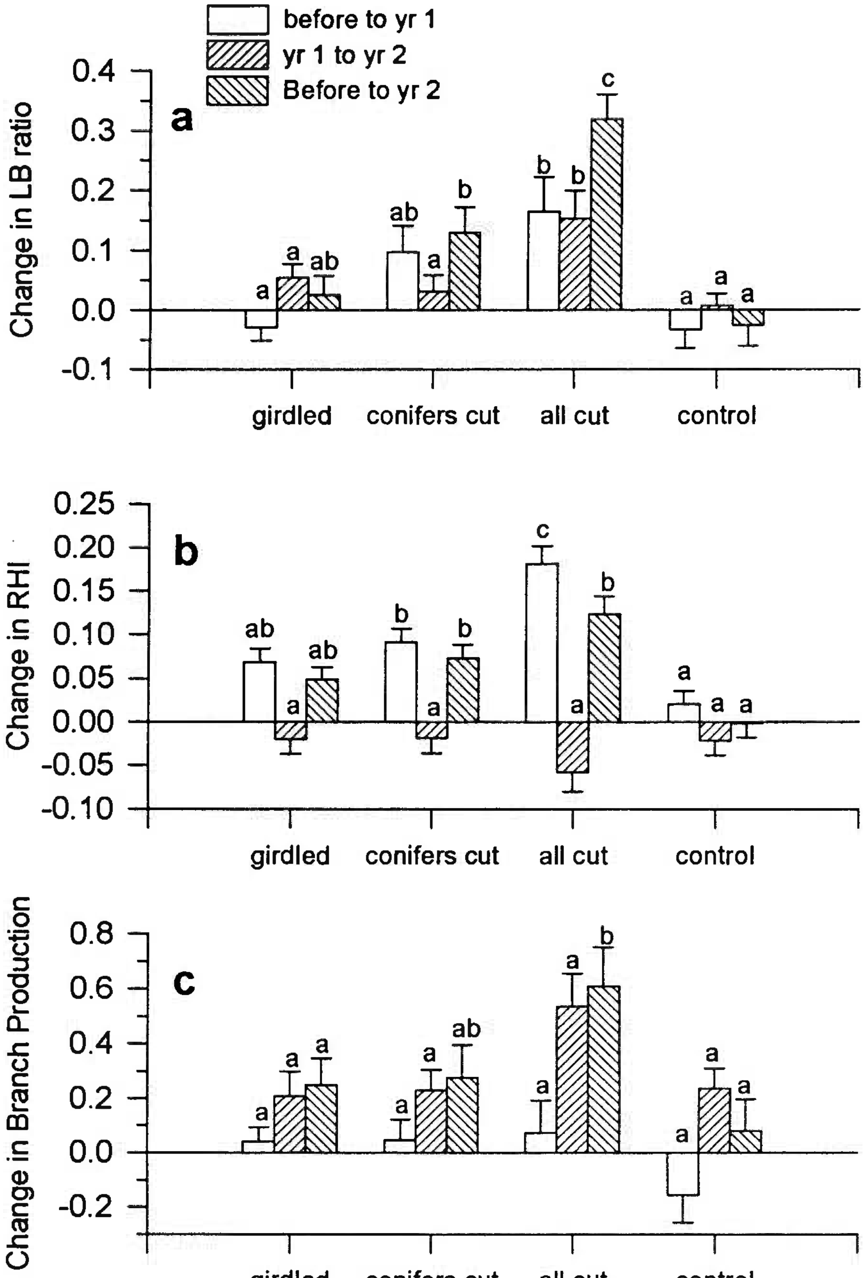

Figure 3.2 Seedling response to the different treatments in terms of changes in the a) LB (leader to branch) ratio, b) the RHI (relative height increment) and c) branch production. Significant differences ($p<0.05$) are noted by different letters.

Table 3.1 Original tree basal area (m^2/ha) by species for each treatment and stand age as well as basal area removed following the treatment. The group conifers is comprised primarily of balsam fir with a small proportion of white spruce. For the treatment girdled the basal area removed is the basal area girdled but remaining in the quadrat. For the other treatments, the trees that are cut are physically removed from the site.

	Control					**Girdled**				
Stand Type	Conifers	Aspen	Birch	Cedar	Removed	Conifers	Aspen	Birch	Cedar	Removed
H	1.3 (1.5)	38.7 (17.5)	4.0 (5.7)	0 (0)	0 (0)	1.4 (0.8)	41.4 (11.0)	1.8 (3.2)	0 (0)	1.4 (0.8)
MH	9.4 (3.4)	20.4 (17.7)	11.1 (15.3)	0 (0)	0 (0)	7.9 (5.3)	22.3 (9.1)	10.1 (5.7)	0 (0)	7.9 (0.8)
MC	16.3 (13.6)	30.1 (5.2)	1.4 (1.1)	0 (0)	0 (0)	8.0 (3.0)	23.2 (5.0)	2.6 (2.6)	0 (0)	8.0 (2.9)
C	19.4 (6.2)	3.9 (6.8)	0 (0)	15.9 (7.0)	0 (0)	21.2 (13.4)	0 (0)	0 (0)	22.4 (10.0)	21.2 (13.4)

	Conifers Cut					**All Cut**				
Stand Type	Conifers	Aspen	Birch	Cedar	Removed	Conifers	Aspen	Birch	Cedar	Removed
H	1.7 (1.8)	30.8 (20.5)	6.5 (9.6)	0 (0)	1.8 (1.8)	3.8 (5.2)	18.1 (13.8)	11.4 (9.0)	0 (0)	33.4 (9.3)
MH	11.7 (8.4)	17.0 (16.2)	8.6 (6.3)	0 (0)	11.7 (8.4)	8.7 (4.0)	0.0 (0.0)	10.5 (1.5)	0 (0)	19.2 (3.6)
MC	14.6 (7.8)	21.7 (15.0)	5.9 (0.9)	0 (0)	14.7 (7.8)	20.5 (11.6)	18.1 (2.0)	2.2 (3.8)	0.2 (0.4)	41.0 (11.5)
C	17.6 (6.1)	0 (0)	0 (0)	17.8 (15.2)	17.6 (6.1)	19.5 (9.9)	3.9 (6.8)	0 (0)	15.9 (7.0)	38.5 (9.3)

Table 3.2 Pre-treatment LB ratio, RHI and branch production values and standard errors for the treatments and stand types.

	LB Ratio	RHI	Branch Production		LB Ratio	RHI	Branch Production
Girdled	0.504 ± 0.022	0.482 ± 0.012	1.356 ± 0.119	H	0.626 ± 0.039	0.494 ± 0.016	1.778 ± 0.157
Conifers Cut	0.511 ± 0.026	0.483 ± 0.010	1.316 ± 0.129	MH	0.525 ± 0.020	0.500 ± 0.010	1.551 ± 0.107
All Trees Cut	0.538 ± 0.032	0.475 ± 0.019	1.264 ± 0.115	MC	0.485 ± 0.023	0.485 ± 0.007	1.104 ± 0.084
Control	0.574 ± 0.029	0.501 ± 0.011	1.457 ± 0.233	C	0.530 ± 0.031	0.462 ± 0.016	0.944 ± 0.129

Table 3.3 Two-way ANOVA's for the growth and architecture indices as well as for seedling recruitment, showing their F-values for Stand, Treatment and interaction effects. Significant probabilities are marked with asterisks such that * < .05, ** <.01 and *** <0.001.

	Leader to Lateral Branch Ratio			**Relative Height Increment**		
	2 yr difference	1 yr difference	2nd - 1st yr diff	2 yr difference	1 yr difference	2nd - 1st yr diff
Treatment	13.049 ***	9.969 ***	3.314 *	5.462 ***	12.006 ***	1.164
Stand	0.870	0.713	0.895	0.979	0.555	0.786
Trtmnt x Std	0.630	3.320 **	1.017	1.551	1.453	1.156

	Branch Number			**Seedling Recruitment**	**Seedling Recruitment to Advance Regeneration Ratio**	**Seedling Mortality**
	2 yr difference	1 yr difference	2nd - 1st yr diff			
Treatment	4.251 **	1.554	4.601 **	1.193	0.610	0.172
Stand	7.154 ***	1.068	3.705 *	3.519 *	0.000 ***	0.793
Trtmnt x Std	2.358 *	1.399	2.917 **	0.908	0.881	0.521

Table 3.4 Regression equations for the different growth and architecture indices based on abiotic and competition variables. These equations were calculated only for those periods that were significantly ($p < 0.05$) affected by the treatments.

	R^2
Leader to Branch Growth Ratio Difference:	
Before treatment to two years after treatment = -2.108 + 1.849 July Soil Moisture + 0.072 June Soil Temperature + 0.3 (2 yr change in total shrub and herb cover)	0.50
Before treatment to one year after treatment = -0.913 + 1.10 July Soil Moisture + 0.012 (1 year change in total herb cover)	0.23
Relative Height Increment Difference:	
Before treatment to two years after treatment = -0.146 + 0.082 Above Shrub Light	0.29
Before treatment to one year after treatment = -0.193 + 0.104 Above Shrub Light + 0.058 Nitrogen Leaching	0.41
Branch Production Difference:	
Before treatment to two years after treatment = -1.073 + 1.573 July Soil Moisture	0.134
Year one to year two = -0.191 + 0.194 Above Shrub Light	0.104

CHAPITRE IV

SPATIAL AND TEMPORAL PATTERNS OF SEEDLING RECRUITMENT WITHIN SPRUCE BUDWORM CAUSED CANOPY GAPS

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4.1 ABSTRACT

Gap dynamics theory suggests that spatial and temporal patterns of species recruitment within canopy gaps may be due to differences in tolerance to shade. Although this theory has been developed in low latitude forests we suggest that it is also applicable to boreal forests. This study investigates temporal and spatial seedling patterns in spruce budworm caused canopy gaps. Five gaps in a 234 year old conifer dominated forest were investigated in the southern part of the boreal forest. All trees were mapped with XY coordinates and seedlings, shrubs and herbs mapped in a grid overlain onto the gap. Seedlings were also aged. Nearest neighbour distances to gap edges and distance to southern gap edge were measured from the centre of all quadrats. Percent cover of shrubs and of herbs was evaluated in all quadrats, and calculated for the quadrat to the south and for all eight adjacent quadrats. Shade tolerant fir and cedar seedlings were found in the southern part of the gaps while intolerant aspen seedlings were correlated to the northern part of the gaps. At the gap level fir seemed to be less abundant where *Acer spicatum* cover was high. This was verified at the smaller scale of individual quadrats where fir seedling density was negatively related to *A.spicatum* cover. A temporal partitioning of gaps into pre and post gap formation also shows a gradient of species establishment related to shade tolerance. The zone of high light in the northern part of large gaps may be one of the mechanisms permitting the maintenance of intolerant species in these forests. However, the small area of this zone and the slowness of gap formation will limit their abundance.

Key Words: shade tolerance, canopy gaps, spatial position, shrub competition, seedling recruitment, balsam fir, trembling aspen, cedar, spruce budworm

Key Phrases: temporal and spatial partitioning of gaps, maintenance of shade intolerant species, competition by *Acer spicatum*, boreal forest stand dynamics, spruce budworm caused canopy gaps

4.2 RÉSUMÉ

La théorie relative à la dynamique des trouées propose que le recrutement spatial et temporel des espèces dans une trouée s'effectue selon leur degré de tolérance à l'ombre. Bien que cette théorie ait été développée dans les forêts du sud, elle peut aussi s'appliquer à la forêt boréale. Cette étude vise à évaluer les patrons spatiaux et temporels de recrutement des semis de différentes espèces dans des trouées causées par la tordeuse des bourgeons de l'épinette (TBE). Cinq trouées ont été étudiées dans des peuplements localisés au sud de la forêt boréale et qui n'étaient pas perturbés par le feu depuis 234 ans. Dans chaque trouée, tous les arbres ont été cartographiés en utilisant un système de coordonnées XY. L'abondance des semis ainsi que les recouvrements arbustif et herbacée ont aussi été mesurés à l'aide d'une grille composée de quadrats de 2m par 2m couvrant l'ensemble de la trouée. Tous les semis ont été âgés au laboratoire. Pour chaque parcelle de 4 m^2, la distance minimale entre son point central et la bordure de la trouée fut mesurée de même que la distance la séparant de la bordure sud de la trouée. Le recouvrement des espèces compétitrices a aussi été évalué dans chaque quadrat et leur influence a été analysée en utilisant une moyenne pour les huits parcelles adjacentes à chaque quadrat de même qu'en utilisant le quadrat localisé immédiatement au sud. Nos résultats indiquent que le sapin et l'épinette, deux espèces tolérantes à l'ombre, se retrouvent au sud des trouées tandis que les semis des espèces intolérantes tel que le tremble, sont associés avec la portion nord des trouées. À l'échelle des trouées, l'abondance du sapin et le recouvrement de l'érable à épis semblent être inversement corrélés et cette relation est verifiée à l'échelle des quadrats. L'analyse des patrons d'établissement temporels des espèces indique un partitionnement selon le degré de tolérance à l'ombre. Les espèces intolérantes à l'ombre s'établissent suite à l'épidémie de la TBE alors que les espèces tolérantes sont, à la fois, recrutées avant et suite à la formation de la trouée. Le maintien des espèces intolérantes dans les forêts âgées est assuré par la grande dimension des trouées. Cependant, elles ne seront pas abondantes car les processus menant à la formation des trouées par la TBE sont lents et parce que la zone recevant de la lumière directe se limite à une petite superficie au nord de la trouée.

4.3 Introduction

Throughout the range of balsam fir (*Abies balsamea*), spruce budworm outbreaks have had a major impact on the structure and development of the forest. Where forests are composed of pure stands of fir, damage caused by this insect results in large scale mortality. A cyclical pattern of fir mortality followed by waves of fir recruitment from abundant advance regeneration has been proposed and subsequently supported for these forests (Baskerville 1975, MacLean 1984, 1988, Morin 1994)

In forests with more diverse species composition the pattern is far more complex. Spruce budworm outbreaks lead to a patchy forest structure in which less vulnerable and non-host tree species survive the outbreak. The forest then becomes a mosaic of forested areas and gaps. Ghent et al. (1957) found that increases or decreases in the ratio of fir to spruce following budworm outbreaks varied from region to region. It has also been suggested that spruce budworm outbreaks may lead to the forest oscillating between birch and fir dominance (Marchand 1990). Successional stage (compositional type) has been found to have a further impact on species recruitment following budworm outbreaks (Kneeshaw and Bergeron in press). In this study, balsam fir, although always the most abundant seedling, decreased in proportion in the older stands while cedar increased. Frelich and Reich (1995) also suggest that cedar, because it is a non-host tree, is able to increase at the expense of fir where fire does not occur for long periods. Even in pure eastern fir forests the budworm may have an impact on relative seedling abundance in different stand types. Hardwood regeneration was found to increase most in mature stands and least in immature stands while fir regeneration decreased most in older stands (Spencer 1985).

Other changes in stand dynamics may be due to interactions with non-tree species. In Minnesota, fir regeneration decreased when overstory mortality exceeded 80% of the initial stand basal area while the abundance of shrubs increased (Batzer and Popp 1985).

Kneeshaw and Bergeron (in press), as well, suggest that fir seedling densities may decrease in large gaps due to increased competition from shrubs.

Temporal patterns in seedling recruitment are also affected by budworm outbreaks. The budworm feeds preferentially on new tissues, including reproductive tissues (Schooley 1978), thus limiting seed production to those trees not attacked by the budworm. Many studies have shown that regeneration following an outbreak is primarily composed of trees established prior to the outbreak (Fye and Thomas 1963, MacLean 1988, Morin and Laprise in press, Osawa 1994). However, other studies have shown that abundant seedling establishment can occur during and after the outbreak (Batzer and Popp 1985, Marchand 1990). The maintenance of intolerant species may also be due to openings in the canopy. Many studies indeed suggest that shade intolerant species may increase in abundance following budworm outbreaks or show that significant numbers of birch and other hardwood invaders are present on the site (MacLean 1984, 1988, Marchand 1990). However, budworm-caused overstory mortality occurs over a period of years and therefore increases in light are gradual. Such gradual increases may be more advantageous to tolerant or semi-tolerant trees or shrubs.

Gap dynamics theory suggests that species differ in the size of gaps in which they are most succesful and in the period of time in which they establish relative to gap formation (Brokaw 1985, 1987, Whitmore 1989). A further extension of this idea is that different locations in the gap will be more favourable to some species than others. Putz (1983) and Brokaw (1985) suggest that shade intolerant trees will be most succesful in the centre of gaps and shade tolerants towards the periphery. These studies, however, come from tropical regions where incident light comes from high angles. In boreal regions sun angles are, on the other hand, lower and direct beam radiation is displaced to the north of the gap (Canham et al. 1990, Ban et al. In review). It can then be hypothesized that northern gap locations should be more favourable for shade intolerant species.

To test this hypothesis and to better understand patterns in seedling regeneration we investigated the spatial relationship of seedlings to the surrounding gap and to vegetation within the gap along a gradient of gap sizes. Similarly, temporal variation in seedling recruitment has also been studied. A number of hypotheses are suggested: 1) that seedling abundance will be greatest at increasing distances from the southern edge of the gap (i.e. where light levels are higher), 2) that seedlings will be most successful where shrubs (see Ghent 1958, Batzer and Popp 1985) are low in abundance and 3) temporally it is expected that most fir and spruce recruitment will be from the pre-outbreak period, that cedar will be recruited continuously and that birch and aspen will be recruited immediately following the period of maximum overstory mortality.

4.4 Study Area

The study area is situated in Quebec's southern boreal forest at a latitude between 48° 15` and 48° 30` North and a longitude of 79^0 15` and $79^0$ 30` West. This region is characterized by clay deposits from the post-glacial lakes Barlow and Ojibway (Vincent and Hardy 1977). The study region, in the forests surrounding Lake Duparquet, is dominated by a rolling clay lowland interspersed by small rocky hills up to 550 m in elevation overlain with reworked till deposits (Bergeron *et al.* 1983). The climate can be classified as cold and continental with an annual average temperature of 0.8^0C and with an average annual precipitation of 857 mm (Anonymous 1993). The average number of frost free days is 64, although frost can occur at any time during the growing season (Anonymous 1993).

The forests of the study area belong to the fir to white birch climax region (Thibault and Hotte 1985) or to Rowe's (1972) Missinaibi- Cabonga section where an association of balsam fir, black and white spruce with paper birch and trembling aspen dominates. Jack pine may also be present on some sites, and where fire has not occurred for long periods white cedar may be abundant (Bergeron and Dubuc 1989).

The fire history of stands in the Lake Duparquet area has been reconstructed using dendroecological techniques (Bergeron 1991, Dansereau and Bergeron 1993). The fire cycle has changed from an estimated 63 years for the pre 1870 period to greater than 99 years in the current period. Gap characteristics described by Kneeshaw and Bergeron (In-Press) show that the proportion of the forest in canopy gap varies from 7% in the youngest hardwood dominated forests to more than 40% in the oldest conifer dominated forests. Gaps in these older forests are caused primarily by mortality resulting from the death of balsam fir trees during the last spruce budworm outbreak. Past epidemics have been reconstructed by Morin *et al.* (1993) with the 1972 to 1987 outbreak resulting in the death of most of the *Abies* trees (Bergeron *et al.*1995). Defoliation due to a 1950's forest tent caterpillar outbreak has also been documented as causing a significant hardwood growth decrease (Bergeron and Charron 1994). Forest harvesting was unimportant until large-scale clear-cuts began in the western part of the region in 1978.

4.5 Methods:

4.5.1 Field Methods

Five gaps of a range of sizes (59 m^2 to 560m^2) were randomly chosen in a conifer dominated forest that had not burned for 234 years (Table 1). The chosen gaps were all greater than 100m from the lake and located on mesic sites with clay soils. Gaps were chosen along a gradient of sizes as a number of researchers have shown that seedling abundance varies with increasing overstory mortality (Kneeshaw and Bergeron In-Press, Batzer and Popp 1985, Osawa 1994).

In the summer or 1994 the perimeter of the expanded gap (EG) which is described by the stems of the live trees bordering the gap was marked off with cord. The vertical projection of the gap onto the ground was evaluated at two metre intervals from the gaps central axis. Similarly, a grid, using 2m by 2m quadrats, was then marked off from the central north-south or east-west axis of the gap. Quadrats were also located in the understory to the north, south east and west of the gap. The position of all live and dead trees (> 2.5 cm DBH) was then mapped and their state (live or dead), their DBH and their species was also recorded. Seedlings (<2.5 cm DBH) were counted by species within each of the gridded quadrats. The tree and seedling species encountered in this study were balsam fir, white spruce, eastern white cedar, trembling aspen and paper birch. Seedlings were generally of sexual origin with the exception of trembling aspen which reprodced in these gaps exclusively from root suckers.

A number of authors have found that seedling height has a stronger relationship to gap opening than seedling density or age (Batzer and Popp 1985, Ghent 1958, Morin and Laprise In-Press, Kneeshaw and Bergeron submitted). Therefore, the height of the tallest, undamaged seedling of each species was also recorded and these seedlings were also harvested so that growth indices could be calculated in the laboratory. The largest seedlings were chosen to represent the individual per quadrat with the greatest chance of being recruited to the tree layer.

Within each of the quadrats the percentage cover of *Acer spicatum, Corylus cornuta, Taxus canadensis, Alnus rugosa, Rubus idaeus*, all other shrub species combined, all herbs combined and total cover was noted. Similarly, the percentage of the quadrat covered by logs, either hard or decomposed, was also recorded.

To determine seedling age structures, all seedlings were harvested in a randomly selected sub-sample of from five to nine of the measured quadrats. The seedlings in these quadrats were tagged and uprooted and taken back to the laboratory for ageing. The aspen suckers were exposed to find the point where the sucker joined the root, the root was then cut on sither side of the sucker and the sucker was separated from the root tissue in the laboratory.

4.5.2 Laboratory Analyses

Initially all fir and spruce seedlings were aged by counting bud scars (cedar, birch and aspen have indeterminate growth forms that prohibit the use of this technique for aging seedlings). Subsequently seedling disks of all five species were cut at the root collar. Morin and Laprise (in press) using stem cross-sections at different heights above and below the point where the stem was in contact with the soil found that maximum age of balsam fir occurred at the root collar. Vegetatively reproduced seedlings were aged where the seedling stem separated from the adult tree tissue. The disks were then sanded and seedling ages determined under a microscope. Except for the very youngest seedlings, ages determined by counting bud scars underestimated the ages determined by counting tree rings and therefore only data obtained from counting tree rings is presented here. Even so, Morin and Laprise (in press) report that there is great difficulty in obtaining accurate age counts of seedlings due to suppressed rings. To mediate this problem seedling data are presented in 5-yr age classes.

To evaluate changes in growth and architecture a number of indices was used. The first, the leader to lateral branch (LB) ratio, reflects changes in architecture. This ratio is calculated as $L/(\text{average}[B_i..B_n])$, where L is the leader length and $B_{i..n}$ are the lengths of the lateral branches produced from the same node as the leader. The second index used was the relative height increment (RHI) defined as the ratio of the height increment in year *n* to the height increment of year *n* plus year *n-1* (Brand 1986). Due to the effect of initial size on height increment response following openings (Hatcher 1964, Ghent 1958), RHI was calculated to permit a comparison in height growth between individuals of different initial size. The final index used was the total number of branches per node, again compared using year to year differences. In detail explanations of the use of these indices can be found in Kneeshaw and Bergeron (in review). It is also noted that balsam fir was the only species evaluated due to its determinate growth form and the small sampling size of the other species.

From the mapped data a matrix of quadrat positions with their associated values was created. To evaluate the impact of vegetation in the current quadrat or in adjacent quadrats, spreadsheet macros, that acted in the same fashion as sliding windows in raster based GIS's, were created for each of the five gaps to calculate the percentage cover of competing species in 1) the quadrat to the south, 2) the average of the current quadrat and the one to the south, and 3) the average of all eight surrounding quadrats.

The mapped grid of quadrat positions was overlain onto the map of gap and expanded gap positions so that quadrat position relative to the gap perimeter could be assessed. The distance from the centre of each quadrat was then measured to the southern border of both the gap and the EG and to the nearest border of the gap and the EG.

4.5.3 Data Analysis

Differences in seedling abundance, between the different gaps, were tested using ANOVA's, based on log-transformed densities where neccessary, with differences between gaps being tested by post-hoc Bonferonni tests. Differences in shrub and herb cover were also tested in the same way, although where transformations failed to correct problems with homogeneity of variance Kruskal-Wallis tests were used. All statistical tests were performed using SPSS version 6.02.

Multiple linear regressions based on the data from all 554 quadrats were used to investigate the relationship between position in the gap and the abundance of balsam fir regeneration. A similar series of regressions investigated the effect of vegetation cover on fir seedling density. Although six groups of shrubs were identified and their cover evaluated, in practice *Rubus* and *Alnus* occurred too rarely to be considered in the analyses. Collinearity analyses were performed on all stepwise regressions to eliminate correlated independent variables. Log transformations were used for fir density and fir's LB ratio. Arcsine square root transformations were used where necessary for the percent cover data.

The four other seedling species (spruce, aspen, birch and cedar) occurred in much lower numbers and were often absent from many of the quadrats. Thus logistic regressions were used to evaluate the factors affecting the presence or the absence of these seedlings from any given quadrat.

In experimentally created gaps the effect of the opening is often evaluated with respect to seedling growth. In this study we therefore also investigated whether seedling height of the tallest seedling per quadrat is related to position using a series of multiple linear regression as described earlier. For balsam fir multiple linear regressions were also used to investigate the relationship between both position in the gap and vegetation cover on the leader to branch (LB) ratio, the relative height index and the number of branches produced in the last whorl. Data are only presented for those relationships that were significant at $\alpha = 0.05$.

4.6 Results

4.6.1 Gap Level Patterns

Balsam fir regeneration densities varied from about 32 000 seedlings per hectare in the smallest gap to an average of 2 500 seedlings per hectare in the largest (Figure 1). The seedling densities of the other gaps were close to the 23 000 seedlings per hectare noted for 234 year old forests of this region (Kneeshaw and Bergeron 1996). The largest gap had a significantly lower density of seedlings than all other gaps, whereas the smallest gap had a significantly greater abundance of seedlings than all gaps except the middle sized 149 m^2 gap (Figure 1). This pattern was the inverse ($p < 0.000$) of that found for *Acer spicatum* which statistically had its greatest cover in the largest gap and its lowest cover in the smallest gap (Figure 2). The other gaps had intermediate *Acer* coverage (from 20 to 30%) that varied inversely with the fluctuations in fir density for these gaps. Although a negative relationship was not noted between fir density and the per cent cover of the other studied vegetation groups (*Taxus canadensis, Corylus cornuta,* all other shrubs grouped together, herbs), it can be observed that herb and shrub cover was low for all species in the smallest gap.

The other tree species were found in much lower numbers than balsam fir (Figure 1). Although seedling abundances for white spruce, cedar, birch and aspen varied from gap to gap the large variation in fir density between the smallest and largest gaps was not repeated with these other species. No trends in spruce, birch and aspen seedling abundances were observed with respect to gap size. On the other hand, cedar was most abundant in the smallest and largest gaps. Although the trend was not linear, fir was generally more abundant in smaller rather than in larger gaps whereas *Acer* was generally more abundant in the larger gaps. The lack of strong patterns with respect to gap size may be due to the small sample size.

4.6.2 Spatial Relationships Within Gaps

Within gaps there is a negative relationship between fir density and the distance to the southern expanded gap boundary and to the nearest expanded gap boundary (Table 3). Fir height and its LB ratio were also highest closest to the southern gap boundary. This relationship is slightly more restrictive than the relationship to the expanded gap boundary. Aspen was the only species to have a positive relationship to distance from the southern edge of the gap. This positive relationship was true for both the probability of finding seedlings and seedling height.

4.6.3 Seedling Relationships to Competing Vegetation

The apparent negative relationship between *Acer* and fir at the whole gap level is verified by multiple linear regression analyses performed at the quadrat level (Table 4). *Acer* cover not only negatively affected fir density but also the height of fir and spruce seedlings. The indices used to evaluate fir's growth and architecture were most affected by total competing vegetation cover, however these relationships were weak. On the other hand, total vegetation cover was more strongly negatively correlated to the height of cedar seedlings. With respect to the other tree species, *Acer* cover had a negative effect on the probability of finding spruce but was positively related to the presence of cedar.

Other positive relationships were noted between the percent cover by *Taxus* and fir height and fir's LB ratio. These positive relationships were noted despite a negative relationship between fir density and *Taxus* cover. This perhaps reflects the fact that the few seedlings that establish and survive must be taller that the *Taxus* cover in quadrats where *Taxus* is abundant.

4.6.4 Seedling Establishment

The balsam fir age distributions show that the largest peaks in seedling establishment occurred in the period slightly preceding or just entering into the outbreak (Figure 3). The last outbreak in this area was established as occurring between 1970 and 1986 with a growth recovery between 1975 and 1979 (Morin *et al.* 1993). A peak in seedling establishment in the 1979 age class in the 146, 217 and 447 m^2 EG's appears to be associated with this period of growth recovery. Only in the 278 m^2 EG is seedling establishment primarily restricted to the pre-outbreak period with 74% of the seedlings being recruited prior to 1970. For the other gaps, ordered by size, the pre-outbreak seedlings comprise 48%, 33%, 34% and 43% of the seedlings respectively. The 447 m^2 EG is the only one of the gaps to maintain a large number of live fir trees. Kolmogorov-Smirnoff tests show that all the age distributions are significantly different from each other ($\alpha < 0.05$) with the exception of the 278 m^2 EG. The age distribution in this gap is only significantly different than that of the 217 m^2 EG.

Although the number of white spruce that were aged is too small to present age structures, average ages suggest that seedling establishement is similar to that of fir (Table 2). An almost equivalent proportion of spruce established in the pre-outbreak vs post-outbreak period (50%, 50%, 56%, 80% and 19% for gaps 1 to 5 respectively). Cedar establishment also follows a pattern similar to white spruce and balsam fir.

Aspen suckers and birch seedlings were, as expected, much younger than the conifer seedlings Table 2). Aspen regeneration began on average in the late 1980's in the period following the end of the outbreak. Paper birch recruitment began on average in the early to mid-80's with only one large seedling dating to the pre-outbreak period.

4.7 Discussion

4.7.1 Position within the gap

The data from our study support the idea that species success will vary with position in the gap. Aspen suckers, the least tolerant species to shade (Perala 1990), were associated with distance towards the northern part of the gap. The position of adult trees should not have affected the position of suckers as adults were found in equal numbers to the north and south of the gaps and because aspen suckers can be produced at distances greater than thirty metres from adult trees (Lavertu et al 1993, Stettler et al 1996). Gaps created by the spruce budworm, due to their large size, may therefore be necessary for the maintenance of intolerant species in areas of the landscape that have not burned for long periods (Baskerville 1975). Only these gaps attain sizes large enough to ensure areas of direct light. In fact, in our study area the distance from the southern border of the gap must be 1.124 times the height of the canopy for direct light to be received at ground level (Kneeshaw and Bergeron In press). Saplings located in the northern part of the gap will, however, grow into this zone of direct light. Nonetheless, the abundance of intolerant species will be limited by the small area of high light found only in the northern part of these gaps.

The pattern of finding a shade intolerant species at the northern edge of gaps contrasts with a study in northern Finland where shade intolerant Scots pine seedlings grew well in the centre of gaps but remained suppressed close to the edges of the gap (Aaltonen 1919 cited in Kuuluvainen 1994). A similar relationship in our study would have been represented by a positive relationship to distance from the nearest edge of the gap.

The shade tolerant species, balsam fir and white spruce (Frank 1990, Sims *et al.* 1991, Coates *et al.* 1995), were, in contrast to aspen, most abundant in the shaded southern parts of the gap. The presence of cedar, another very tolerant species (Johnston 1990), was also correlated to the southern part of the gap in independent regression analyses for the two largest gaps ($p<0.009$ and $p<0.000$, analyses not shown). A number of studies investigating seedling abundance have demonstrated that fir and other shade tolerant seedlings are found in greater number under canopies than in gaps while the inverse is true for species such as birch (Abe 1995, Perkins *et al.* 1992, White *et al.* 1985).

The greater abundance of the coniferous species in the shaded part of the gap may in part be due to the higher moisture levels found in these areas that are not exposed to direct light. Balsam fir, white spruce and cedar are vulnerable to dessication and in fact, for the germination of balsam fir, moisture has been noted to be more important than light (Frank

1990). It has also been noted that fir recruitment following fire was severely limited until after the development of a vegetation cover (Galipeau *et al.* 1997). In forested conditions a number of studies have documented the greatest survival and or abundance of fir as occurring under partial canopy cover (Osawa 1994, Batzer and Popp 1985, McLaren and Janke 1996, Côté and Bélanger 1991). For example, McLaren and Janke (1996) found that balsam fir seedling germination and survival was greatest under 40-79% cover. Even seedling growth follows a similar pattern, for in an experimental study the largest fir seedlings were found at intermediate light conditions (Logan 1969).

Our results, showing that spatial position within gaps influences species recruitment, empirically verify those derived from a forest simulation model suggesting that the spatial distribution of trees is important in explaining species patterns in the forest mosaic (Pacala and Deutschman 1995). Furthermore, in a spatially explicit study of stand dynamics in boreal forests of Minnesota it was found that at large-scales succession appeared convergent towards a number of tolerant species but at a small-scale small clusters of different species occurred (Frelich and Reich 1995). Although our study did not explicitly investigate the effect of spatial scale our observations are consistent with their results. At the gap level, stands are dominated by fir; a species that is ten times more abundant than any other individual species in most gaps. At a smaller scale, within gaps, aspen is associated with the northern portion and fir, spruce and cedar with the southern part of the gap. It has also been noted that small patches of adult aspen are often encountered in these older conifer dominated forests (personal observation).

4.7.2 Competing species

In the budworm literature, shrubby species have often been identified as being linked to areas of poor seedling recruitment (Ghent *et al.* 1957, Batzer and Popp 1985, Osawa 1994). Unlike Osawa's (1994) study, raspberry and pin cherry were unimportant competitors in our region following the last budworm outbreak although raspberry has been recognized as an important shrub following cutting in our study region (Harvey *et al.* 1995). Instead the greatest shrub response, in budworm created gaps of this region, is from *Acer spicatum*

(Degrandpré et al. 1993). It has also been suggested that *Acer* and other shrubs are most abundant when overstory mortality is highest (Batzer and Popp 1985). At both the gap level and the quadrat level *Acer* had a strong negative impact on balsam fir abundance and height. The use of a gap size gradient in this study also suggests a gap size relationship, with larger gaps generally having a higher *Acer* cover than small gaps where fir was abundant. In earlier research we suggested that such a relationship may explain the negative correlation of fir to gap size.

Although fir is negatively affected by *Acer*, cedar is not and both Kneeshaw and Bergeron (in press) and Frelich and Reich (1995) have noted that, in the absence of fire, the proportion of cedar relative to fir may increase as cedar is a long-lived, non-host species to the spruce budworm. The ability to recruit where fir recruitment is reduced may therefore confer an added advantage on cedar.

Interactions with shrub species, as recognized following forest harvesting, will also have a large impact on forest patchiness at different scales. Shrub abundance and their negative impact on seedling growth will also slow down the transition to a new forested state following budworm outbreaks.

It is also interesting to note the importance of considering not only shrub competition in the same quadrat as the tree seedlings but also in adjacent quadrats. Traditionally, only the direct impact of shrub competition is considered. In our study, the taller shrubs found in adjacent quadrats had a strong negative impact on seedling presence, height and density. This impact is not only observed for quadrats to the south, because of shading, but also from all surrounding quadrats. This may be due to the high latitudes of these forests and the many angles from which sunlight is received during the growing season.

4.7.3 Period of recruitment

Observations of the temporal recruitment of seedlings show a partitioning of species into periods of post and pre- gap formation. Aspen recruitment occurs almost entirely in the post-outbreak period i.e. after 1987 (Morin *et al.* 1993). Birch establishment occurred on average in the early 1980's during the period of heaviest fir mortality (Bédard 1993, Plourde 1994). The greatest period of conifer seedling establishment was in the early seventies although a number of seedlings of each of these species established as early as the 1930's following the first budworm outbreak this century (Morin et al 1993). Ghent (1958) has also shown that fir seedling banks begin building up 20 to 30 years before the onset of an outbreak. Shade tolerant species such as fir that are abundant in the understory therefore have an advantage in gaps that are formed by the slow mortality of the overhead trees. Indeed, many authors have suggested that the large balsam fir seedling banks are responsible for a cycling of fir forests following budworm outbreaks (Baskerville 1975, MacLean 1984, Morin 1994). The results from this study concord with these earlier studies to the extent that balsam fir will remain the most abundant species following spruce budworm outbreaks.

In our study area, however, balsam fir seedling densities are much lower than in the relatively pure balsam fir stands to the east (Kneeshaw and Bergeron 1996 vs Morin and Laprise in press). Competition on our productive and more species rich sites may limit the abundance of advance regeneration. In such areas, a lack of abundant post-outbreak regeneration may limit the degree to which a pure fir stand may develop. Such an hypothesis would also support the moisture-shade relationship suggested earlier, as fir germination and young seedlings are more vulnerable to moisture stress than established seedlings. These post-outbreak seedlings, which comprise about 50% of the observed regeneration in both our study and that of Batzer and Popp (1985), should therefore be more abundant in the shaded parts of the gap.

The observation that aspen establishment occurs only after 1987 may be explained by the slow formation of gaps following spruce budworm outbreaks. The budworm prefers current year foliage and therefore continuous defoliation over a number of years is required before tree death occurs. In mature stands trees begin dying after 4 to 5 years and in immature stands after 7 to 8 years with the completion of mortality after approximately 12 years (MacLean 1980). This slow formation of gaps may therefore be another factor limiting the abundance of aspen recruitment following budworm outbreaks.

In conclusion, our study not only shows that the spruce budworm has an important role in the maintenance of mixed woods in this part of the boreal forest but that spatial patterns are important in understanding changes in tree composition. In the absence of budworm outbreaks, we suggest that small gaps formed by the senesence of individuals or small groups of trees would result in the increasing dominance of balsam fir. Early successional trees would not be able to recruit and with time would slowly disappear from the forest. The budworm by creating large canopy gaps therefore permits the maintenance of the boreal mixed-wood even in the absence of stand-destroying fires.

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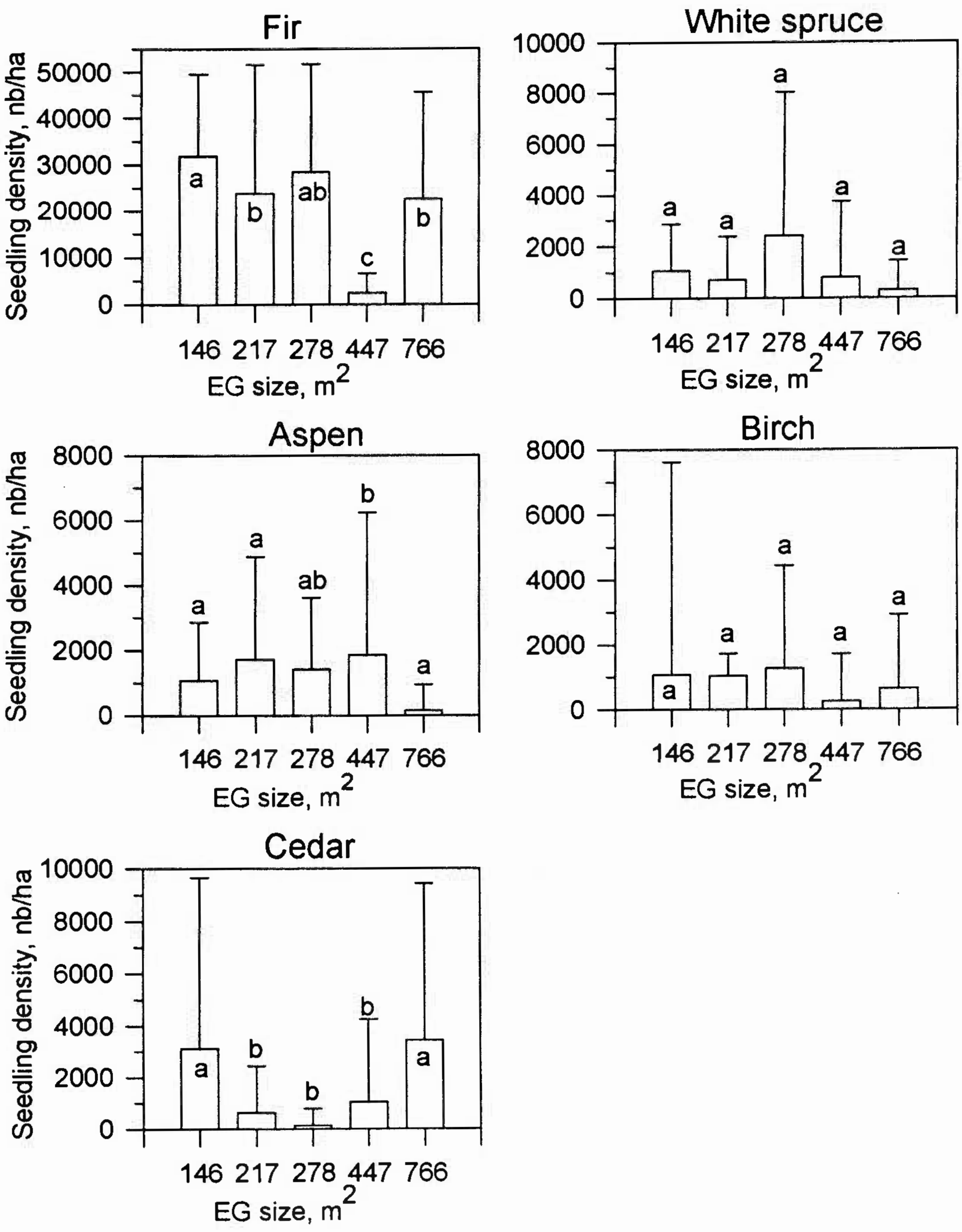

Figure 4.1 Average seedling densities and standard deviation for the five species in the studied gaps. Bars with different letters are statistically different, $p<0.05$

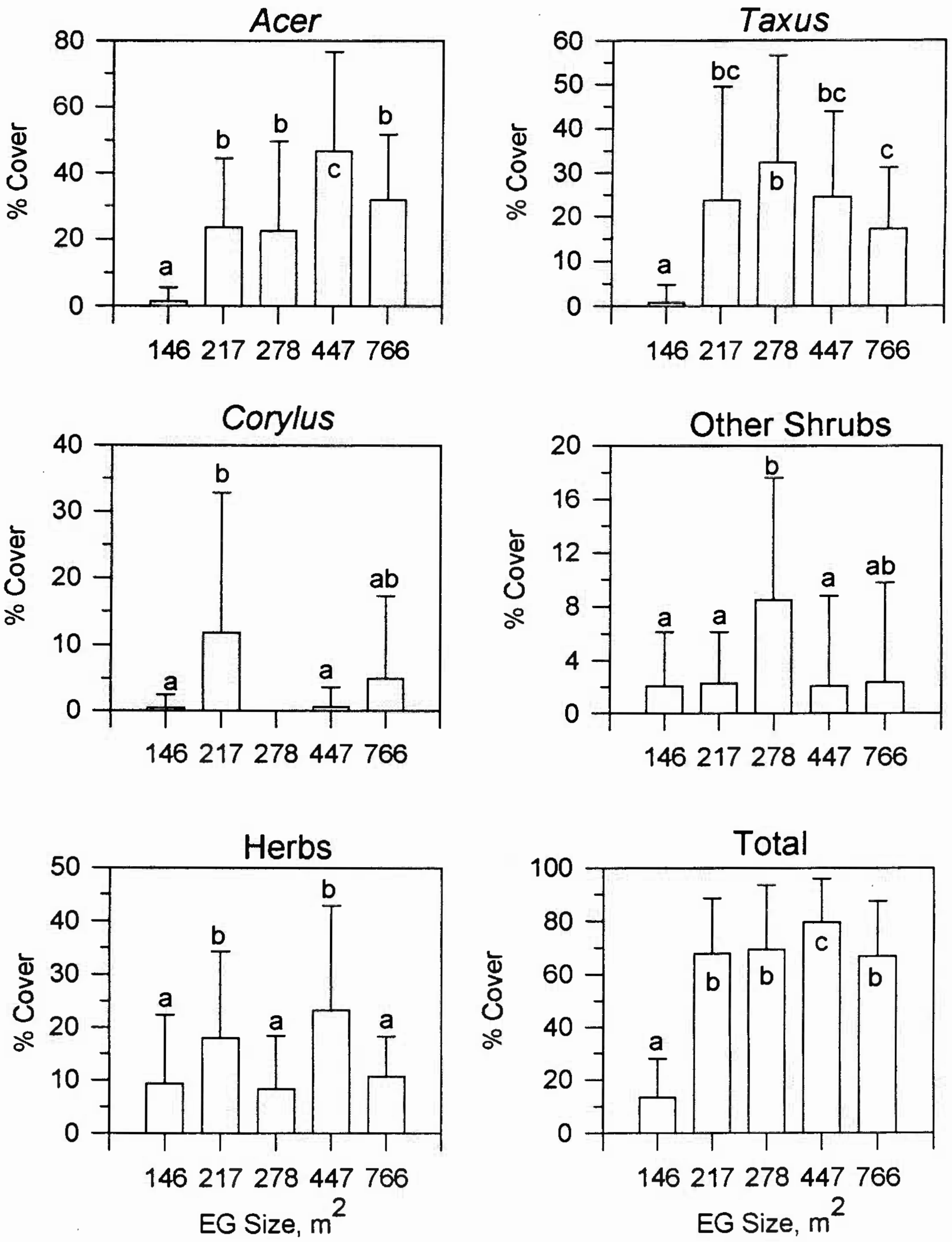

Figure 4.2 Average percent cover and standard deviation for individual species and groups of vegetation in each of the five studied gaps. Bars with different letters are statistically different, $p < 0.05$.

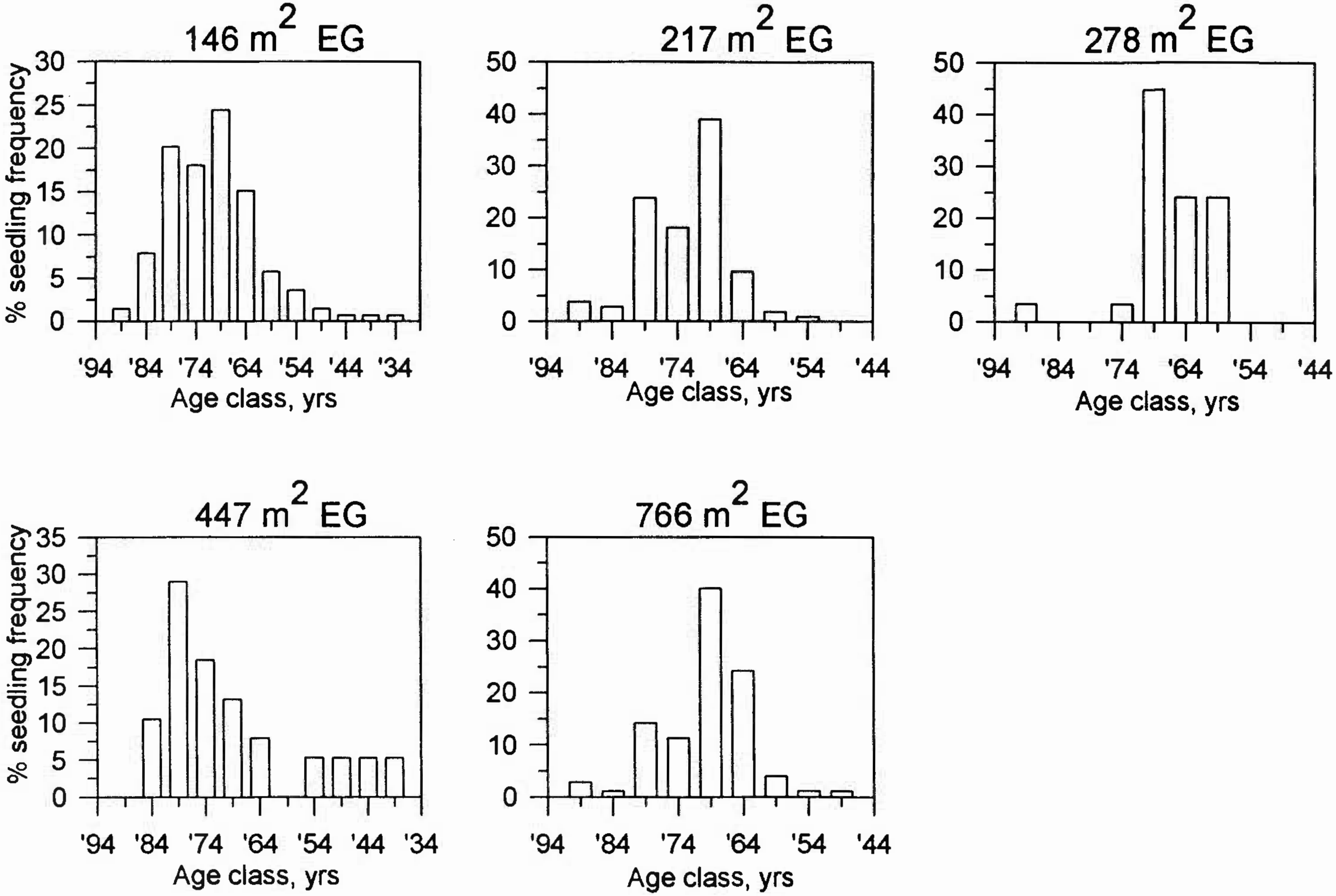

Figure 4.3 Balsam fir seedling age structures in the five studied gaps.

Table 4.1 Gap and expanded gap sizes for each of the studied gaps.

	EG size, m^2	Gap size, m^2
Gap 1	278	149
Gap 2	766	560
Gap 3	217	89
Gap 4	447	281
Gap 5	146	59

Table 4.2 Age characteristics of the different species in each of the gaps.

	Fir	W. Spruce	Aspen	Birch	Cedar
146 m^2 EG					
avg age	21,5	15,9	2,3	7,9	27,8
std dev	9,2	7,4	0,8	2,6	16,7
min	1	5	1	5	11
max	57	26	3	11	66
n	139	16	6	11	12
217 m^2 EG					
avg age	22,4	23,5	4,0	10,3	25,8
std dev	7,0	4,6	2,9	6,2	5,3
min	3	15	1	6	16
max	54	30	15	22	31
n	180	9	30	8	10
278 m^2 EG					
avg age	25,5	24,9	5,6	15,3	18, 7
std dev	5,6	17,8	2,1	6, 7	9,9
min	5	3	3	4	5
max	33	47	12	32	31
n	27	14	21	15	6
447 m^2 EG					
avg age	23,0	26,9	3,6	12,2	18,3
std dev	13,1	14,9	1,1	2,3	5,9
min	8	4	1	9	12
max	53	55	6	15	26
n	38	10	38	6	15
766 m^2 EG					
avg age	25,5	20,1	4,8	8,2	26,2
std dev	5,6	11,2	1,7	5,1	11,4
min	5	4	3	3	12
max	33	32	8	14	54
n	27	10	8	11	24

Table 4.3 Regressions between fir density, and growth indices, the seedling height of all species and distance to gap boundaries. The probability of seedling presence of the other four species at different distances from gap boundaries was investigated in the second part of the table using logistic regressions.

Mulitple linear regressions			
Dependent variable	Equation	R^2	α
Fir Density	3.33 - 0.14 EGnear - 0.47 EGsouth	0.20	0.0000
Fir Height	4.56 - 0.17 GapNear - 0.15 GapSouth	0.06	0.0013
Fir LB ratio	0.8 + 0.8 EGnear - 0.7 GapSouth	0.11	0.0005
Aspen Height	260.0 + 44.3 EGsouth	0.11	0.0275
Logistic regressions			
Dependent	z		α
White spruce	- 0.12 -0.66 EGsouth		0.0140
Aspen	- 1.86 + 0.53 GapNear + 0.43 GapSouth		0.0011

* Egnear = the distance to the nearest expanded gap boundary, Egsouth = the distance to the southern expanded gap boundary, GapNear = the distance to the nearest gap boundary, GapSouth = the distance to the southern gap boundary

Table 4.4 Regressions between fir density, and growth indices, the seedling height of all species and shrub and herb cover. The probability of seedling presence of the other four species in relationship to herb and shrub cover was investigated in the second part of the table using logistic regressions.

Multiple Linear Regressions

Dependent variable	Equation	R^2	α
Fir Density	2.65 - 0.02 adj*Acer* - 6.0 *Taxus*	0.28	0.0000
RHI	0.57 - 0.002 southTotal	0.07	0.0020
LB ratio	-0.01 -0.006 adjTotal + 2.3 *Taxus*	0.08	0.0068
No. Branches	2.3 - 0.008 adjTotal	0.03	0.0402
Fir Height	4.8 - 0.01 adj*Acer* - 0.01 Total + 0.004 avg*Taxus*	0.24	0.0000
Spruce Height	4.6 - 0.01 adj*Acer* - 9.6 Total	0.26	0.0000
Cedar Height	4.9 - 14.9 Total	0.24	0.0000
Aspen Height	167.9 - 1.0 southTotal	0.08	0.0018

Logistic Regressions

Dependent	z	α
Spruce Presence	-0.6 - 8.7 *Acer*	0.0008
Cedar Presence	-0.2 - 0.04 adjTotal + 13.2 *Acer*	0.0000
Birch Presence	0.8 - 0.9 Herbs	0.0015

* adj*Acer* = average percent cover of *Acer* in all eight surrounding quadrats, southTotal = % cover of all herbs and shrubs in the quadrat directly to the south of the measured quadrat, adjTotal = average total % cover of all eight adjacent quadrats, avg*Taxus* = average cover of *Taxus* in current quadrat and the quadrat to the south

CONCLUSION GÉNÉRALE

Entre deux feux successifs, les épidémies de la tordeuse des bourgeons de l'épinette (TBE) sont responsables de la formation de trouées et ont ainsi une grande influence sur la composition de la forêt boréale. Même si la formation de ces trouées n'est pas continue mais périodique, certains conclusions peuvent être tirées des observations faites au moment de cette étude. Des trouées de dimension considérables permettent le maintien des espèces intolérantes à l'ombre dans les vieilles forêts conifériennes. Par contre, la formation lente de la trouée et l'angle faible du soleil dans la forêt boréale sont des facteurs qui assurent le maintien des espèces tolérantes à l'ombre, notamment le sapin. En raison de sa tolérance à l'ombre, de sa longévité et du fait que cette espèce n'est pas un hôte de la TBE, lors de longs intervalles sans feu, le thuya pourrait augmenter en abondance.

En fait, il a été démontré que seule l'abondance des semis du thuya semble augmenter constamment avec le temps écoulé depuis le dernier feu. La régénération du tremble demeure plus ou moins constante au sein de cette période alors que les semis des deux espèces hôtes, le sapin baumier et l'épinette blanche, de même que ceux du bouleau, sont plus abondants lors des stades de mi-succession et diminuent par la suite dans les vieux peuplements. Malgré cette diminution, les semis du sapin demeurent dominants dans tous les peuplements étudiés.

L'abondance des semis n'a été que faiblement influencée par les facteurs abiotiques malgré leur utilisation dans les classifications écologiques (Bergeron et al 1983, Bergeron et Dubuc 1989). Par contre, les facteurs biotiques ont une influence importante sur l'abondance des semis conifériens. En fait, la densité de la régénération du sapin baumier, de l'épinette blanche et du thuya augmente avec l'abondance de semenciers ce qui suggère que ces espèces devraient augmenter en abondance avec le temps depuis le feu.

Cependant, avec l'avancement des stades successionels, les trouées sont plus grandes et couvrent un pourcentage plus important de la forêt. L'abondance des semis du sapin diminue avec la dimension des trouées. Ces relations laissent supposer que le sapin ne pourrait jamais dominer complètement les forêts et donc que ces forêts n'ont pas encore atteint un stade d'équilibre. Ceci s'avère donc en contradiction avec les modèles de la dynamique des forêts développé pour les sapinières des maritimes qui suggèrent que les épidémies de la TBE causent un remplacement cyclique du sapin par le sapin (Baskerville 1975, MacLean 1984).

La modélisation des patrons de succession utilisant les matrices de transition suggèrent que la proportion du sapin augmente jusqu'au moment où le thuya commence à prendre plus d'importance. Le sapin demeurerait l'espèce dominante mais sa proportion diminuerait dans la forêt. L'épinette blanche, le tremble et le bouleau pourraient se maintenir en petites proportions. Le thuya n'est pas adapté au feu mais nos résultats suggèrent qu'il pourrait augmenter en abondance, en présence de la TBE. Frelich et Reich (1995) proposent aussi que la dominance du sapin serait limitée par les épidémies de la TBE mais qu'en absence de feu, il n'y ait pas de contrainte pour le thuya. De plus, les évidences paléoécologiques suggèrent que le thuya fut plus abondant durant les périodes où de longs intervalles entre les feux furent notés (Richard 1993, Liu 1990).

Le maintien des autres espèces est aussi en partie dû aux épidémies de la TBE. Le tremble est une espèce intolérante à l'ombre et ne s'installe donc pas dans le sous-bois. Ainsi, son maintien dépend des grandes. Dans les hautes latitudes, l'angle du soleil est faible et la lumière directe atteint les drageons seulement dans la partie nord des trouées. L'abondance de ces drageons est donc limitée par la petite zone de lumière directe et possiblement par le nombre réduit de trembles adultes dans les forêts âgées. La période de recrutement est aussi affectée. En fait, les drageons de tremble s'installent à la fin de l'épidémie, lorsque tous les arbres sont morts, probablement en raison de la formation lente des trouées suite aux infestations de la TBE. Même la réponse des semis du sapin, en terme de croissance et de changements d'architecture, est lente dans les trouées formées sur une période de quelques années.

En absence des épidémies de la TBE, les trouées formées par la mortalité d'arbres isolés ou de petits groupes d'arbres seraient trop petites pour le maintien des espèces ayant besoin de lumière directe. Le maintien de l'abondance du sapin et du tremble, avec le temps depuis le dernier feu, corroborent les résultats d'un modèle qui suggèrent que les épidémies de la TBE changent les patrons de succession dans les forêts de l'Abitibi (Bergeron et Dansereau 1993).

Quant aux semis des espèces tolérantes à l'ombre, ils apparaissent moins abondants dans les grandes trouées des forêts conifériennes, sous lumière directe. Ceci pourrait être associé à leur besoin d'humidité (Frank 1990, McLaren and Janke 1996). Dans les grandes trouées, non seulement il y a plus de lumière directe mais d'autres facteurs, telle la présence d'espèces compétitrices pourrait limiter l'abondance des espèces tolérantes à l'ombre. Nos observations et celles élevées dans la littérature (Batzer et Popp 1985, Ghent et al. 1957), démontrent l'importance de l'augmentation de l'*Acer spicatum* suite à la présence de grandes trouées dans les forêts conifériennes. La compétition des arbustes semble en fait être associée à une réduction de la densité totale des semis et à une diminution du rapport entre la régénération et la mortalité d'arbres dans les trouées des forêts âgées. Ces résultats suggèrent d'une part que le développement du prochain peuplement pourrait être plus long que le temps de développement de la forêt actuelle ou d'autre part, que les prochains peuplements seront moins denses.

En plus d'une meilleure compréhension des processus écologiques, ces résultats s'avèrent importants pour l'aménagement forestier puisque la régénération après les épidémies de TBE s'apparente aux méthodes sylvicoles basées sur la régénération préétablie. Au Québec, les opérations forestières s'inspirent de plus en plus des perturbations naturelles. De plus, les exigences pour une foresterie durable sont telles que les méthodes imitant les processus naturels deviennent de plus en plus à la mode.

Au lieu de favoriser les peuplements conifériens, les opérations sylvicoles pourraient viser à maintenir les forêts mixtes où la régénération préétablie est plus abondante, particulièrement en ce qui concerne le sapin. D'autres études démontrent aussi que la mortalité causée par la TBE est moindre dans les forêts ayant une proportion importante de feuillus (Bergeron et al 1995). De plus, nos résultats indiquent que la hauteur des sapins augmente et que cette espèce améliore son architecture pour favoriser sa croissance, dans les petites ouvertures tandis que dans les grandes ouvertures, les semis sont moins abondants. Une stratégie sylvicole prometteuse pour le sapin consiste donc à créer des ouvertures de petite dimension dans des zones d'abondante régénération, au sein de forêts mixtes.

Cependant, pour maintenir les forêts mixtes, une stratégie recommandée pour notre région (Bergeron et Harvey 1997), les grandes trouées, telles celles créées dans le passé par les feux, sont aussi nécessaires. Pour une gestion écosystémique basée sur les régimes de perturbations, les gestionnaires doivent connaître la distribution des grandeurs de trouées et la distribution spatiale des trouées à l'échelle du paysage. Pourtant, cette dernière information et son influence sur les processus contrôlant la mosaïque forestière demeure inconnue et devrait donc être l'objet de recherches à venir.

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