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**LA RÉGÉNÉRATION DU THUYA APRÈS COUPES
PARTIELLES EN PEUPLEMENTS MIXTES**

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Résumé

Les facteurs affectant la régénération de thuya occidental (*Thuja occidentalis* L.) après des coupes partielles en peuplements mixtes sur station mésique ont été étudiés à l'aide de trois approches. Premièrement, des coupes de jardinage par pied d'arbre (25 % de la surface terrière récoltée) et par trouées (trouées de $1,5H \times 1,5H$; 625 m^2), ainsi qu'une coupe d'ensemencement (50 % de la surface terrière récoltée) ont été suivies durant trois ans en Outaouais (Québec, Canada) pour mesurer l'abondance, l'établissement et la croissance à court terme d'une nouvelle cohorte de régénération. Deuxièmement, une étude rétrospective effectuée dans d'anciennes coupes partielles en Outaouais, dans la réserve faunique Papineau-Labelle (Québec, Canada) et à Penobscot Experimental Forest (PEF, Maine, États-Unis) a permis de mesurer la croissance diamétrale et en hauteur des semis, des marcottes et des petites gaules de thuya dans des régions ayant des densités variables de cerfs de Virginie (*Odocoileus virginianus* Zimmerman). Troisièmement, l'abondance et le recrutement des semis, ainsi que les taux de passage et la mortalité des gaules de thuya ont été étudiés dans des peuplements aménagés par des coupes partielles répétées sur un horizon de 40 ans à PEF. Ces trois approches ont permis de déterminer que les petits semis de thuya (< 15 cm de hauteur) sont présents sous plusieurs intensités de coupes partielles, mais la meilleure combinaison de conditions d'établissement est une proximité des semenciers, une coupe de jardinage par pied d'arbre, un substrat minéral exposé et un faible niveau de compétition. La croissance en hauteur est influencée par la région et la disponibilité de la lumière, tandis que la croissance diamétrale est augmentée par des coupes partielles. En présence d'une densité élevée de cerfs, la croissance des semis au-delà de 30 cm de hauteur et le recrutement au stade gaulis sont faibles, limitant ainsi la densité de tiges. À la lumière de ces résultats, il est préférable de préétablir la régénération de thuya par des coupes partielles de faible intensité ou de travailler avec la régénération préétablie naturellement. Dans un deuxième temps, une ouverture plus grande du couvert peut libérer les semis et les gaules et permettre une augmentation de la croissance en hauteur et en diamètre. Il peut être nécessaire de contrôler le broutement selon la densité des populations de cerfs.

Abstract

Factors affecting the regeneration of northern white-cedar (*Thuja occidentalis* L.) after partial cuts in mixedwood stands on mesic sites were studied using three distinct approaches. Firstly, single-tree selection cutting (25% of basal area removed), shelterwood seed-cutting (50% of basal area removed), and group selection cutting (gaps of $1.5H \times 1.5H$; 625 m^2) were monitored over three years in the Outaouais Region (Quebec, Canada) to measure the abundance, establishment, and short-term growth of a new regeneration cohort. Secondly, a retrospective study was conducted in partial cuts in the Outaouais Region, Papineau-Labelle wildlife reserve (Quebec, Canada), and at the Penobscot Experimental Forest (PEF, Maine, United States) to compare diameter and height growth of white-cedar seedlings, layers, and small saplings in regions with different densities of white-tailed deer (*Odocoileus virginianus* Zimmerman). Thirdly, the abundance and recruitment of seedlings, and turning rates and mortality of white-cedar saplings, were studied in stands managed by repeated partial cutting over a 40-year period at the PEF. These three approaches demonstrated that small white-cedar seedlings (< 15 cm high) are present under many intensities of partial cuts, but the best combination of conditions to establish seedlings are: proximity of seed trees, partial opening of the canopy (single-tree selection cutting), exposed mineral soil, and low competition level. Height growth appears to be primarily a function of the region and light availability, and diameter growth increases following partial cutting. With a high density of deer, recruitment of seedlings over 30 cm high and to sapling stage is low, limiting density of saplings. In light of these results, it is preferable to pre-establish white-cedar regeneration by partial cutting of low intensity, or to work with naturally pre-established regeneration. After seedlings are established, a wider canopy opening can release seedlings and saplings and increase height and diameter growth. It may be necessary to control browsing pressure according to deer population densities.

Avant-Propos

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Merci aux professionnels de recherche et aux étudiants-chercheurs du laboratoire de sylviculture pour leur aide et leur soutien. Merci aussi aux étudiants de premier et de deuxième cycle en foresterie qui ont participé aux inventaires sur le terrain. Un merci tout spécial va à Mme Sabrina Morissette avec qui j'ai partagé un dispositif, un été de terrain, plusieurs discussions et une amitié. Merci au Ministère des Ressources naturelles et de la Faune (MRNF) et à mes collègues de la Direction de la recherche forestière (DRF) pour leur soutien. Merci à tous ceux qui ont pris le temps de réviser et de commenter mes écrits.

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Insertion d'articles

Tout d'abord, l'information contenue dans l'introduction générale de cette thèse a été partiellement reprise dans un document sur la raréfaction du thuya produit par le Ministère des ressources naturelles et de la faune à la Direction de la recherche forestière et à la Direction de l'environnement forestier.

Larouche, C. 2006. Raréfaction du thuya. Chapitre 5 (addenda) du document : Les enjeux de biodiversité relatifs à la composition forestière, P. Grondin et A. Cimon, coordonnateurs. Ministère des Ressources naturelles, de la Faune et des Parcs, Direction de la recherche forestière et Direction de l'environnement forestier, 32 p.

De plus, cette thèse est composée de quatre chapitres, chacun étant un article à caractère scientifique dont je suis l'auteure principale. Dans tous les cas, j'ai réalisé la majeure partie des analyses statistiques, de l'interprétation des résultats et de la rédaction des textes. Les dispositifs à court et à moyen terme ont été planifiés conjointement par Jean-Claude Ruel, Jean-Martin Lussier et moi-même, tandis que j'ai effectué l'installation et la collecte des données sur le terrain avec l'aide de nombreux assistants. Les données du quatrième chapitre m'ont été transmises par le U.S. Forest Service, mais j'ai toutefois effectué les analyses et quelques inventaires complémentaires sur le terrain, notamment pour caractériser l'environnement écologique des parcelles et le broutement.

Les quatre articles n'auraient pas la même qualité sans l'aide des coauteurs. Mon directeur de recherche, Jean-Claude Ruel, est coauteur de tous les articles, car il a supervisé mes travaux ainsi que révisé et commenté tous mes écrits. Mon codirecteur, Jean-Martin Lussier, est coauteur des trois premiers articles, car il a aussi bonifié mes écrits grâce à ses commentaires. Finalement, ma codirectrice, Laura S. Kenefic, est la première coauteure du quatrième chapitre, puisque les travaux, les analyses et la rédaction ont été effectués sous sa supervision.

Chapitre I :

Larouche, C., Ruel, J.-C., and Lussier, J.-M. Factors affecting northern white-cedar (*Thuja occidentalis* L.) seedling establishment and early growth in mixedwood stands.

Une version antérieure de l'article a été soumise à la Revue canadienne de recherche forestière le 25 avril 2008, puis refusée, à la suite d'une décision partagée des réviseurs, le 20 août 2008. Par contre, l'éditeur acceptera une seconde soumission du manuscrit après des révisions majeures apportées à la structure de l'article et la présentation des résultats. La pertinence de l'étude, le caractère novateur et le dispositif expérimental n'avaient pas été remis en question. À la suite d'une réécriture complète de l'article, il sera soumis de nouveau prochainement sous sa forme actuelle, incluant les révisions majeures apportées à la structure et à la présentation des résultats.

Chapitre II :

Larouche, C., Ruel, J.-C., and Lussier, J.-M. Early establishment dynamics and species composition three growing seasons after canopy treatments in mixedwood stands.

L'article sera soumis prochainement à la revue scientifique Forest Ecology and Management.

Chapitre III :

Larouche, C., Ruel, J.-C., and Lussier, J.-M. Height and diameter growth of northern white-cedar (*Thuja occidentalis* L.) seedlings, layers, and small saplings in mixedwood stands under partial cutting management.

L'article sera soumis prochainement à la revue scientifique The Forestry Chronicle.

Chapitre IV :

Larouche, C., Kenefic, L.S., and Ruel, J.-C. Northern white-cedar (*Thuja occidentalis* L.) regeneration dynamics on the Penobscot Experimental Forest in Maine: 40-year results

L'article a été accepté avec révisions mineures dans la revue scientifique Northern Journal of Applied Forestry le 2 septembre 2009. L'article sera publié dans le numéro de décembre 2009 ou mars 2010.

À mon père, Laurent

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Introduction générale

Le thuya occidental (*Thuja occidentalis* L.) est utilisé par l'homme depuis plusieurs siècles pour les propriétés de son bois – légèreté et résistance à la moisissure, à l'humidité et aux insectes – et les vertus médicinales de son feuillage (Johnston 1990; Naser et al. 2005). Les premiers colons l'avaient d'ailleurs surnommé l'*Arborvitae* : l'arbre de vie (Johnston 1990; Hannah 2004). De nos jours, le thuya a encore de multiples usages, dont les plus répandus sont les revêtements extérieurs (communément appelés « bardes de cèdre »), le sciage, le paillis ornemental et les panneaux de particules agglomérées. Il s'agit toutefois de l'essence arborescente commerciale résineuse la moins étudiée en Amérique du Nord (Curtis 1946; Scott et Murphy 1987; Hofmeyer 2008).

Selon plusieurs auteurs, la présence du thuya a diminué dans le temps sur la majorité de son aire de distribution (Siccama 1971; Lorimer 1977; Smith et Borczon 1981; Miller et al. 1991; Schaffer 1996; Heitzman et al. 1997, 1999; Cornett et al. 2000a, 2000b; Cogbill et al. 2002; Etheridge et al. 2005; Boucher et al. 2009). La faible abondance des gaules de thuya dans certaines régions est très préoccupante pour le renouvellement de cette essence, ce qui constitue un enjeu important pour la conservation de la biodiversité en ce qui a trait à la composition forestière (Grondin et Cimon 2003; Hannah 2004; Larouche 2006). Selon toute vraisemblance, la raréfaction du thuya pourrait découler non seulement d'une régénération déficiente résultant de l'utilisation de régimes sylvicoles inadaptés, mais aussi de l'accroissement et du déplacement vers le nord des populations de cervidés (Grigal et Ohmann 1975; Chimner et Hart 1996; Côté et al. 2004). La régénération des peuplements actuels semble problématique (Cornett et al. 2000a) et les facteurs propices au succès de l'établissement et du recrutement des semis demeurent méconnus (Heitzman et al. 1997, 1999). Conséquemment, la diminution du succès de reproduction peut entraîner la réduction de l'étendue ou de l'occurrence de l'essence (Beardmore et al. 2006).

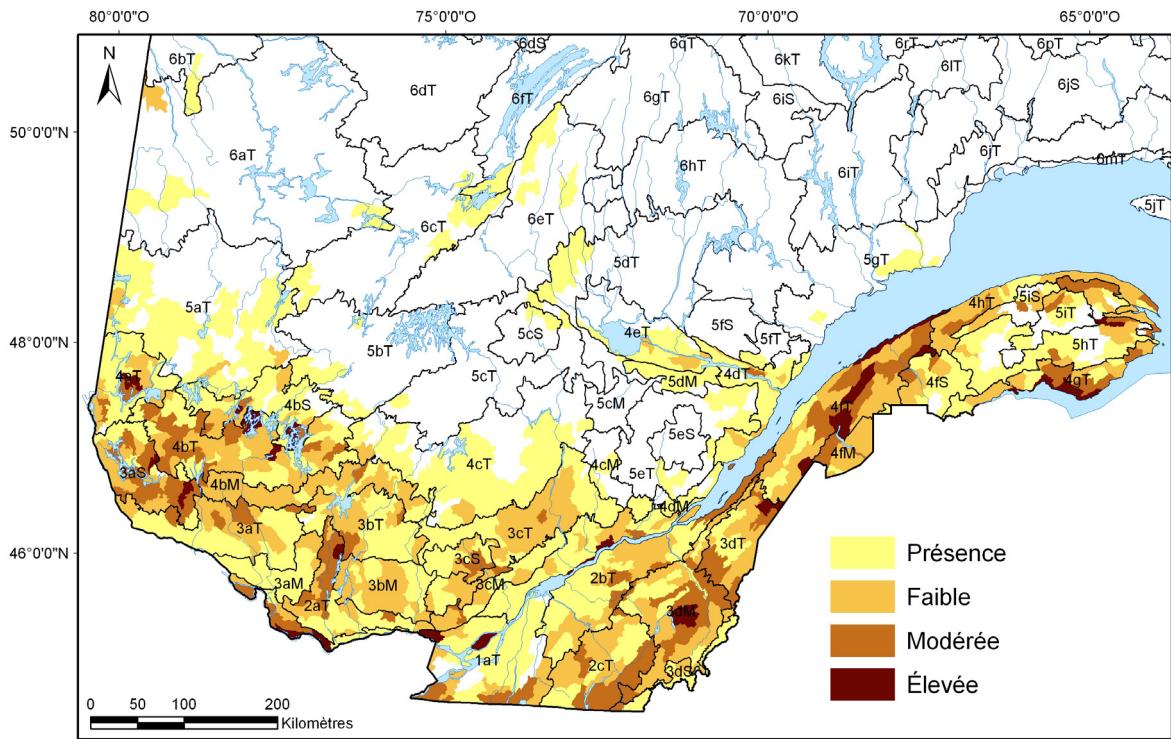
Cette introduction présente la répartition géographique du thuya, l'état actuel des connaissances sur les modes de reproduction, ainsi que les conditions de croissance aux stades semis et gaulis. Elle expose également la dynamique du thuya dans les peuplements mixtes et l'effet escompté des procédés de régénération généralement utilisés dans ces peuplements.

La répartition géographique du thuya et les espèces associées

Le thuya est une espèce indigène commune au Canada et aux États-Unis (Johnston 1990; Miller 1992). En territoire nord-américain, il est présent dans la région des Grands Lacs et la Nouvelle-Angleterre, tandis qu'au Canada, il occupe le sud-ouest du Manitoba jusqu'à l'océan Atlantique (Johnston 1990; Miller 1992). Au Québec, le thuya est largement répandu au sud du 48^e parallèle (Figure 1) dans les domaines bioclimatiques de l'érablière et de la sapinière (MRNF 2008, *données non publiées*). Il est présent sur tous les types et les qualités de station (Scott et Murphy 1987; MRNF 2008, *données non publiées*), mais ce sont les stations mésiques qui offrent les meilleures conditions de croissance et qui alimentent le plus l'industrie en tiges de qualité (Curtis 1946; Verme et Johnston 1986; Johnston 1990). Le thuya est aussi présent sur toutes les positions topographiques, mais il est plus abondant dans les dépressions et sur les terrains plats, dont le drainage varie d'imparfait à très mauvais (Habeck 1958; MRNF 2008, *données non publiées*). Il occupe autant les sols organiques que minéraux (Johnston 1990; Heitzman et al. 1999; Cornett et al. 2000a), peu importe la texture du dépôt (MRNF 2008, *données non publiées*) et jusqu'à des pH aussi bas que 3,0 (Kell 2009).

Le thuya forme rarement des cédrières pures, sauf sur des stations mal drainées et sur des falaises (Lamy et al. 1999; Matthes-Sears et Larson 1999; Hofmeyer 2008). Il se retrouve donc principalement comme essence compagne dans des peuplements mixtes sur l'ensemble de son aire de distribution (Figure 1) (Habeck 1958; Johnston 1990; Larouche 2006). Selon les régions et les types écologiques, la dominance des peuplements et les espèces associées varient (Johnston 1990; Farrar 1996). Sur les stations imparfaitement drainées à saturées, le thuya est généralement accompagné du sapin baumier (*Abies balsamea* (L.) Mill.), de l'épinette noire (*Picea mariana* (Mill.) B.S.P.), de l'épinette rouge (*Picea rubens* Sarg.), de l'épinette blanche (*Picea glauca* (Moench) Voss), du mélèze laricin (*Larix laricina* (Du Roi) K. Koch) et de l'érable rouge (*Acer rubrum* L.). Sur les stations mésiques à très sèches, en plus des essences précédentes, il se retrouve avec le bouleau jaune (*Betula alleghaniensis* Britt.), le bouleau à papier (*Betula papyrifera* Marsh.), l'érable à sucre (*Acer saccharum* Marsh.), le chêne rouge (*Quercus rubra* L.), la pruche du Canada (*Tsuga canadensis* (L.) Carrière) et le pin blanc (*Pinus strobus* L.). Dans

la partie sud de son aire de distribution, il est aussi en association avec l'érable argenté (*Acer saccharinum* L.), le frêne noir (*Fraxinus nigra* Marsh.), l'orme d'Amérique (*Ulmus americana* L.) et le peuplier à grandes dents (*Populus grandidentata* Michx).



Source : Larouche (2006)

Figure 1. Répartition et importance relative du thuya occidental dans les sous-régions écologiques du Québec méridional.

Note : L'importance relative a été déterminée grâce à la surface terrière des peuplements. À partir de l'ensemble des placettes d'échantillonnage réalisées lors de l'inventaire écoforestier du MRNF, un recouvrement total de thuya a été calculé par district écologique. Par la suite, ce recouvrement a été divisé par la superficie forestière productive du district. Les résultats obtenus ont été transformés en classes (Présence = 0,01 à 4,53 %, Faible = 4,54 à 11,07 %, Modérée = 11,08 à 21,50 % et Élevée = 21,51 à 45,77 %).

La reproduction du thuya

Le mode de reproduction sexuée

Le succès de régénération du thuya par voie sexuée dépend simultanément de la production, de la viabilité, de la dispersion et de la prédateur des semences, ainsi que de la disponibilité d'un environnement microclimatique adéquat pour la germination, l'établissement et la

survie des semis. Chez le thuya, la production massive de cônes débute dès l'âge de 30 ans (Johnston 1990; Schaffer 1996), mais elle est très variable selon les années. Lors d'une bonne année semencière, dont la fréquence oscille entre trois et cinq ans (Godman et Mattson 1976; Johnston 1990), un thuya mature peut produire jusqu'à 260 000 semences (Johnston 1990). Les distances de dissémination relativement courtes sont de l'ordre de deux à trois hauteurs d'arbre (Johnston 1990; Miller 1992). Conséquemment, l'abondance de semis est conditionnelle au nombre et à la distribution des semenciers (Cornett et al. 1997; Rooney et al. 2002), ainsi qu'à la quantité de semences produites. En conditions naturelles, le taux de germination des semences de thuya est généralement bas, même si la prédatation par les petits mammifères est rarement observée (Gashwiler 1967; Bartlett et al. 1991). Des recherches supplémentaires sont nécessaires afin de connaître le rôle possible des parasites et des pathogènes réduisant la viabilité des semences.

Les semences étant de petite taille (2 à 3 mm; 1,2 mg), les réserves nutritives sont limitées et les semences demeurent viables durant moins d'une année sur le parterre forestier (Johnston 1990). Il n'y a donc pas de banque de semences enfouies dans le sol. La dormance légère des semences est levée par la fonte de la neige et les plantules émergent entre la fin du mois de mai et le début du mois d'août (Johnston 1990). Par contre, les taux d'établissement et de survie des semis sont faibles et dépendent des conditions environnementales. Une forte abondance de semis n'est pas garante d'un succès de régénération. Seulement 4 % de ceux-ci atteignent, au fil du temps, une hauteur de 25 cm (Scott et Murphy 1987) et le taux de mortalité est très élevé durant les 2 à 3 premières années (Jones et al. 1994; DeLong et al. 1997). Par la suite, les chances de survie augmentent annuellement.

Les semis sont vulnérables à la dessiccation et au gel hâtif et tardif (Curtis 1946; Nelson 1951; Johnston 1990), ainsi qu'à la compétition par la végétation herbacée, les arbustes et les autres essences ligneuses (Chimner et Hart 1996). Les meilleures conditions d'établissement et de survie des semis semblent être rencontrées sur les gros débris ligneux (Scott et Murphy 1987; Cornett et al. 1997; Rooney et al. 2002), les substrats forestiers perturbés (Zasada et al. 1992; Heitzman et al. 1997; Rooney et al. 2002) et la matière organique brûlée (Verme et Johnston 1986). L'élément reconnu comme le plus critique

pour cette phase est la disponibilité en eau du substrat (Cornett et al. 2000a). Les débris ligneux conservent l'humidité, tandis que le sol minéral exposé a une conductivité hydraulique accrue (Marquis 1965; Winget et Kozlowski 1965). Comme d'autres essences ayant de petites graines, un substrat non perturbé n'est généralement pas favorable à l'établissement de semis (Godman et Mattson 1976).

Puisque la teneur en humidité du substrat est inversement proportionnelle à l'ouverture de la canopée, un léger couvert peut augmenter les chances de survie en évitant la dessiccation des semis (Johnston 1990). De plus, l'ombrage partiel du sol diminue les extrêmes de température (Schaffer 1996; Raymond et al. 2003) et limite la compétition par les espèces à croissance rapide (Smith et al. 1989).

Dans les peuplements mixtes, la germination des semences de thuya peut aussi être contrainte physiquement par la présence de litière feuillue par-dessus la semence (Bartlett et al. 1991). La dissémination des semences débutant à la mi-août (Johnston 1990), les feuilles mortes les ensevelissent et limitent physiquement l'émergence des plantules au printemps suivant. La chute automnale des feuilles peut aussi être fatale pour les semis de moins de trois ans (Johnston 1990). Ce phénomène est d'autant plus important chez le thuya en raison de la petite taille des semences (2 à 3 mm, 1,2 mg) et des plantules comparativement aux autres conifères associés (semence de sapin baumier : 3 à 6 mm, 7,6 mg; mélèze laricin : 3 à 4 mm, 6,3 mg; épinette blanche : 2 à 4 mm, 2,3 mg) (Burns et Honkala 1990; Farrar 1996; Simard 1999).

Le mode de reproduction asexuée

Selon la littérature, la reproduction asexuée (principalement le marcottage) est le principal mode de régénération utilisé par le thuya dans les milieux humides. En ce sens, Nelson (1951), Verme et Johnston (1986) et Bergeron (2000) affirment que plus de la moitié des arbres retrouvés sur ces stations sont d'origine végétative. Par contre, davantage d'études sont nécessaires pour généraliser cette affirmation à l'ensemble des stations colonisées par le thuya. Il n'y a d'ailleurs pas de consensus dans la littérature quant au mode de reproduction privilégié sur les stations mésiques (Stanek 1961; Johnston 1990; Chimner et Hart 1996; Bergeron 2000).

Comme pour l'épinette noire, le succès du marcottage du thuya dépend du contact entre n'importe quelle partie d'une branche ou d'une tige et un milieu suffisamment humide pour qu'elle puisse s'enraciner (Curtis 1946; Stanek 1961; Johnston 1990). La branche peut provenir d'un arbre-mère âgé de plus de 5 ans (Johnston 1990), d'un arbre renversé ou d'un arbre poussant dans un peuplement où la densité et la structure permettent de conserver des branches basses (Stanek 1961; Doucet 1987). Généralement, les peuplements peu denses et à structure irrégulière ou inéquienne ont un meilleur succès de marcottage. Le seuil minimal d'humidité nécessaire à la surface du substrat pour permettre l'enracinement n'a toutefois pas été déterminé. Par contre, les autres facteurs abiotiques affectent peu le succès de ce type de régénération (Kneeshaw et Bergeron 1998). Quant aux drageons et aux rejets de souche, ils sont peu fréquents et rarement rapportés dans la littérature (Blanchet 1982; Anderson et al. 1990; Johnston 1990).

Lorsque le lien enfoui entre l'arbre-mère et la marotte est encore connecté, l'origine asexuée d'un arbre est indiscutable (Lussier et al. 1992). Avec le temps, le lien est détruit par l'action de la pourriture ou mécaniquement durant les opérations forestières (Stanek 1961). Il devient alors difficile d'identifier le mode de reproduction duquel un arbre provient (Stanek 1961; Doucet 1987; Lussier et al. 1992). Ni la forme du système racinaire, ni celle de la tige ne sont caractéristiques du mode de reproduction utilisé. De la même manière que l'épinette noire et le sapin, les semis de thuya peuvent ramper au sol et développer un système racinaire asymétrique, ainsi qu'une courbure prononcée en forme de « J » à la base du tronc (Vincent 1965; McCarthy et Weetman 2006). Les semis et les gaules peuvent également être rabattus au sol sous le poids de la neige et de la glace, donnant l'impression d'une origine asexuée (Plourde 1999). Toutefois, une analyse destructive de la tige permet de calculer l'accroissement en hauteur de la première année de croissance. Celui-ci est toujours inférieur à 5 cm, qu'il s'agisse d'un semis poussant en conditions naturelles (Simard 1999) ou en serre (Habeck 1958; Harry et al. 1987), tandis qu'une marotte aura une croissance supérieure attribuable à la longueur de la pousse annuelle d'une branche. Par contre, cette méthode d'identification n'est pas infaillible. Deux autres pistes d'identification du mode de reproduction demeurent à explorer pour quantifier l'ampleur de l'utilisation du mode de reproduction asexuée selon les types de station : i) les analyses pour l'identification génétique des arbres peuvent permettre

d'associer les marcottes et les arbres-mère comme des clones (Prat et al. 2006; White et al. 2007) et ii) comme l'épinette noire, l'anatomie initiale des branches et des racines est différente et une étude anatomique au microscope de rondelles provenant du système racinaire pourrait permettre de distinguer les deux organes (Stanek 1961). Cette deuxième méthode peut toutefois être inappropriée pour les essences développant des racines adventives, comme c'est le cas pour l'épinette noire et le sapin (Desrochers et Gagnon 1997; Parent et al. 2000).

Les conditions et les taux de croissance

La vie d'un arbre peut être divisée en stades de développement selon les dimensions atteintes. Le nom et le nombre de stades diffèrent dépendamment des ouvrages consultés, mais il y a généralement : i) le stade semis, ii) le stade gaulis, iii) le stade perchis et iv) le stade futaie (OIFQ 2002; RNC 2008). Lors des deux premiers stades, les arbres sont considérés comme de la régénération, tandis qu'ils deviennent marchands pour les deux stades suivants. Par conséquent, seuls les stades semis et gaulis du thuya seront abordés dans le présent document.

Au stade semis

Le stade semis débute par la phase d'établissement. Celle-ci s'étend de la germination de la semence jusqu'à ce que la mortalité juvénile de masse ne soit plus à craindre, que les semis n'aient plus besoin d'une protection particulière (RNC 2008) et qu'ils soient en mesure de réagir à l'ouverture du couvert forestier. Cette phase semble particulièrement difficile pour les semis de thuya et les facteurs permettant sa réussite demeurent nébuleux (Heitzman et al. 1997, 1999). Pour l'épinette blanche et le sapin, les semis sont considérés établis lorsqu'ils ont atteint une hauteur de 30 cm (Baldwin 1977; Côté et Bélanger 1991). La phase d'établissement demande donc généralement entre 5 et 15 ans pour les résineux nord-américains, c'est-à-dire l'épinette blanche, l'épinette noire, la pruche du Canada et le sapin baumier, poussant en conditions naturelles (Anderson et al. 1990; Nienstaedt et Zasada 1990; Côté et Bélanger 1991). Cette information n'est toutefois pas disponible dans la littérature sur le thuya, mais il est généralement reconnu que la croissance en hauteur de celui-ci commence à des taux plus bas que les autres essences (Hannah 2004).

Après la phase d'établissement, le taux de croissance des semis de thuya est grandement affecté par la productivité du site (Johnston 1990; Hannah 2004) et la quantité de lumière disponible. La croissance en hauteur et la qualité des tiges sont meilleures sur les stations mésiques où les sols minéraux calcaires sont frais et riches en nutriments et en carbonates (Curtis 1946; Johnston 1990; Pregitzer 1991; Heitzman et al. 1999). La tolérance à l'ombre du thuya est variable dépendamment de la taille et de l'âge de l'arbre. Selon les auteurs et les stades de développement, il peut être classé comme intermédiaire, tolérant et très tolérant à l'ombre (Johnston 1990). Le thuya est généralement considéré moins tolérant que le sapin baumier et la pruche du Canada, mais plus que l'épinette noire (Godman et Lancaster 1990; Davis et al. 1998). Les auteurs ne sont toutefois pas unanimes à ce sujet, car Johnston (1990) et Kneeshaw et al. (2006) affirment que les thuyas peuvent être plus tolérants que le sapin aux stades semis et gaulis. Les semis ont une tolérance à l'ombre intermédiaire, tandis que les marcottes et les arbres matures ont la capacité de demeurer vigoureux durant de longues périodes d'oppression (Curtis 1946; Heitzman et al. 1999; Hofmeyer 2008). Dans ces conditions, la croissance diamétrale et en hauteur des semis sont considérablement réduites, tandis que la cime a tendance à s'étaler latéralement (Simard 1999) comme le fait l'épinette rouge (*Picea rubens* Sarg.) (Dumais et al. 2007). Selon des études en environnement contrôlé, la croissance maximale en hauteur des semis de thuya (hauteur totale > 30 cm) est atteinte sous 45 % de pleine lumière où elle serait d'environ 21,7 cm/an (Logan 1969). Elle est toutefois autour de 9,6, 16,4 et 19,8 cm/an à des intensités de 13 %, 25 % et 100 % de pleine lumière. Sous 100 % de pleine lumière, les semis de thuya âgés de 9 ans atteignent une hauteur totale inférieure à l'épinette noire et supérieure à l'épinette blanche et au sapin baumier (épinette noire : 221 cm; thuya : 178 cm; épinette blanche : 160 cm; sapin baumier : 119 cm; Logan 1969). Ces résultats restent néanmoins à valider à l'aide d'expériences *in situ* dans les peuplements naturels.

Au stade gaulis

Au Québec, une gaule se définit comme un arbre vivant dont la hauteur est supérieure à 1,3 m et dont le diamètre à hauteur de poitrine est supérieur à 1 cm et inférieur à 9,1 cm (MRNFP 2003). Comme pour l'épinette noire, les marcottes et les semis naturels de thuya poussant sur des stations comparables devraient avoir la même croissance en hauteur, en

diamètre et en volume (Lussier et al. 1992; Paquin et Doucet 1992a, 1992b; Paquin et al. 1999). La perception que les marcottes ont une croissance plus lente que les semis naturels proviendrait d'observations effectuées sur des stations pauvres, peu favorables au développement des arbres (Doucet 1987). De plus, à ce stade de développement, la croissance des semis et des marcottes est régie par les mêmes facteurs (Stanek 1961), soit la productivité de la station et les ressources disponibles.

Durant ce stade, la croissance en hauteur du thuya est d'environ 8 cm/an dans le sud de son aire de distribution (Johnston 1990; Hofmeyer 2008). Elle peut toutefois être inférieure à 6 cm/an sur des sols organiques saturés en eau (Johnston 1977). Dépendamment de la qualité de station, Hannah (2004) rapporte une croissance entre 15 et 30 cm/an dans des jeunes peuplements de structure régulière de 6 m de hauteur exempts de broutement. Ces taux de croissance en hauteur du thuya sont généralement inférieurs à ceux des autres conifères associés sur les mêmes stations (U.S. Forest Service, *données non publiées*).

Les taux de croissance diamétrale sont rarement disponibles pour les gaules, mais une étude rétrospective récente, effectuée sur des stations de qualité moyenne au Maine, a rapporté des accroissements diamétraux d'environ 0,1 cm/an pour des tiges de thuya de 1,3 à 11,3 cm au diamètre à hauteur de poitrine (Hofmeyer 2008). Ce taux de croissance diamétrale est largement inférieur à celui des gaules des autres résineux associés, c'est-à-dire l'épinette rouge, la pruche du Canada et le sapin baumier (Fowells 1965; Anderson et al. 1990; Hofmeyer 2008).

Moins massive qu'au stade semis, la mortalité est quand même un facteur pouvant moduler l'abondance et la répartition des gaules de thuya. De la même manière que pour les autres résineux, elle peut être causée par la récolte du peuplement mature (Mitchell et Beese 2002), le broutement, l'autoéclaircie, la sécheresse, les insectes et les maladies (Anderson et al. 1990; Burns et Honkala 1990). L'importance relative de ces causes de mortalité est variable selon les régions, ainsi que la composition et la structure du peuplement. Les insectes et les maladies affectant les gaules de thuya sont peu connus, mais les mites (*Oligonychus* spp.) et les mineuses (*Argyresthia* spp.) sont des causes potentielles de mortalité (Rose et al. 2000).

Le broutement préférentiel par les herbivores

En plus des facteurs limitatifs énumérés précédemment, il faut aussi considérer le broutement par les herbivores comme une cause importante du manque de recrutement de thuya aux stades semis et gaulis (Alverson et al. 1988; Pregitzer 1991; Cornett et al. 2000b). Le broutement cause des dommages sévères et la mortalité des semis et des gaules, ce qui va jusqu'à décaler la structure diamétrale de la composante de thuya vers les gros diamètres (Côté et al. 2004; Hannah 2004) et en compromettre la présence dans les futurs peuplements (Johnston 1972, 1977; Grigal et Ohmann 1975; Cornett et al. 2000b). Le broutement préférentiel désavantage le thuya et les essences ayant un faible taux d'acide tannique et de terpènes (Borgmann et al. 1998; Samson et al. 2002; Brugerolle 2004). Conséquemment, les espèces non consommées ont un avantage pour leur croissance en hauteur et peuvent augmenter en proportion dans les peuplements mixtes.

Le cerf de Virginie (*Odocoileus virginianus* Zimmerman), le lièvre d'Amérique (*Lepus americanus* Erxleben) et l'orignal (*Alces alces* Gray) peuvent nuire à la régénération de thuya (Curtis 1946; Johnston 1972, 1990; Davis et al. 1998; Rooney et al. 2002). Le cerf est sans aucun doute la plus néfaste des trois espèces (Heitzman et al. 1997). Le thuya représente une essence de prédilection pour ce mammifère en fournissant un excellent couvert thermal et une nourriture hivernale nutritive (Verme 1965; Verme et Johnston 1986).

Selon Pregitzer (1991), la dynamique actuelle de régénération pourrait être totalement différente de celle qui avait cours avant la colonisation. En effet, la population de cervidés était alors moins élevée et une abondante régénération préétablie de thuya pouvait être présente, ce qui n'est plus le cas de nos jours. Notons que les populations de cerfs dans le nord-est des États-Unis sont particulièrement élevées (5,8 à 9,7 cerfs/km² en 2007 dans le centre du Maine; MDIFW 2007) et que leur rôle dans la dynamique de régénération du thuya pourrait être différent dans la forêt mixte du Québec où le cerf se retrouve plus près de sa limite nordique de distribution (aucune présence en 2005 dans le secteur nord de la région de l'Outaouais; 5,5 cerfs/km² en 2005 dans la Réserve faunique Papineau-Labelle; MRNF 2007a). Toutefois, aucune étude ne nous permet de conclure à cet égard malgré l'importance capitale que pourrait revêtir cette différence. Les changements climatiques

pourraient aussi entraîner un déplacement et une expansion vers le nord des populations de cervidés due à une diminution de l'épaisseur du couvert de neige (Bourque et Simonet 2007). En outre, la densité des populations d'herbivores n'est pas constante sur un territoire donné. À la suite d'un traitement sylvicole, le broutement par les herbivores peut s'intensifier à cause de l'abondance de la nourriture disponible ou devenir inexistant parce que les animaux ont fui le peuplement durant les opérations forestières (Verme et Johnston 1986; Bujold 2004).

Qu'il s'agisse de peuplements purs ou mixtes, de ravages ou d'aires d'alimentation occasionnelles, le broutement de la régénération limite la croissance en hauteur et le développement de la cime en plus d'affaiblir les arbres. Dépendamment de l'épaisseur du couvert de neige, les arbres peuvent être susceptibles au broutement tant qu'ils n'ont pas atteint une hauteur de 3 m (Alverson et al. 1988; Lanasa et Zuidema 1991; Pregitzer 1991). De plus, les essences à croissance lente, comme le thuya, tolèrent plus difficilement le broutement répété que les essences à croissance rapide (Côté et al. 2004). Selon Aldous (1949), le broutement répété mène à la mort des arbres si 15 à 20 % de son feuillage est brouté annuellement. Plusieurs études menées dans des régions occupées par le cerf rapportent l'absence de semis et de marcottes de thuya mesurant plus de 25 cm de hauteur (Cornett et al. 1997; Saunders et Puettmann 1999a; Cornett et al. 2000b). Cette lacune s'explique par le broutement préférentiel du cerf défavorisant les arbres compris entre 30 cm et 130 cm de hauteur (Beals et al. 1960; Saunders et Puettmann 1999a). Même si les petits semis peuvent bénéficier d'une protection contre le broutement grâce au couvert de neige et à la protection physique par les essences compétitives non consommées (Borgmann et al. 1998), ils deviennent vulnérables dès qu'ils les dépassent (Davis et al. 1998).

Certains auteurs ont démontré une interaction entre la densité du couvert et l'impact du broutement (McLaren et Janke 1996; Saunders et Puettmann 1999b; Cornett et al. 2000b). Même si les semis de thuya peuvent survivre sous un couvert fermé, ils demeurent plus sensibles au stress additionnel causé par le broutement et le taux de mortalité y est plus élevé (Cornett et al. 2000b). Des études au Michigan et au Minnesota ont d'ailleurs démontré que le taux de survie des semis résineux sévèrement broutés est plus faible sous

une canopée dense que dans les peuplements ouverts (McLaren et Janke 1996; Saunders et Puettmann 1999b). Dans des cas comme ceux-ci, la perte de seulement 20 % du feuillage pourrait entraîner la mortalité des thuyas (Schaffer 1996).

Notons aussi que le broutement par les herbivores peut influencer le développement des semis d'essences non broutées par le piétinement excessif (Miller 1992; Borgmann et al. 1998; Aubin et al. 2007). Les exclos, limitant l'accès à la régénération d'un peuplement, peuvent donc avoir un impact positif sur la croissance de toutes les essences présentes à l'intérieur de ceux-ci (Borgmann et al. 1998; Cornett et al. 2000b). Selon Miller (1992), le taux de croissance en hauteur de la régénération peut être jusqu'à quatre fois supérieur à l'intérieur des exclos par rapport à l'accroissement de la régénération non protégée. Cornett et al. (2000b) ont aussi trouvé significativement plus de semis et de marcottes de thuya mesurant plus de 1,2 m dans les exclos qu'à l'extérieur de ceux-ci.

La dynamique du thuya dans les peuplements mixtes

Les études tentant d'élucider l'impact de l'aménagement sur la régénération du thuya proviennent principalement de peuplements purs de thuya croissant sur des stations humides (Heitzman et al. 1997; Cornett et al. 2000b; Rooney et al. 2002). Dans la majorité des cas, les résultats sont contradictoires et leur extrapolation aux peuplements mixtes sur station mésique est difficile et peu souhaitable. En outre, les semis de thuya s'établissant difficilement sur la litière feuillue, pouvant disparaître sous la couverture de feuilles mortes et ayant un taux de croissance inférieur aux essences associées (Schaffer 1996; Simard 1999), l'abondance de la régénération de thuya est généralement plus faible sur les parterres des peuplements mixtes que sous des peuplements résineux (Kneeshaw et Bergeron 1998; Bergeron 2000) et les cédrières pures.

Les peuplements naturels

En règle générale, la régénération du thuya dans les peuplements mixtes semble critique. C'est grâce à sa longévité, son absence de vulnérabilité à la tordeuse des bourgeons d'épinette (*Choristoneura fumiferana* (Clem.)), sa tolérance à l'ombre et sa réaction de croissance après l'ouverture que l'abondance du thuya augmente à mesure que les

peuplements vieillissent. Selon Heitzman et al. (1999) et Bergeron (2000), si la fréquence des perturbations naturelles majeures est faible et que le renouvellement du peuplement se fait par des perturbations à petite échelle, les thuyas préétablis bénéficieront de conditions de croissance adéquates et de suffisamment de temps pour se développer. Ainsi, cette essence va augmenter sa dominance dans les peuplements avec le temps.

À tous les stades de développement, les tiges de thuya sont généralement dominées par d'autres essences dans les peuplements mixtes (Johnston 1990; Heitzman et al. 1997; Bergeron 2000). Aux stades semis, gaulis et perchis, les taux de croissance en hauteur sont plus faibles que ceux des essences associées (Hannah 2004; Hofmeyer 2008), tandis qu'à maturité, le thuya atteint des hauteurs plus faibles que les autres essences, soit une moyenne de 12 à 15 m (Johnston 1990; Farrar 1996). Selon l'étude de Scott et Murphy (1987), environ 60 % des plus grandes tiges de thuya dans les parcelles ont été dépassées par d'autres essences. Ces compétiteurs ont généralement une croissance plus rapide et une longévité plus courte que le thuya (Heitzman et al. 1997), ce dernier demeurant latent dans les étages et les classes de cime inférieurs (Miller 1992; Heitzman et al. 1999). Lorsque les peuplements mixtes avancent en âge, il apparaît alors une forte variabilité dans la succession (Bergeron 2000) et une irrégularité spatiale tant verticale qu'horizontale avantageuse à l'égard du thuya.

Les peuplements aménagés

Dans la forêt publique québécoise, la stratégie d'aménagement des peuplements mixtes est généralement axée sur le maintien dans le temps et dans l'espace des essences commerciales prioritaires (MRNFP 2003). La proportion de la surface terrière occupée par les essences principales est alors en hausse, tandis que celle des essences secondaires tend à décroître. La composition des peuplements résultants est donc altérée par rapport à la forêt naturelle. Conséquemment, des problèmes d'enfeuillage et de raréfaction de certaines essences, telles le thuya, l'épinette rouge, l'épinette blanche et le pin blanc, peuvent être identifiés comme des enjeux de biodiversité relatifs à la composition forestière (Grondin et Cimon 2003).

Dans un contexte d'aménagement écosystémique ayant pour but de conserver la biodiversité et les processus qui la régissent, les pratiques forestières s'inspirant des perturbations naturelles doivent être privilégiées (MRNF 2007b). Le fait de court-circuiter l'évolution naturelle des forêts mixtes modifie la dynamique structurale des peuplements et les interactions interspécifiques entre les essences comparativement aux peuplements naturels. La composition et la structure du nouveau peuplement seront dépendantes du niveau de perturbation de la canopée et de la régénération naturelle préétablie (Doucet et Gagnon 1994; Kneeshaw et Bergeron 1998). Généralement, la régénération de thuya est plus abondante dans les vieux peuplements (Bergeron 2000) contenant une composante importante de gros débris ligneux (Scott et Murphy 1987; Cornett et al. 2000a). Par contre, la diminution de l'intervalle de temps entre deux récoltes cause une importante baisse de la quantité de bois mort sur le sol forestier (Hély et al. 2000). Cette situation peut interférer avec l'établissement des conifères (Simard et al. 2003) et engendrer un enfeuillage des peuplements mixtes (Déry 1995; Grondin et Cimon 2003).

Plusieurs études rapportent un manque de régénération de thuya après des coupes totales ou partielles (Grigal et Ohmann 1975; Johnston 1977; Davis et al. 1998; Heitzman et al. 1999). Cette situation est attribuable aux lits de germination inadéquats, au manque de disponibilité des ressources, à la compétition avec des essences à croissance plus rapide et au broutement par les herbivores (Verme et Johnston 1986; Johnston 1990). Il est fréquent que le sapin baumier remplace le thuya dans les peuplements exploités, car le sapin est moins exigeant en termes de lits de germination, aussi tolérant à l'ombre et moins soumis au broutement (Grigal et Ohmann 1975; Frank 1990; Davis et al. 1998; Simard et al. 2003).

La plantation et le regarni pourraient aider à maintenir la proportion de thuya dans les peuplements mixtes aménagés, mais la régénération naturelle est la méthode généralement favorisée au Québec et au Canada (Haddon 1997). Au Québec, seulement quelques pépinières produisent des plants de thuya et le reboisement est peu fréquent. En 2004-2005, sur les terres publiques québécoises, 165 200 plants de thuya ont été mis en terre, comparativement à 8 333 100 plants d'épinette blanche et 46 484 500 plants d'épinette noire (MRNF 2008). En outre, c'est uniquement dans la région administrative du Bas-St-

Laurent que des thuyas ont été plantés sur les terres publiques (MRNF 2008). Quant aux forêts privées, les superficies reboisées en thuya demeurent marginales.

Les procédés de régénération dans les peuplements mixtes

Les peuplements mixtes peuvent être aménagés sous le régime de la futaie équienne, inéquienne et irrégulière. En ce sens, les procédés de régénération pouvant être utilisés sont les coupes totales, les coupes progressives (régulières et irrégulières) et les coupes de jardinage (Smith et al. 1997). Par contre, aucun de ces procédés de régénération ne semble avoir fait ses preuves pour maintenir la composante de thuya dans les peuplements mixtes sur station mésique (Davis et al. 1998; Heitzman et al. 1999).

Les coupes totales

Il existe des études rapportant une régénération de thuya suffisante après des coupes totales, mais elles étaient effectuées dans des peuplements purs jouissant d'une abondante régénération composée de thuyas préétablis (Thornton 1957; Benzie 1963; Verme et Johnston 1986). L'exposition soudaine de la régénération de thuya préétablie peut entraîner une mortalité élevée à cause des brûlures, du stress hydrique et des dommages résultant du passage de la machinerie (Thornton 1957; Verme et Johnston 1986), mais l'abondance de la régénération après la coupe peut tout de même être suffisante pour reconstituer le futur peuplement.

Si la régénération n'est pas préétablie, la coupe totale fournit des résultats plutôt décevants pour la reproduction sexuée du thuya (Heitzman et al. 1997) et la rareté de la régénération après coupe est préoccupante (Grigal and Ohmann 1975; Davis et al. 1998; Beardmore et al. 2006). Même après une préparation de terrain, l'absence de couvert de protection augmente la sécheresse et la température du sol, ainsi que l'abondance de végétation compétitive (Archambault et al. 1998). De plus, les coupes totales diminuent la présence des arbres semenciers à proximité du parterre à régénérer. Selon une étude effectuée au Wisconsin en 1980 dans une cédrerie à sapin sur une station hydrique, les sites ayant subi des coupes totales se sont régénérés principalement en sapin baumier (Davis et al. 1998). Cinq ans après la coupe, le pourcentage de régénération sur les parterres était de 66,3 %

pour le sapin baumier, 19,3 % pour l'épinette noire et 14,4 % pour le thuya, comparativement à 61,4 % pour le thuya, 37,1 % pour le sapin et 1,5 % pour l'épinette noire avant la coupe. C'est après une préparation de terrain par brûlage dirigé succédant à une coupe totale que la régénération de thuya semble la plus présente, mais elle demeure généralement très inférieure à celle du sapin et de l'épinette (Davis et al. 1998).

Dans le contexte de la forêt mixte sur station mésique, la structure généralement irrégulière ou inéquienne des peuplements ainsi que la multitude d'essences présentes justifient rarement l'utilisation de ce procédé de récolte favorisant l'établissement d'une seule cohorte de régénération (Smith et al. 1997). Les régimes sylvicoles basés sur les coupes partielles, s'approchant davantage de la dynamique naturelle des perturbations partielles dans les peuplements mixtes, sont généralement plus appropriés (Bergeron et al. 2007; Fraver et al. 2009). De plus, sachant que la proportion de thuya a tendance à augmenter avec le temps depuis la dernière perturbation majeure (Bergeron 2000), la longueur de la révolution entre deux coupes totales est généralement trop courte pour assurer le maintien de la proportion de thuya.

Les coupes progressives

Un procédé de régénération par coupes progressives permet d'ouvrir graduellement le couvert pour favoriser l'établissement de la régénération naturelle des essences semi-tolérantes et tolérantes à l'ombre tout en limitant l'envahissement par la végétation compétitive (Côté et Bélanger 1991; Miller et al. 1991; Smith et al. 1997). Jusqu'à maintenant, aucune étude de régénération mettant la coupe progressive en application dans des peuplements purs ou mélangés contenant du thuya n'a été trouvée dans la littérature.

Par contre, la proximité des thuyas semenciers et les conditions de croissance pourraient améliorer le succès de régénération du thuya avant la coupe finale si le couvert n'est pas trop ouvert (Miller et al. 1991; Schaffer 1996; Asselin et al. 2001). Puisque la teneur en humidité du substrat est inversement proportionnelle à l'ouverture de la canopée, un couvert partiel améliorera la survie des semis en limitant la dessiccation et l'abondance de la végétation compétitive (Johnston 1990; Schaffer 1996). Une préparation de terrain peut aussi améliorer les chances de succès de la régénération résineuse, surtout si les opérations

de récolte ont été effectuées en saison hivernale (Pothier et Prévost 2008) et que le sol n'a pas été perturbé.

Une attention particulière doit toutefois être portée à l'intervalle de temps entre la coupe d'ensemencement et la coupe finale. Selon le Manuel d'aménagement forestier (MRNFP 2003), le délai maximal entre la première et la dernière intervention d'une coupe progressive régulière ne doit pas excéder 10 ans. Cet intervalle pourrait être trop court pour l'établissement adéquat de la régénération d'essences résineuses pouvant mettre plus de 15 ans avant d'atteindre une hauteur de 30 cm (Anderson et al. 1990; Nienstaedt et Zasada 1990; Côté et Bélanger 1991). Or, la coupe progressive irrégulière offre une période allongée pour l'installation de la régénération (Raymond et al. *sous presse*), ce qui pourrait laisser suffisamment de temps aux semis de thuya pour s'établir. En outre, la coupe progressive irrégulière à couvert continu et la coupe progressive irrégulière à régénération lente maintiennent et favorisent les essences ayant une croissance lente au stade semis, comme c'est le cas pour le thuya, l'épinette rouge et la pruche (Raymond et al. *sous presse*).

Les coupes de jardinage

De la même manière que les coupes progressives, le procédé de régénération par jardinage permet la conservation d'un couvert partiel qui filtre la lumière et réduit les pertes de régénération dues à la compétition par les feuillus à croissance rapide demandant plus de lumière disponible que le thuya (Johnston 1990; Miller 1992). De plus, la conservation d'un couvert forestier à perpétuité pourrait avantager grandement le thuya, lequel a une bonne tolérance à l'ombre. Or, aucune étude n'offre de résultats concrets sur l'utilisation du jardinage dans les peuplements contenant du thuya. Les avantages et les inconvénients présumés doivent plutôt être basés sur l'autécologie du thuya.

Selon Johnston (1990), la reproduction sexuée du thuya est meilleure dans les coupes par pied d'arbre que dans les coupes par trouées ou par bandes. Or, le jardinage par trouée est fréquemment utilisé pour la régénération des peuplements mixtes (Brewer et Merritt 1978; Barden 1979; Runkle 1981). Selon la dimension des trouées, ce traitement permet de régénérer une plus grande diversité d'essences ayant des tolérances variables à l'ombre

(Brewer et Merritt 1978; Barden 1979; Runkle 1981; Scott et Murphy 1987). Le centre des trouées est principalement colonisé par des espèces intolérantes à l'ombre, tandis que les bordures permettent la régénération des essences ayant une tolérance intermédiaire. Toutefois, à l'intérieur des trouées, les fluctuations de température du sol, les faibles taux d'humidité et les conditions de pleine lumière pourraient freiner l'établissement et la survie des semis enracinés superficiellement (Raymond et al. 2003). Ainsi, les plus nombreux et les plus grands thuyas sont régulièrement observés le long des bordures plutôt qu'au centre des ouvertures (Verme et Johnston 1986; Scott et Murphy 1987).

De la même manière que pour les coupes progressives, la longueur de l'intervalle entre deux coupes consécutives de jardinage dans un peuplement influence grandement la régénération des essences. Comme cela a déjà été dit, les rotations longues et la présence de débris au sol favorisent grandement le thuya (Scott et Murphy 1987; Cornett et al. 2000a). La période de rotation est primordiale, car des interventions trop fréquentes semblent diminuer la proportion de thuya. Dans la littérature, aucune longueur de rotation idéale n'a été avancée pour cette essence.

La démarche méthodologique

Ce projet de recherche combine trois approches complémentaires qui ont permis de développer rapidement de nouvelles connaissances sur l'abondance, l'établissement et la croissance de la régénération de thuya dans les peuplements mixtes sur station mésique. L'objectif général de la thèse était de répondre à la question suivante :

« Quels sont les facteurs favorisant l'abondance, l'établissement et la croissance des semis et des gaules de thuya à court, moyen et long terme dans les peuplements mixtes sur station mésique et aménagés par des régimes de coupes partielles dans le sud-ouest québécois et le nord-est américain? »

Dans un premier temps, un dispositif expérimental a été établi dans la région de l'Outaouais (Québec, Canada) pour comprendre les facteurs affectant l'abondance et la croissance initiale des semis naturels et plantés de thuya. Cette étude à court terme a permis de cerner les facteurs limitatifs et les processus critiques pour la régénération du thuya. Ces résultats

sont présentés dans les chapitres I et II où la dynamique d'établissement et de croissance, ainsi que la composition et la stratification verticale de la régénération sont analysées trois saisons de croissance après des coupes partielles d'intensité variable.

Le deuxième volet du projet est constitué d'une étude à caractère rétrospectif dans des peuplements mixtes aménagés avec des coupes partielles dans les régions de l'Outaouais (Québec, Canada), des Laurentides (Québec, Canada) et du centre du Maine (Penobscot Experimental Forest, États-Unis). Sans permettre une étude aussi poussée des processus de régénération que l'approche précédente, le chapitre III présente la croissance diamétrale et en hauteur de semis et de petites gaules de thuya poussant dans des régions ayant des densités variables de cerfs de Virginie.

Finalement, le chapitre IV vise la compréhension de la dynamique de croissance et de mortalité des semis et des gaules de thuya sur un horizon de trente à quarante ans dans une forêt expérimentale ayant une forte densité de population de cerfs de Virginie (Penobscot Experimental Forest, Maine, États-Unis). En plus d'analyser l'abondance et la distribution par classe de hauteur des semis, un suivi des tiges individuelles depuis trente ans a permis de quantifier le recrutement, les taux de passage et la mortalité des gaules selon leur classe de diamètre.

Chapitre I

Factors affecting northern white-cedar (*Thuja occidentalis* L.) seedling establishment and early growth in mixedwood stands

Abstract

Regeneration of northern white-cedar (*Thuja occidentalis* L.) is often deficient after harvesting in mixedwood stands growing on mesic sites even where browsing pressure is low. Three yellow birch-softwood uneven-aged stands were selected at the northern limit of the range of white-tailed deer (*Odocoileus virginianus* Zimmerman) (Quebec, Canada). We compared the effectiveness of silviculture treatments on establishment and early growth of white-cedar after single-tree selection cutting (25% of basal area removed), shelterwood seed-cutting (50% of basal area removed), and group selection cutting (gaps of 625 m²); pre-established regeneration was removed prior to treatment. Three years after harvesting, the best combination of factors for the highest abundance of white-cedar seedlings was single-tree selection cutting with artificial seeding on exposed mineral seedbeds (68.8% of plots were stocked with white-cedar). Early growth of planted white-cedar seedlings (40 cm tall) and biomass production were proportional to light availability, e.g., best under group selection cutting (mean height increment = 14.8 cm/yr; mean root collar diameter increment = 3.0 mm/yr). Browsing pressure has regional impacts depending on herbivore occupancy of the area. Deer were absent, while snowshoe hare (*Lepus americanus* Erxleben) did not have a consistent effect on seedling abundance and early survival, limiting height growth only during the first year following planting.

Keywords: single-tree selection cutting, group selection cutting, shelterwood, regeneration, seedbed, browsing, seeding treatment, early growth, eastern white cedar, *Thuja occidentalis*, *Lepus americanus*, *Odocoileus virginianus*

Résumé

La régénération de thuya occidental (*Thuja occidentalis* L.) est déficiente sur les stations mésiques exploitées où il se retrouve en mélange avec d'autres espèces, même si la pression de broutement est faible. Trois bétulaies jaunes résineuses inéquiennes ont donc été sélectionnées dans la partie nord de l'aire de distribution du cerf de Virginie (*Odocoileus virginianus* Zimmerman) (Québec, Canada), afin d'étudier l'efficacité d'une coupe de jardinage par pied d'arbre (25 % de la surface terrière récoltée), d'une coupe de jardinage par trouées (trouée de 625 m²) et d'une coupe progressive d'ensemencement (50 % de la surface terrière récoltée) pour l'établissement et la croissance initiale de la régénération du thuya. La régénération préétablie a été enlevée avant la récolte. Trois ans après la récolte, la meilleure combinaison de conditions pour la régénération du thuya est la coupe de jardinage par pied d'arbre avec un ensemencement artificiel sur un sol minéral exposé (68,8 % des parcelles ont au moins un semis de thuya). Quant à la croissance et la production de biomasse des semis plantés de thuya mesurant 40 cm initialement, elles sont proportionnelles à la disponibilité de la lumière, i.e. la meilleure après la coupe de jardinage par trouées (accroissement moyen en hauteur = 14,8 cm/an; accroissement moyen en diamètre au collet = 3,0 mm/an). Le broutement a un impact variable selon les régions, dépendamment de la densité des populations d'herbivores. Le cerf était absent du territoire d'étude, tandis que le lièvre d'Amérique (*Lepus americanus* Erxleben) n'a pas eu un effet systématique sur l'établissement et la survie des semis. Il a seulement limité la croissance en hauteur des plants durant la première année suivant la plantation.

Mots clés: jardinage par pied d'arbre, jardinage par trouées, coupes progressives, régénération, lit de germination, broutement, ensemencement, croissance initiale, *Thuja occidentalis*, *Lepus americanus*, *Odocoileus virginianus*

Introduction

Northern white-cedar (*Thuja occidentalis* L.) occurs across a wide variety of habitats (Scott and Murphy 1987). It can reproduce on organic soils, but its development is best on mesic mineral soils (Johnston 1990; Miller 1992) where it rarely forms pure stands (Johnston 1990; Miller 1992). Consequently, an important part of the white-cedar wood supply comes from mixedwood stands (Johnston 1990). Major concerns for white-cedar management are the scarcity of its reproduction after harvesting (Grigal and Ohmann 1975) and browsing pressure, which inhibits white-cedar abundance and development (Heitzman et al. 1997; Cornett et al. 2000b). Although some knowledge regarding white-cedar regeneration has been gained from wet sites, white-cedar-dominated stands, and areas with high herbivore densities (Johnston 1990; Miller 1992; Rooney et al. 2002), silvicultural practices that ensure its adequate regeneration and development after harvesting are lacking.

On wet sites, vegetative reproduction accounts for more than fifty percent of white-cedar saplings (Verme and Johnston 1986; Johnston 1990; Bergeron 2000), but sexual reproduction (seed origin) dominates on mesic sites (Scott and Murphy 1987). White-cedar sexual regeneration is potentially limited by many biotic and abiotic factors. Availability of seeds is conditioned by the number and distribution of seed trees (Cornett et al. 1997; Greene and Johnson 1998; Rooney et al. 2002) and by the frequency of seed production. This aspect can be crucial for white-cedar regeneration abundance in mixedwood stands where seed trees are scarce (Zarnovican 2003).

Seedbed moisture is a key environmental factor for germination and early development of white-cedar. Mineral soil is an adequate seedbed (Simard et al. 2003), but decayed wood seems to be the superior seedbed for white-cedar seedling survival (Scott and Murphy 1987; Cornett et al. 1997; Rooney et al. 2002). Woody debris may become sparse in managed forests (Kohm and Franklin 1997); consequently white-cedar reproduction is reported to be limited by the absence of adequate seedbeds in harvested areas (Kneeshaw and Bergeron 1996; Cornett et al. 1997).

Seedling mortality remains high during the first three years after germination (DeLong et al. 1997; Simard et al. 2003) and only 4% of established white-cedar seedlings reach a

height of 25 cm (Scott and Murphy 1987). In addition, light availability is also an important factor for seedling development. Although white-cedar is considered extremely shade-tolerant, height growth of white-cedar regeneration should be best at 45% of full sunlight, compared to 13%, 25%, and 100% (Logan 1969). Seedling development can also be hampered by competition from the regeneration of faster growing species, which can be quite abundant in mixedwood stands (Scott and Murphy 1987; Johnston 1990; Chimner and Hart 1996), and by browsing damage caused by white-tailed deer (*Odocoileus virginianus* Zimmerman) or snowshoe hare (*Lepus americanus* Erxleben) (Johnston 1972, 1990). Deer are the most important predators of white-cedar seedlings and saplings, especially in winter.

Mixedwood stands can be managed under many approaches depending on forest management objectives, species composition, and stand structure (Smith et al. 1997). One approach uses low intensity cutting treatments, such as single-tree selection cutting, that promote the establishment of shade-tolerant species (Raymond et al. 2003) and which could favor white-cedar abundance by providing partial shelter of the forest floor, high soil moisture, and seed tree proximity (Miller 1992; Schaffer 1996; Asselin et al. 2001). Because of its wider range of canopy gap sizes, group selection cutting is frequently used as a second approach, which promotes a greater diversity of species with different shade tolerances (Runkle 1981; Scott and Murphy 1987). White-cedar seedlings and saplings are regularly observed at the edges of gaps (Verme and Johnston 1986; Scott and Murphy 1987). Finally, the seed-cutting is a common first stage of a shelterwood regeneration system and creates enough vacant growing space to allow the installation of new seedlings (Smith et al. 1997). However, large canopy openings could cause high mortality of white-cedar seedlings through the effects of drought (Verme and Johnston 1986) and competition from intolerant fast-growing species (Smith et al. 1997). All these canopy reduction treatments could favor white-cedar regeneration abundance and early growth, but they have not been fully tested in mixedwood stands.

The objective of this study was to determine the factors limiting white-cedar seedling establishment and early growth in order to develop adequate regeneration strategies in mixedwood stands. We examined the combined influence of partial harvesting intensities,

browsing control treatments, seedbed disturbances, seeding types, and environmental factors. The following hypotheses were tested: (i) white-cedar seedlings are the most abundant in single-tree selection cutting combined with exposed mineral seedbeds; (ii) growth of seedlings is the fastest under partial canopy openings (about 45% of full sunlight); and (iii) damage or mortality of white-cedar seedling caused by browsing will mask the effect of other factors.

Methods

Study site

The study was conducted in the Outaouais Region of western Quebec, 120 km northwest of Fort-Coulonge ($46^{\circ}51'N$, $77^{\circ}23'W$). It is located in the Balsam fir-Yellow birch bioclimatic domain, Ecological Region 4b-M (Gosselin et al. 1998). The continental humid climate is associated with a mean annual temperature ($\pm SD$) of $2.6 \pm 0.4^{\circ}\text{C}$ and a total annual precipitation of $1037 \pm 115 \text{ mm}$ (1971-2000; *data from BioSIM*, Régnière 1996). In 2005-2006 on the study area, the frost-free period was 144 consecutive days, with a total of 223 days without frost.

Three contiguous uneven-aged stands were selected on the basis of a significant white-cedar component. These stands were growing on moderately well-drained sites, and which had not experienced recent harvesting (last partial cut in 1963 for all stands). There was no major perturbation reported, although the fir component was probably affected by the two most recent spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks (Morin 1998). Mean stand basal area ranged from 21.2 to 26.5 m^2/ha (diameter at breast height $\geq 9.1 \text{ cm}$). Dominant canopy species included: yellow birch (*Betula alleghaniensis* Britton), 32% of basal area; white-cedar, 25%; red (*Acer rubrum* L.) and sugar maple (*Acer saccharum* Marsh.), 24%; white spruce (*Picea glauca* (Moench) Voss), 7%; paper birch (*Betula papyrifera* Marsh.), 7%; and balsam fir (*Abies balsamea* (L.) Mill.), 5%. Horizontal stand structure was heterogeneous with an intimate mix of species and aggregations of white-cedar, while the vertical structure was irregular, including multiple layers. The understory was composed of mountain maple (*Acer spicatum* Lamb.) and squashberry viburnum (*Viburnum edule* (Michx.) Raf.) (both combined = 35.6% cover), together with red and

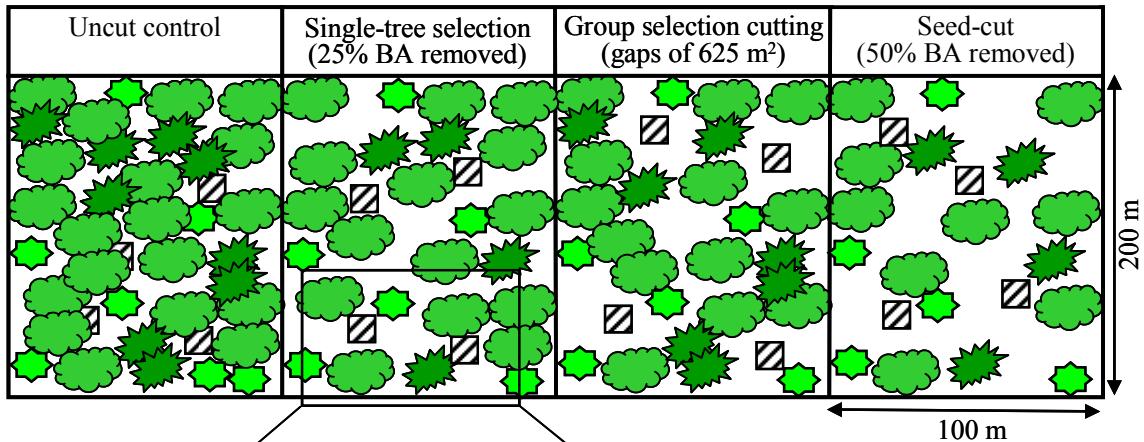
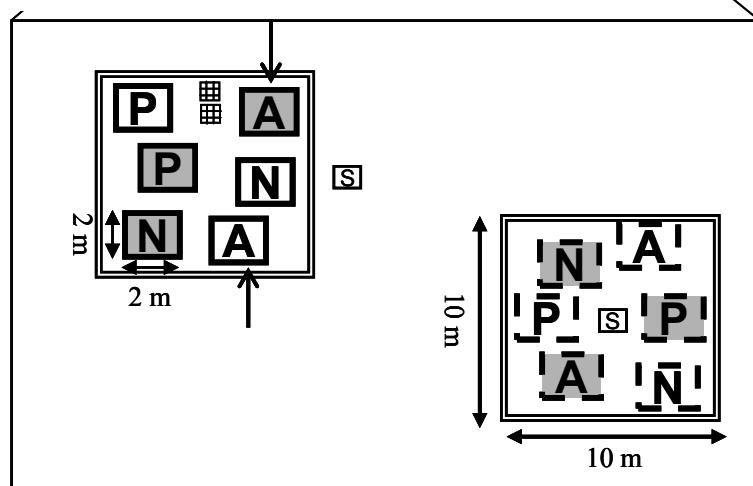
sugar maple, balsam fir, yellow birch, and white-cedar. The thin organic layer (6 cm) is developed on a 50-100 cm deep soil, with a sandy-loam to loamy-sand texture in the podzolic B-horizon. The pH (\pm SD) of organic and mineral layers were 3.3 ± 0.5 and 4.0 ± 0.3 respectively.

The study area was located in the northern part of the white-tailed deer range, in a region where moose (*Alces alces* Gray) are also present. In 2004, large mammal population densities were estimated as: no deer recorded; 3.4 moose/10 km² (Lamontagne and Lefort 2004), and about 6 hares/10 km² (Godbout 1998). The density of hare is low, while that of moose is high compared to other administrative regions of the province (MRNF 2007a). No browsing was observed on white-cedar regeneration at the time when sites were selected. Little information is available on small mammal populations in the study area.

Design and data collection

Four rectangular 8-ha blocks were established in 2003, and partially harvested in June of the following year (Figure 2a). To compare the post-harvest regeneration of different cutting intensities, each block was divided into four 2-ha canopy treatments: (i) control without harvesting; (ii) single-tree selection cutting (20% marking of basal area, and 5% for losses and operational purposes); (iii) seed-cutting (40% marking, and 10% for losses and operational purposes); and (iv) group selection cutting, with five square gaps of 625 m² ($1.5H \times 1.5H$, where H is the dominant height of white-cedar = 16.7 m). The number of gaps in the group selection cutting was set for experimental purposes; harvest rate was more intensive than operational group selection system (see Nyland 2002). The seed-cutting is a common first stage of a shelterwood regeneration system, aiming to open the canopy while retaining seed trees and partial cover during the establishment of a new regeneration cohort (Smith et al. 1997). In single-tree selection cutting and seed-cutting, harvesting was done across all diameter classes, thereby maintaining species size-class proportions. However, all trees were cut in the gaps, while the adjacent residual canopy remained intact. Gaps were located so that they had at least one white-cedar seed tree within 10 m of the edge, with a distance ≥ 35 m between gaps. Felling was done with a single-grip harvester and whole-trees were hauled by cable skidder.

(a) One 8-ha block including four 2-ha canopy treatments

(b) Two 100-m² whole-plots**Figure 2.** Example of one 8-ha block including four 2-ha canopy treatments, and two 100-m² whole-plots including six 4-m² subplots with or without enclosure.

Note: In 100-m² whole-plot (double lines): solid square, 4-m² subplot without enclosure; dash square, 4-m² subplot with enclosure; white filling, undisturbed seedbed; gray filling, disturbed seedbed; A, artificial seeding; N, natural seeding; P, planted; arrow, subplot with environmental monitoring (monthly abundance of seedlings, soil moisture, soil temperature, nutrients); S, seed trap; checked square, predation trap.

The experimental design is a split-plot with repeated measures. It includes four square 100-m² whole-plots per canopy treatment ($n = 64$; Figure 2a). Whole-plot location guidelines were: (i) ≥ 10 m from the block edges; (ii) ≤ 10 m from a white-cedar seed tree; (iii) semi-randomly distributed in the single-tree selection cutting, seed-cutting, and control treatment; (iv) in gap centres in the group selection cutting; and (v) avoidance of humid depressions. Basal area by species was inventoried with a prism (basal area factor = 2) around the center of each whole-plot. Each whole-plot included six square 4-m² subplots (Figure 2b). In half of the whole-plots, subplots had browsing control treatments that were created by erecting animal exclosures. Exclosures were 1-m high, and constructed with a wood frame covered by metal screening (hexagonal mesh apertures of 8 cm²). The bottom of the screen was flattened on the ground to prevent intrusions by digging rodents. The screen covered the top in 2004 only. In all whole-plots, subplots had two seedbed types (3 disturbed and 3 undisturbed). Soil disturbance was carried out manually with a rake after harvesting (July 2004) to remove the humus and expose the superficial mineral horizon (Ae). One-third of the subplots (1 disturbed and 1 undisturbed) was left to natural seeding. Manual seeding of white-cedar was done on another third (seed lot THO-A0-061-3-0 provided by the Ministry of Natural Resources of Quebec; 72% seed germinability) in August 2004 and 2005 with 1.76 g of seed (ca. 1000 viable seeds subplot). On each of the remaining one-third of the subplots, four 2-year-old nursery-grown white-cedar seedlings (IPL 45-110; 2+0) were planted in July 2004. Initial height (\pm SD) of the seedlings averaged 40.6 ± 3.2 cm, while initial root collar diameter (RCD) was 3.8 ± 0.5 mm. In each subplot, the pre-established regeneration of all woody species, including shrubs, was cut just after the harvesting to minimize its influence during the periods of germination and establishment of the post-harvest regeneration. Exclosure, seedbed, and regeneration treatments were assigned randomly among canopy treatments.

Regeneration measurements were carried out at the end of August 2005 and 2006. Regeneration of all species was counted yearly by 5-cm height classes in all 4-m² naturally and artificially seeded subplots. RCD and height of planted white-cedar seedlings were monitored in August 2004, 2005, and 2006. Browsing on each seedling was also monitored by the percentage of total foliage consumed (0 = absence of browsing; 1 = 1-25%; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%). In August 2006, planted seedlings were harvested for

root, stem, and foliage dry mass analyses (*see* Logan 1969). Foliar analyses of the terminal shoot (last 5 cm) were also conducted to relate seedling nutrition, canopy treatment, and seedbed type. Total nitrogen (N) in acid tissue digests was determined by flow-injection analyzer (QuikChem Method 13-107-06-2-D, Zellweger Analytic Inc., Milwaukee, WI). Phosphorus (P), potassium (K), calcium (Ca), and magnesium (Mg) concentrations were determined by inductively coupled plasma spectrometry (ICAP-9000, Thermo Jarrell Ash, Franklin, MA, USA). In May 2005, 2006, and 2007, white-cedar natural seed rain was monitored with 64 1-m² seed traps covered with galvanized screen (square mesh of 1 cm²; Hughes et al. 1987; *see* Chapter 2). Each seed trap was paired with a whole-plot and was placed within or near this whole-plot (Figure 2b). White-cedar basal area was inventoried in a 20 m-radius circular plot around each trap. Total light availability under the forest canopy, expressed as a percentage of total photosynthetic photon flux density (%PPFD), was estimated on cloudy days in July 2004. To do so, we used numerical hemispherical photographs of the forest canopy taken from a point 1.5 m above the centre of each whole-plot (Rooney et al. 2002). The photographs were analyzed with the Gap Light Analyser (GLA) (Fraser et al. 1999).

Over 12 months, seed predation was assessed using 8 pairs of square 0.1-m² predation traps (*see* Côté et al. 2003). Each trap was constructed with a 5-cm high wood frame, and fitted with a mesh screen bottom (1-mm² mesh size). They were buried and filled with local forest floor material and seeded to mimic the manually seeded subplots (25 viable seeds/trap; total of 35 seeds (72% seed germinability)). One half was covered with a galvanized wire screen (square mesh apertures of 1 cm²). At the end of August 2006, the entire contents of each trap were collected individually and germinants and residual seeds were retrieved from the forest floor material and counted in the laboratory.

Two blocks were randomly chosen for detailed monitoring of seedling demography and selected environmental factors. An exploratory analysis was performed to evaluate the importance of water, light, and nutrient availability on intra-annual variation in seedling abundance. Seedbed properties were monitored in the uppermost 10 cm; two pairs of artificially seeded subplots without exclosures (1 disturbed and 1 undisturbed) were randomly selected from each canopy treatment including the control (Figure 2b). In 2005

(June, July, and August) and 2006 (May, June, July, and August), seedling density was recorded on a monthly basis for all species. During the same period, volumetric soil water content in the uppermost 10 cm was monitored (16 records subplot/month) via time-domain reflectrometry (Field Scout TDR 100, Spectrum Technologies Inc., East-Plainfield, IL). Soil temperature was recorded at 2-hour intervals at a depth of 6 cm with 16 data-loggers (WatchDog Model 100, Spectrum Technologies Inc.) from May 2004 to October 2006. In July 2005, 80 pairs (5 pairs subplot) of plant root simulator (PRS) TM-probes (Western Ag Innovations Inc., Saskatoon, SK; one anion probe, one cation probe) were buried for 60 days to determine soil nutrient availability ($\mu\text{g}/10\text{ cm}^2/60\text{ days}$; Hangs et al. 2004). Nutrients that were monitored with the ion-exchange resin membranes included available inorganic-N ($\text{NH}_4^+ \text{-N}$ and $\text{NO}_3^- \text{-N}$), Ca, Mg, K, P, iron (Fe), manganese (Mn), copper (Cu), zinc (Zn), boron (B), sulphur (S), and aluminium (Al). Laboratory analyses were conducted by Western Ag Innovations Inc. according to Hangs et al. (2004).

Statistical analyses

Mixed analysis of variance models (PROC MIXED, SAS 9.1, SAS Institute Inc., Cary, NC, USA) were constructed to examine the effects of canopy treatments, exclosure treatments, seedbed types, seeding treatments, and time on plant and soil responses. Response variables included (i) annual white-cedar seedling abundance, (ii) abundance of competing species, (iii) height increment of planted white-cedar seedlings, (iv) RCD increment of planted white-cedar seedlings, (v) planted white-cedar seedling dry mass, (vi) monthly white-cedar seedling abundance, (vii) soil water content, (viii) mean monthly soil temperature, (ix) total light availability (%PPFD), and (x) cation and anion supply rates in the soil. Natural log-transformation with an optimized constant was performed on seedling abundance and soil moisture data to correct for heterogeneity of variance among treatments (Quinn and Keough 2002). The remaining variables were not transformed.

In ANOVA models, canopy treatments, seedbed types, seeding treatments, exclosure treatments, and time, together with their interactions, were considered fixed effects, while blocks and replicates were random effects. Each block included two identical whole-plots (replicates) that were analyzed as nested factors. After initial ANOVAs, some covariance

parameters (random effects) and nonsignificant four-way and five-way interactions were eliminated to improve fitting and robustness of the model (Voss 1999), and to simplify their ecological interpretation. Degrees of freedom were calculated using Satterthwaite's method. Orthogonal contrasts were performed when significant main effects or interactions were detected (Mize and Schultz 1985). Descriptive statistics were used for seed predation and percentage of total foliage consumed.

Results

Establishment of white-cedar seedlings

The abundance of white-cedar seedlings was influenced by canopy treatment, animal exclosure, seedbed type, seeding treatment, and time since cutting as simple main effect or multiple interactions (Table 1; Figure 3). When we dissect the Canopy treatment \times Exclosure treatment \times Year interaction, contrasts show that, in 2005, white-cedar seedlings had the same abundance in all canopy treatments without exclosures, while seedlings were more abundant within exclosures in the harvesting treatments than in the control treatment. However, the opposite was observed in 2006, where highest seedling abundances were in subplots without animal exclosures in the control treatment. Group selection cutting had fewer seedlings than the single-tree selection cutting and seed-cutting in 2006 (Figure 3a). The two-way interaction of Canopy treatment \times Seeding treatment suggested greater success of artificial seeding in the single-tree selection cutting and seed-cutting compared to the control treatment and group selection cutting (Figure 3b). For both years and among all canopy treatments including the control, white-cedar regeneration was higher with artificial seeding on disturbed seedbeds relative to natural seed rain (Figure 3c). Stocking of white-cedar regeneration in subplots that were naturally seeded, which was calculated as a percentage of subplots with at least one white-cedar seedling, was 14.1% in 2005 and 18.0% in 2006. For the same years, stocking in artificially seeded subplots was 39.1% and 43.0%, respectively.

Table 1. ANOVA of the effects of canopy treatments, exclosure treatments, seeding treatments, and seedbed types on the abundance of white-cedar seedlings over 2 years.

Source of variance	dfn ^a	dfd ^b	p-Value ^c
Canopy treatment (C)	3	56	0.049
Exclosure treatment (E)	1	56	0.279
C × E	3	56	0.165
Seedbed type (S)	1	171	0.046
Seeding treatment (G)	1	171	<0.001
S × G	1	171	0.005
C × S	3	171	0.984
C × G	3	171	0.009
G × (UC vs. S25, S50, and GAP) ^d	(1)	171	0.054
G × (GAP vs. S25 and S50)	(1)	171	0.007
G × (S25 vs. S50)	(1)	171	0.378
C × S × G	3	171	0.214
E × S	1	171	0.135
E × G	1	171	0.240
E × S × G	1	171	0.317
C × E × S	3	171	0.990
C × E × G	3	171	0.245
Year (Y)	1	237	0.041
C × Y	3	237	<0.001
E × Y	1	237	0.026
C × E × Y	3	237	0.009
Y × E (UC vs. S25, S50, and GAP)	(1)	237	0.007
Y × E (GAP vs. S25 and S50)	(1)	237	0.047
Y × E (S25 vs. S50)	(1)	237	0.566
S × Y	1	237	0.615
G × Y	1	237	0.586
S × G × Y	1	237	0.296
C × S × Y	3	237	0.761
C × G × Y	3	237	0.690
E × S × Y	1	237	0.186
E × S × Y	1	237	0.070

Note: Orthogonal contrasts performed for significant interactions between sources of variance.

^a Numerator degrees of freedom.

^b Denominator degrees of freedom.

^c Natural log-transformation of seedling abundance ($y = \ln(\text{seedlings} + 1)$).

^d UC, uncut control; S25, single-tree selection cutting (25% basal area removed); S50, seed-cutting (50% basal area removed); GAP, group selection cutting.

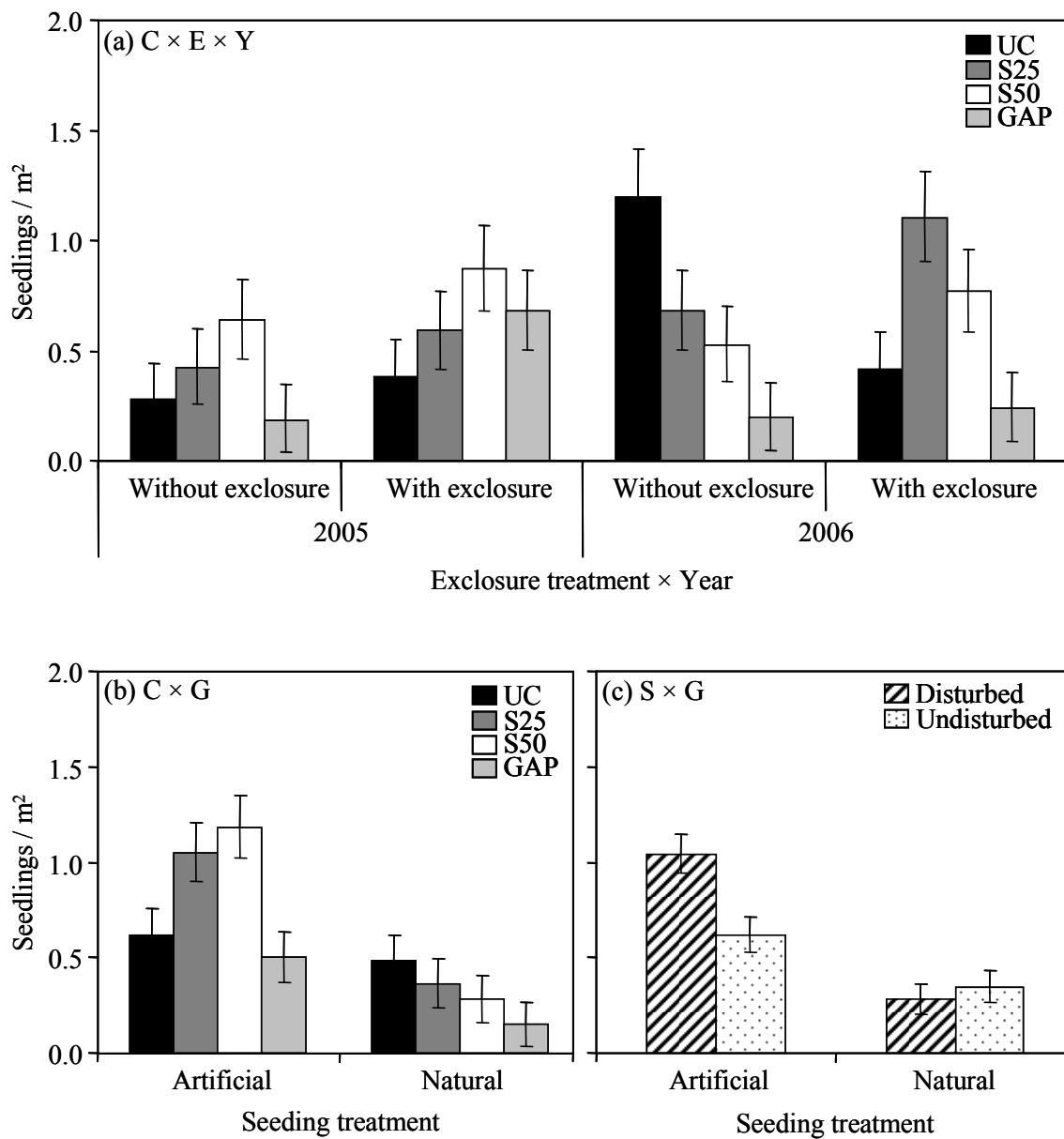


Figure 3. Abundance of white-cedar seedlings in significant interactions including canopy treatments, exclosure treatments, seeding treatments, seedbed types, and time (see Table 1). Error bars show 95% confidence intervals. Same legend as Table 1.

Canopy treatment directly influences seed rain and environmental conditions governing the abundance of seedlings. The best seed crop was in 2006 ($F_{2,60} = 27.60$, $p < 0.001$; 2006 vs. 2004-2005, $p < 0.001$), while 2005 was better than 2004 (2005 vs. 2004, $p = 0.037$). No viable seed of white-cedar was collected in the traps from the 2004 seed crop. Mean abundances were 1 and 158 viable seeds/m² in 2005 and 2006, respectively. In 2005, more seeds were recorded in seed traps in subplots without exclosures of the control treatment (20 viable seeds/m²), compared to other seed traps (16 viable seeds/m²). The basal area of white-cedar seed trees around whole-plots in subplots without exclosures of the control treatment was higher at 24.3 m²/ha, compared to 11.5 m²/ha, 5.0 m²/ha, 3.6 m²/ha, and 1.3m²/ha in control subplots with exclosures, single-tree selection cutting, seed-cutting, and group selection cutting, respectively ($F_{3,43.3} = 3.54$, $p = 0.022$; Control vs. GAP+S25+S50, $p = 0.018$). However, canopy treatment did not affect seed rain during the poor seed year.

In the predation traps that were protected from predators, a mean of 36.1 white-cedar seeds and germinants were recovered, which is one more seed than the initial seeding rate. In traps without screen covers, the number of seeds that were found ranged from 20 to 33. More seeds disappeared in group selection cutting (-35.7%) than in seed-cutting (-24.3%), single-tree selection cutting (-22.9%), and control treatment (-8.6%), suggesting a higher predation rate in group selection. None of the recovered seeds germinated in growth chambers, after being buried for 12 months in the traps.

Canopy treatment also affects environmental conditions such as soil water content, soil temperature, and light availability. The control treatment had the lowest soil water content and soil temperature compared to harvested treatments (Table 2; Figures 4a and 4b). Soil water content was the same for single-tree selection cutting, seed-cutting, and group selection cutting, while soil temperature and light transmission were higher in group selection than in the other treatments (Figures 4b and 4c). Light availability above the shrub layer depended on canopy treatment ($F_{3,12} = 134.36$; $p < 0.001$). Control treatment, single-tree selection cutting, and seed-cutting did not differ with respect to the percentage of total light (GAP vs. Control+S25+S50, $p < 0.001$; Control vs. S25+S50, $p = 0.083$; S25 vs. S50, $p = 0.290$).

Table 2. ANOVAs of the effects of canopy treatments and seedbed types on the monthly abundance of white-cedar seedlings, soil water content, and soil temperature over 2 growing seasons.

Source of variance	dfn ^a	White-cedar abundance		Soil water content		Soil temperature	
		dfd ^b	p-Value ^c	dfd	p-Value ^d	dfd	p-Value
Canopy treatment (C)	3	4	0.781	11.6	0.003	9.1	0.006
UC vs. S25, S50, GAP ^e	(1)	---	---	8.4	<0.001	9.1	0.025
GAP vs. S25 and S50	(1)	---	---	8.4	0.320	9.1	0.003
S25 vs. S50	(1)	---	---	8.4	0.069	9.1	0.297
Seedbed type(S)	1	4	0.485	6	0.071	6.4	0.274
C × S	3	4	0.426	6	0.062	6.4	0.314
Year (Y)	1	48	<0.001	24.3	<0.001	7.6	<0.001
Month (M(Y))	5	48	0.022	24.3	<0.001	7.6	<0.001
June (2005 vs. 2006)	(1)	48	0.020	---	---	7.6	0.003
July (2005 vs. 2006)	(1)	48	0.004	---	---	7.6	0.337
August (2005 vs. 2006)	(1)	48	0.996	---	---	7.6	<0.001
C × Y	3	48	0.052	24.3	0.331	7.6	0.997
C × M(Y)	15	48	0.615	24.3	0.304	7.6	0.516
S × Y	1	48	0.016	1704	0.151	8	0.624
S × M(Y)	5	48	0.206	1704	0.005	8	0.710
S × May	(1)	---	---	1704	0.036	---	---
S × June(2005 vs. 2006)	(1)	---	---	1704	<0.001	---	---
S × July(2005 vs. 2006)	(1)	---	---	1704	<0.001	---	---
S × Aug(2005 vs. 2006)	(1)	---	---	1704	<0.001	---	---
C × S × Y	3	48	0.194	1704	0.921	8	0.862
C × S × M(Y)	15	48	0.791	1704	0.247	8	0.277

Note: Orthogonal contrasts performed for significant main effects and interactions between sources of variance.

a, b, c, e Same legend as Table 1.

d Natural log-transformation of soil water content ($y = \ln(\text{soil water content} + 0.1)$).

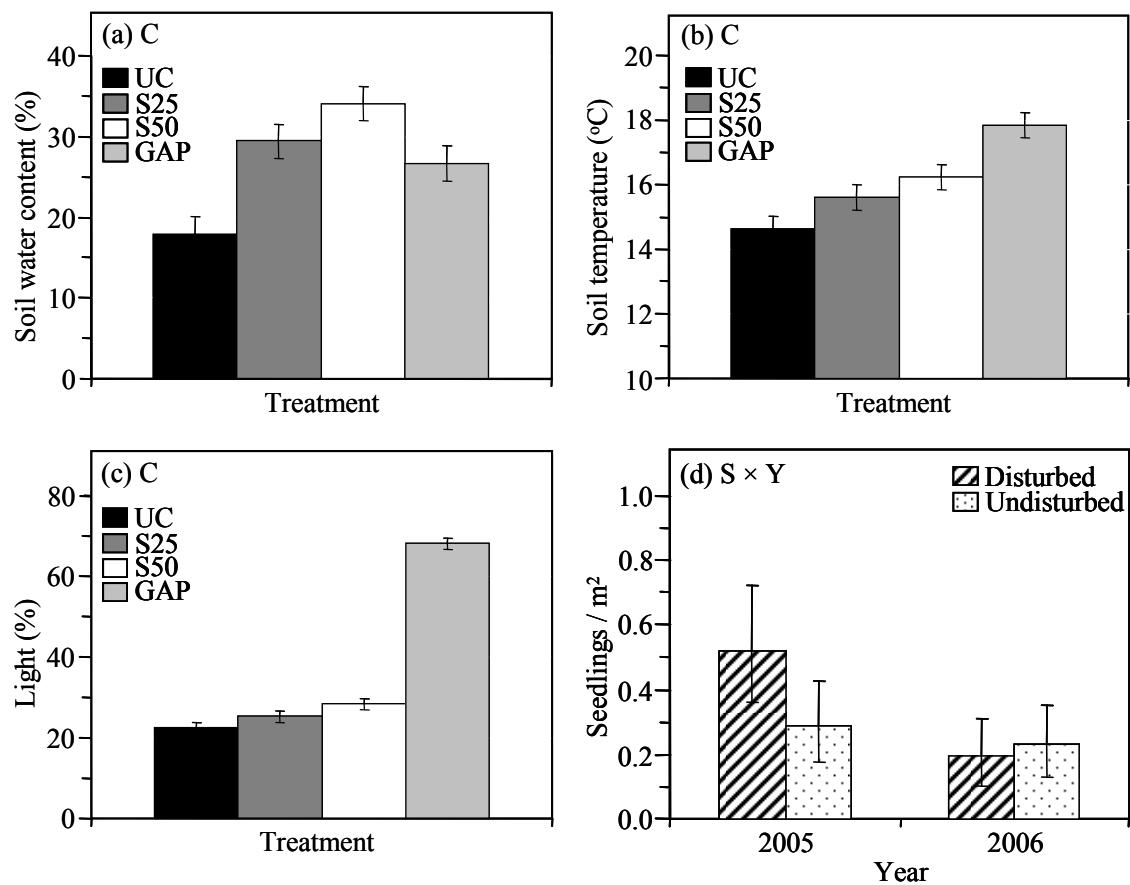


Figure 4. Soil water content, soil temperature, and light availability by canopy treatment, and abundance of white-cedar seedlings by seedbed types over two years (see Table 2). Error bars show 95% confidence intervals. Same legend as Table 1.

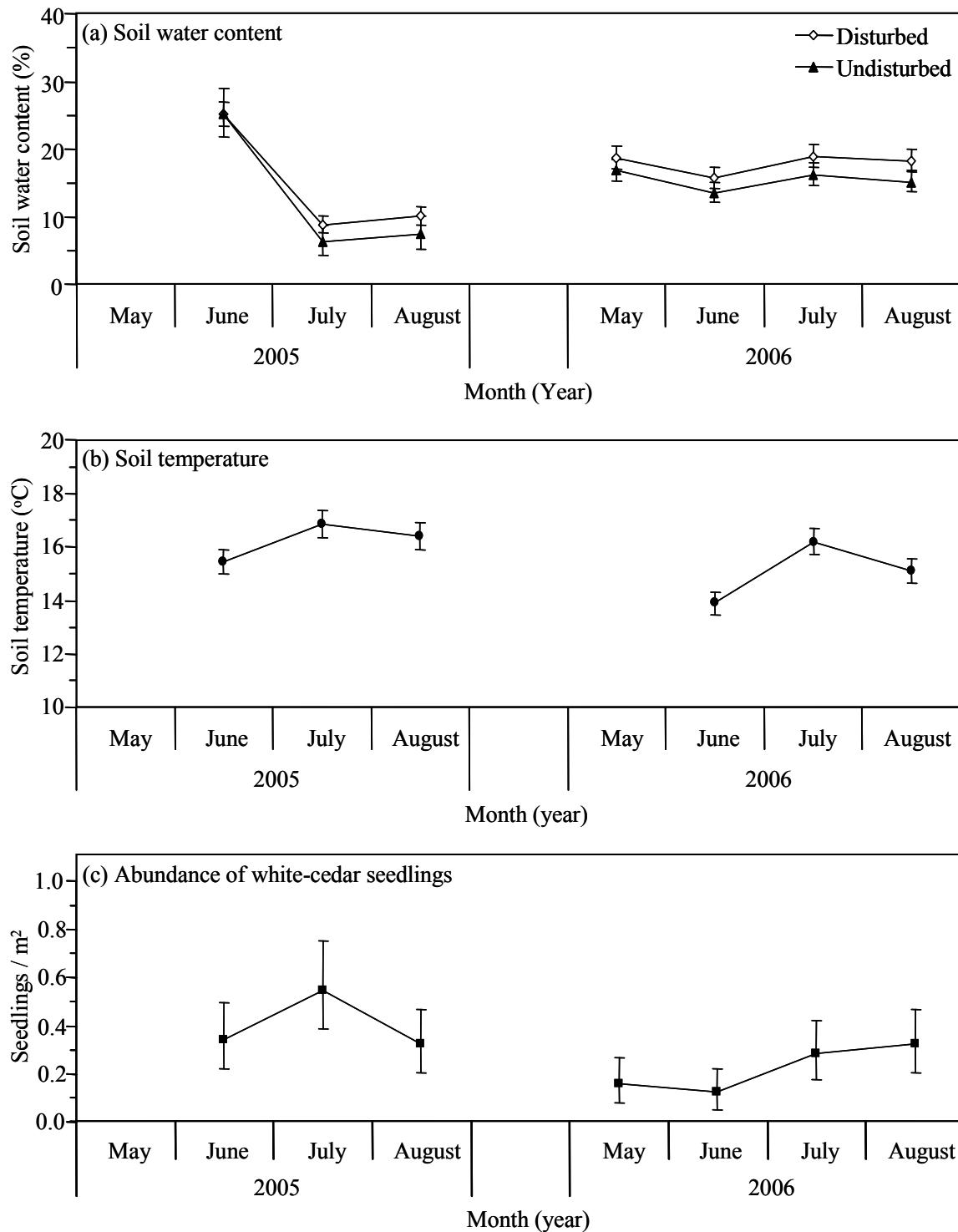


Figure 5. Evolution of soil water content, soil temperature, and abundance of white-cedar seedlings by month over two growing seasons. Error bars show 95% confidence intervals.

In all canopy treatments (including the control), monthly soil moisture patterns differed greatly between the two years (Table 2; Figure 5a). The growing season of 2005 was particularly dry, with a sharp decline in soil water content between June and July/August. In 2006, soil water content was much more stable throughout the growing season. During the drought of July and August 2005, more moisture was retained in the uppermost 10 cm of soil in the disturbed than in the undisturbed seedbeds (Figure 5a). During that period, white-cedar abundance was higher in the disturbed seedbeds compared to the undisturbed ones (Table 2; Figure 4d). Mean soil temperature was the same in July across the two growing seasons, but higher in June and August 2005, compared to 2006 (Figure 5b). Periods with mean temperatures above 0°C were May 16 to September 28, 2005, and May 1 to October 4, 2006, without difference among the canopy treatments including the control. However, frost occurred on August 30, 2005 (early frost) and May 26, 2006 (late frost).

Monthly monitoring showed that establishment of new white-cedar seedlings was high between June 14 and July 12, 2005, with substantial mortality between July 12 and August 14, 2005, without differences among canopy treatments (Table 2; Figure 5c). Approximately 85% of 1-year-old white-cedar seedlings did not survive until the following spring. In 2006, there was a progressive increase in seedling abundance throughout the growing season with a lower rate of seedling establishment compared to the previous year (Figure 5c). Overall, seedling density was comparable at the end of both growing seasons, despite the difference in demographical patterns.

Nutrient absorption by the ion-exchange probes did not differ among canopy treatments including the control. However, seedbed disturbance increased N availability for root uptake (disturbed = $62.63 \pm 12.06 \mu\text{g}/10 \text{ cm}^2/60 \text{ days}$ vs. undisturbed = $42.50 \pm 7.47 \mu\text{g}/10 \text{ cm}^2/60 \text{ days}$; $F_{1, 4} = 10.16$, $p = 0.033$), while the availability of other nutrients that were tested remained unaffected.

In 2006, all natural white-cedar seedlings were smaller than 20.0 cm (mean height of 3.7 cm; $0.1 \pm 0.05 \text{ seedlings/m}^2$). The subplots were dominated by maples (11.0 cm; $7.8 \pm 0.6 \text{ seedlings/m}^2$), yellow birch (17.4 cm; $4.1 \pm 1.0 \text{ seedlings/m}^2$), paper birch (26.3 cm; $0.2 \pm 0.1 \text{ seedlings/m}^2$), balsam fir (8.1 cm; $0.1 \pm 0.01 \text{ seedlings/m}^2$), white spruce (5.8 cm;

0.03 ± 0.01 seedlings/m²), and a number of other tree species (34.5 cm; 0.6 ± 0.2 seedlings/m²), including trembling aspen (*Populus tremuloides* Michx.), American beech (*Fagus grandifolia* Ehrh.), mountain maple, eastern white pine (*Pinus strobus* L.), pin cherry (*Prunus pensylvanica* L.), red oak (*Quercus rubra* L.), and black ash (*Fraxinus nigra* Marsh.) (see Chapter 2). Moreover, abundance of white-cedar seedlings was negatively correlated with the percent cover of red raspberry (*Rubus idaeus* L.), shrub, herbaceous, and fern, and with the abundance of other tree species for both growing seasons ($r = -0.095$, $p = 0.032$). The area of competition-free soil (e.g., the percentage of soil surface available for establishment of tree species) was influenced by canopy treatments ($F_{3,53.4} = 27.48$, $p < 0.001$). The percent of disturbed and undisturbed subplot area that was occupied by shrub, herbaceous, and fern species was 10.2% in the control treatment, 19.4% in single-tree selection cutting, 21.4% in seed-cutting, and 71.1% in the group selection cutting (see Chapter 2).

Early growth of planted white-cedar seedlings

Over the three years of monitoring planted white-cedar seedlings, mean heights were 42.6 cm, 46.4 cm, and 55.9 cm in August 2004, 2005, and 2006, respectively. Height and RCD increment was the highest for group selection cutting and the lowest for the control treatment (Table 3; Figure 6). Mean white-cedar height decreased in the control treatment in 2005, mainly due to hare browsing. Height growth was greater in 2006 for all canopy treatments, and group selection cutting had the highest increase (Figure 6a). The opposite response was observed for RCD increment where all canopy treatments (including the control) induced higher growth in 2005, with little difference between treatments in 2006 (Figure 6b). Exclosure treatments demonstrated that browsing inhibited white-cedar height and RCD growth (Table 3). Seedlings planted in subplots with exclosures had height and RCD growth higher by 3.2 cm and 2.5 mm, respectively, than planted seedlings that were potentially exposed to herbivory. Seedbed type did not affect height increment, but it slightly increased RCD increment for all canopy treatments (Table 3) with higher growth on disturbed seedbeds (1.8 mm vs. 1.4 mm).

Table 3. ANOVAs of the effects of canopy treatments, exclosure treatments, and seedbed types on height and root collar diameter (RCD) increments of planted white-cedar seedlings over 2 years.

Source of variance	dfn ^a	Height increment		RCD increment	
		dfd ^b	p-Value	dfd	p-Value
Canopy treatment (C)	3	48	<0.001	43.4	<0.001
Exclosure treatment (E)	1	48	0.001	43.4	0.018
C × E	3	48	0.993	43.4	0.823
Seedbed type (S)	1	48	0.110	34.2	0.005
C × S	3	48	0.307	34.2	0.135
E × S	1	48	0.184	34.2	0.787
C × E × S	3	48	0.900	34.2	0.987
Year (Y)	1	179	<0.001	153	<0.001
C × Y	3	179	0.018	152	0.001
Y × (UC vs S25, S50, and GAP) ^c	(1)	179	0.739	150	<0.001
Y × (GAP vs. S25 and S50)	(1)	179	0.002	152	0.352
Y × (S25 vs. S50)	(1)	179	0.622	156	0.176
E × Y	1	179	0.051	153	0.833
C × E × Y	3	179	0.582	152	0.679
S × Y	1	179	0.847	149	0.236
C × S × Y	3	179	0.445	149	0.481
E × S × Y	1	179	0.517	149	0.678

Note: Orthogonal contrasts performed for significant interactions between sources of variance.

^{a, b, c} Same legend as Table 1.

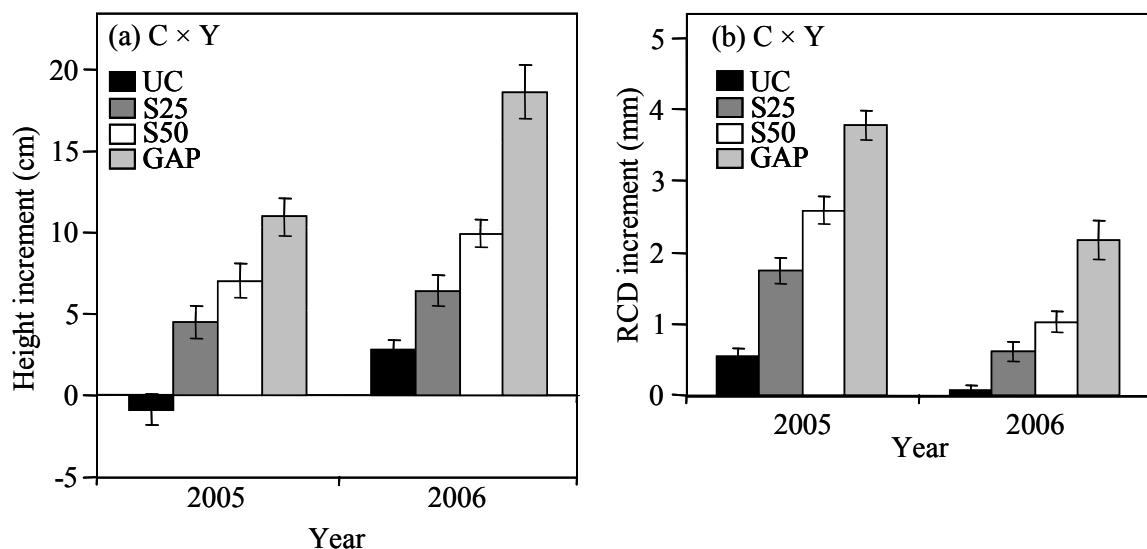


Figure 6. Annual height and root collar diameter (RCD) increment of planted white-cedar seedlings over two years in canopy treatments, including the control, in significant interactions (*see* Table 3). Error bars show 95% confidence intervals. Same legend as Table 1.

In 2006, seedling dry mass analyses confirmed our growth monitoring results (Table 4). Aboveground parts (foliage, branch, and stem) and roots had a lower mass in the control than in harvested treatments, and dry masses were maximal in group selection cutting (Table 4). In addition, animal exclusion resulted in the highest foliage and branch dry mass (12.80 ± 1.13 g vs. 9.71 ± 1.03 g) among treatments. The greatest root masses were found on disturbed seedbeds (3.98 ± 0.29 g vs. 3.28 ± 0.24 g).

Table 4. ANOVAs of the effects of canopy treatments, exclosure treatments, and seedbed types on the dry mass of foliage and branches, main stem, and roots of planted white-cedar seedlings 3 growing seasons after planting; and mean masses by canopy treatment in 2004.

(a) ANOVAs of dry mass

Source of variance	dfn ^a	Foliage and branches		Main stem		Roots	
		dfd ^b	p-Value	dfd	p-Value	dfd	p-Value
Canopy treatment (C)	3	56.6	<0.001	54.9	<0.001	50.6	<0.001
UC vs. S25, S50, GAP ^c	(1)	57.5	<0.001	56.4	<0.001	49.1	<0.001
GAP vs. S25 and S50	(1)	56.1	<0.001	54.1	<0.001	51.3	<0.001
S25 vs. S50	(1)	56.1	0.110	54.1	0.115	51.3	0.037
Exclosure treatment (E)	1	56.6	0.023	54.9	0.199	50.6	0.068
C × E	3	56.6	0.761	54.9	0.819	30.6	0.689
Seedbed type (S)	1	29.8	0.067	33.8	0.077	30.6	0.010
C × S	3	29.8	0.376	33.8	0.434	30.6	0.293
E × S	1	29.8	0.274	33.8	0.333	30.6	0.103
C × E × S	3	29.8	0.956	33.8	0.974	30.6	0.814

(b) Mean masses (g ± SD)

Canopy treatment	Foliage and branches	Main stem	Roots
UC	3.54 ± 0.38	2.27 ± 0.12	1.79 ± 0.16
S25	8.56 ± 0.74	4.30 ± 0.32	2.88 ± 0.21
S50	11.54 ± 0.81	5.57 ± 0.33	3.83 ± 0.21
GAP	21.47 ± 1.71	10.60 ± 0.71	6.06 ± 0.40

Note: Orthogonal contrasts performed for significant main effect of sources of variance.

^{a, b, c} Same legend as Table 1.

Foliar analyses of the planted seedlings showed a difference between nutrient concentrations prior to planting (2004) and at the end of the study for all canopy treatments including the control (Table 5). Concentrations of P ($F_{1,14} = 80.04$, $p < 0.001$), and Mg ($F_{1,14} = 25.02$, $p < 0.001$) were higher in 2004, while N ($F_{1,14} = 0.02$, $p = 0.898$) and K ($F_{1,14} = 0.09$, $p = 0.769$) concentrations remained unchanged. Calcium concentrations increased ($F_{1,14} = 27.17$, $p < 0.001$) after three growing seasons in the field. At the end of the study, foliar concentrations of Ca and P were the same in all planted seedlings, while N, K, and Mg were different among canopy treatments, without consideration for seedbed types (Table 5). K was the highest in the control treatment. N was the highest in the group selection cutting, while Mg was lower in that treatment. N was the only nutrient correlated with seedling dry mass ($r = 0.596$, $p < 0.001$).

Browsing damage on white-cedar was absent from all artificially seeded subplots, all subplots with animal exclosures, and 46.9% of the unprotected planted subplots. Considering only unprotected planted subplots, hare browsing was observed in all canopy treatments including the control. Control subplots experienced the highest frequency of damage ($F_{1,31} = 11.07$, $p = 0.002$; Control vs. S25+S50+GAP, $p < 0.001$), with 37.5% of browsed subplots compared to 15.6% for harvested treatments. Neither deer nor moose browsing was observed on planted white-cedar seedlings. With respect to the severity of browsing, 21.6% (control subplots) and 17.2% (harvested subplots) of damaged planted seedlings were in class 1 (1-25% of the total foliage consumed), 11.2% and 10.3% were in class 2 (26-50%), 12.1%, 11.2% were in class 3 (51-75%), and 11.2% and 5.2% were in class 4 (76-100%).

Table 5. ANOVAs of the concentration of nutrients in foliage of the terminal shoot (last 5 cm) of planted white-cedar seedlings 3 growing seasons after planting; and mean concentration of nutrients before planting and 3 growing seasons after planting by canopy treatment.

(a) ANOVAs of concentration

Source of variance	dfn ^a	Total nitrogen		Phosphorus		Potassium		Calcium		Magnesium	
		dfd ^b	p-Value	dfd	p-Value	dfd	p-Value	dfd	p-Value	dfd	p-Value
Canopy treatment (C)	3	49.1	0.002	12.1	0.063	50.4	< 0.001	51.2	0.272	24.2	0.009
UC vs. S25, S50, and GAP ^c	(1)	52.8	0.606	---	---	54.4	< 0.001	---	---	24.7	0.034
Gap vs S25 and S50	(1)	45.1	< 0.001	---	---	46	0.386	---	---	24	0.014
S25 vs S50	(1)	50	0.561	---	---	51.5	0.636	---	---	24	0.138
Exclosure treatment (E)	1	49.1	0.453	12.1	0.519	50.5	0.553	51.4	0.061	24.2	0.917
C × E	3	49.1	0.777	12.1	0.749	50.4	0.639	51.2	0.563	24.2	0.525
Seedbed type(S)	1	56.7	0.079	99.2	0.062	58.2	0.159	60.3	0.079	87.5	0.627
C × S	3	56.7	0.942	99.2	0.982	58.2	0.748	60.2	0.839	87.5	0.603
C × E × S	3	56.7	0.697	99.2	0.704	58.2	0.476	60.2	0.465	87.5	0.754

(b) Mean concentration (mg/g)

Canopy treatment	Total nitrogen	Phosphorus	Potassium	Calcium	Magnesium
Before planting (2004)	18.70 ± 0.37	2.96 ± 0.08	8.66 ± 0.19	6.59 ± 0.13	2.66 ± 0.12
UC (2006)	18.30 ± 0.53	1.77 ± 0.06	9.95 ± 0.33	8.81 ± 0.28	1.80 ± 0.03
S25 (2006)	17.17 ± 0.41	1.47 ± 0.04	7.94 ± 0.19	9.59 ± 0.35	1.78 ± 0.05
S50 (2006)	17.79 ± 0.67	1.41 ± 0.07	7.69 ± 0.34	9.39 ± 0.30	1.65 ± 0.06
GAP (2006)	21.28 ± 0.94	1.71 ± 0.09	8.18 ± 0.49	9.60 ± 0.34	1.52 ± 0.05

Note: Orthogonal contrasts performed for significant main effect of sources of variance.

^{a, b, c} Same legend as Table 1.

Discussion

Establishment of white-cedar seedlings

In the present study, the best combination of factors for the establishment of white-cedar seedlings was single-tree selection cutting with artificial seeding on exposed mineral seedbeds (68.8% of subplots with presence of white-cedar), while the worst combination was group selection cutting with natural seeding on both seedbed types (0% of subplots with presence of white-cedar). White-cedar is the least studied commercially valuable tree species in North America (Scott and Murphy 1987). Consequently, the study had to include many different explanatory factors. Moreover, a powerful experimental design with many degrees of freedom was necessary to comprehend regeneration dynamics of this secondary species present in low abundance under a mixedwood canopy (white-cedar < 2 500 seedlings/ha; yellow birch = 41 000 seedlings/ha; maples = 78 000 seedlings/ha) (*see Chapter 2*). However, the small component of white-cedar in mesic mixedwood stands is essential to maintain natural composition and dynamics, conserve wildlife habitats and food resources, and sustain the forest industry.

Artificial seeding greatly improved seedling abundance under all canopy treatments when seed rain was poor or moderate. The positive effect of artificial seeding, even in group selection cutting and on undisturbed seedbeds (Figures 3b and 3c), strongly suggests that the seed rain limited white-cedar regeneration, in contrast to other studies that have demonstrated the importance of appropriate microsite for establishment as the primary limiting factor (Cornett et al. 1997). In fact, the seeding effect was by far the most important factor when considering the ANOVA on seedling abundance (Table 1).

Uneven-aged silviculture systems, such as single-tree selection cutting, maximize the availability of seed in time and space by keeping a continuous number of seed trees close to the area where regeneration is desired, compared to even-aged systems, such as uniform shelterwood or clearcut systems, which require predictable, frequent, and heavy seed crops to ensure proper regeneration. Seed supply is even more important since there is no white-cedar seed bank in the soil and seeds remain viable for less than one year on the forest floor (Johnston 1990). In the same study area, results from Désy (2007) demonstrated that the

number of seeds monitored in the seed traps was correlated with the basal area of white-cedar within 20 m ($r = 0.513$, $p = 0.01$), but this correlation was not observed in a year of low seed production. In autumn 2005, control subplots without exclosures had high seedling abundance, mainly due to the proximity of productive seed trees. There were twice as many seed trees near control subplots compared to harvested treatments, which translated into more seeds inventoried in the seed traps. These differences in seed availability tended to mask canopy effects under natural seeding in 2006 (Figure 3a).

Because of the short duration of the study, we cannot infer the frequency of seed years for white-cedar in this region, but the literature suggests that very good seed crops are less frequent for this species than for its competitors (ca. every 5 years) (Godman and Mattson 1976; Johnston 1990). However, artificial seeding density was higher than the seed rain of the best seed crop observed in our study; therefore, we consider that this study provided a density of regeneration higher than that could be expected after a good seed year in these mixedwood stands.

Seed predation is more prevalent in group selection cutting than in other canopy treatments, but the low abundance of seedlings cannot be attributed solely to predation. Small mammals can eat white-cedar seeds (Johnston 1990), but seed predation is uncommon for white-cedar due to its small seed size (ca. 12 mm^2 ; 1.23 mg) (Johnston 1990; Simard et al. 2003). More research is required regarding the possible roles of parasites and pathogens in reducing the viability of white-cedar seeds and seedlings.

Moderate environmental conditions that were created by protection cover in the control treatment, single-tree selection cutting, and seed-cutting combined with disturbed seedbeds, maintain soil water content, soil temperature, and light availability at an acceptable level for establishment of white-cedar seedlings (Figures 3a and 4). However, higher abundance of white-cedar seedlings in 2006 compared to 2005 does not signify the absence of mortality. The detailed analysis of demography shows two sharp declines in white-cedar abundance (Figure 5c) for all canopy treatments (including the control), which were mostly attributed to environmental conditions.

In July and August 2005, 41% mortality was observed in one-year-old seedlings (Figure 5c). This decrease was likely caused by low soil water content and high soil temperatures (Figures 5a and 5b). Newly germinated seedlings are highly susceptible to drought, and consequently, maintenance of soil moisture levels is essential for their establishment and early survival (Cornett et al. 2000a). In mesic sites with mineral soils, precipitation during the growing season directly influenced water availability. Over the period of May 1 to August 31, the summer of 2005 was drier (299.7 mm of precipitation) than the summer of 2006 (450.5 mm) (*data from BioSIM*, Régnière 1996). Tolerance limits of white-cedar seedlings have not been defined, but in our study less than 10% soil water content was associated with high seedling mortality.

The second reduction in abundance of white-cedar seedlings (51% mortality; Figure 5c) occurred between August 2005 and June 2006, and was possibly due to litterfall and frost. At the soil level, the frost-free period is usually from mid-May to late-September in the study region (Gosselin et al. 1998), but there were unusual frosty days on August 30, 2005 and May 26, 2006 in all canopy treatments. One-year-old white-cedar seedlings can be killed by early and late frosts, thereby decreasing regeneration abundance (Johnston 1990). This high mortality rate means that about 50% of the seedlings monitored in 2006 originated probably from the seed crop of 2005 and were only one-year-old at the end of the study. Consequently, they are still extremely vulnerable to mortality.

When viable seeds were abundant, such as was the case with artificial seeding, more seedlings established on disturbed than on undisturbed seedbeds under all canopy treatments (Figures 3c and 4d). Soil disturbance, through the removal of the humus and exposure of the mineral soil, slightly increased available water in the uppermost 10 cm of the soil during seasonal moisture deficiencies and increased seedling survival (Figure 5a). The lowest soil moisture under the control treatment may have been due to substantial transpiration or increased rain interception by canopy vegetation (Figure 4a). These lowest soil moisture levels explained the impact of scarification under an intact canopy. It is generally recognized that humus decreases hydraulic conductivity during drought days and improves moisture retention in the mineral horizons (Marquis 1965; Winget and Kozlowski 1965).

Group selection was the worst canopy treatment (Figure 3a) for meeting the light requirements of white-cedar seedlings early survival; a light canopy cover should be better than full sunlight conditions. Partial shading is often considered necessary to moderate extreme temperatures and keep soil moisture at an acceptable level for seedlings during summer days (Schaffer 1996; Raymond et al. 2003). Group selection cutting, with the highest soil temperature and available light under the canopy (Figures 4b and 4c), reduced the establishment of seedlings, even on artificially seeded areas (Figure 3b).

Moreover, competition from fast-growing shrubs, herbs, and ferns is proportional to the percentage of canopy opening and compromised white-cedar seedling survival, especially in the group selection cutting. Generally, competition restricts the access of white-cedar to water, light and nutrient resources (Oliver and Larson 1997). This result is similar to that obtained by Chimner and Hart (1996), who found an exponential diminution in abundance of white-cedar seedlings when shrub density increased on humid sites in Michigan ($r^2 = 0.70$, $p < 0.01$). Interspecific competition that hinders white-cedar regeneration has also been observed in large natural openings in boreal forests (Kneeshaw and Bergeron 1996) and after clearcutting in humid mixedwood stands (Verme and Johnston 1986).

Early growth of planted white-cedar seedlings

Single-tree selection cutting is appropriate to promote establishment and early growth of white-cedar in mesic mixedwood stands, but the optimal canopy reduction treatment that is required was not the same for early growth of established seedlings.

High light levels favored planted white-cedar seedling growth and biomass production. Consequently, group selection cutting with the highest %PPFD (Figure 4c) allowed greater height and RCD increments (Figure 6) and higher foliage, stem, and root production (Table 5) than the control treatment, single-tree selection cutting, and seed-cutting. Regarding tolerance limits to shade, our results showed that seedling diameter and height growth were still possible at %PPFD as low as 20%, and that the growth rate continued to increase until 70% full sunlight. In modelling height growth of white-cedar seedlings, there is an increase in height increment with light availability between 15 and 36% of indirect light (see Chapter 3). According to Logan (1969) and Johnston (1990), seedlings exhibit prolific

branching under high light availability, thereby increasing the leaf area. A high light intensity is best not only for foliage and root development (Logan 1969), but also for height growth, which is contrary to Logan's results (Logan 1969). This height-light relationship is also consistent with literature reports from humid sites, where white-cedar seedlings remain quiescent under the canopy until it is opened by some disturbance (Verme and Johnston 1986). Thus, white-cedar seedlings taller than 25 cm have been exclusively observed adjacent to or within natural canopy gaps (Scott and Murphy 1987).

Soil disturbance improved root development and RCD increment of planted seedlings in all canopy treatments (Table 3). According to Thiffault et al. (2003), seedbed disturbance may stimulate nitrifier activity during the years following harvesting and lead to an increase in soil mineral N availability. This nutrient can then be taken up by more developed root systems in disturbed seedbeds, which would increase foliar concentrations of N (Table 5) and improve production of foliage (Gloser et al. 2009).

Nutrient status of planted seedlings also influenced growth (Table 5). Before planting, white-cedar seedlings were boosted with mineral nutrients to reach nursery growing standards (Girard et al. 2001). High concentrations of mineral nutrients are beneficial for growth, but boosted white-cedar seedlings are highly attractive to herbivores after planting (Radvanyi 1987). This could explain why seedling height growth was affected by hare browsing pressure only during the first year following plantation. At that time, animal exclusion improved height and RDC increments of planted seedlings, while browsing reduced foliage and branch mass (Table 4). However, hare damage could be less critical for white-cedar seedlings that originate from natural seeding, which has been observed for other softwood species (Radvanyi 1987; Rodgers et al. 1993).

Deer were practically absent from our study area, hare density was low with evidence of browsing present only on planted seedlings, and moose appeared to browse white-cedar only when other food was scarce (Grigal and Ohmann 1975), which was not the case here. In contrast to other studies with high deer densities in Maine, Wisconsin, Michigan, and Minnesota (Johnston 1972; Heitzman et al. 1999; Cornett et al. 2000b; Chapter 4), herbivore control is likely not required to successfully regenerate white-cedar in the current study region.

Management considerations

Conducting partial cutting treatments in an area with low deer population levels avoids excessive browsing as a major driver of regeneration density and allows the exploration of silvicultural treatments. Consequently, the lack of white-cedar regeneration is due to other biotic and abiotic factors. Understanding these factors can allow foresters to modify management practices accordingly.

Planting may maintain white-cedar proportions in mixedwood stands, but natural regeneration methods are generally favored in Canada. This study showed that the establishment of new regeneration is possible using partial cutting, as long as an adequate seed source is present, browsing is low, and pre-established regeneration did not prevent new seedlings.

Uncertainty surrounding the seed production cycle of white-cedar favors silviculture systems that ensure a more or less continuous presence of mature white-cedar seed trees if natural seeding is used. Regeneration of white-cedar needs a gradual opening of the canopy. Thus, irregular or uneven-aged systems, such as single-tree selection or irregular shelterwood, with a regeneration period lasting many decades, are therefore preferable to promote establishment of seedlings compared to even-aged systems, such as regular shelterwood and clearcutting systems.

Conclusion

In contrast to studies in the southern part of the white-tail deer range, browsing is not the most important factor limiting regeneration of white-cedar seedlings. In the absence of pre-established seedlings, sexual regeneration of white-cedar is mainly restricted by the timing and availability of viable seeds. After a good seed year or an artificial seeding, seedling establishment and early survival on mesic sites are assured by constant soil moisture and soil temperatures (without early and late frosts). Limitation of competition also improves early survival. Planted seedling early growth and biomass production are favored by high sunlight, soil disturbance, and N availability in the soil. Based on these results, single-tree selection systems, in conjunction with spot scarification, followed by creating gaps after establishment of seedlings are the most suitable systems for a sustainable management of

white-cedar using sexual regeneration. More studies are needed to evaluate the role of vegetative regeneration in stand renewal. Deer density varies across white-cedar's range and it is essential to further explore silvicultural approaches in regions with higher deer population levels. Furthermore, medium- and long-term growth of established seedlings should also be investigated by a detailed demographic study.

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Chapitre II

**Early establishment dynamics and species composition
three growing seasons after canopy reduction treatments
in mixedwood stands**

Abstract

This study determined the impact of three regeneration methods on the establishment dynamics and early growth of yellow birch (*Betula alleghaniensis* Britton), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh.), northern white-cedar (*Thuja occidentalis* L.), balsam fir (*Abies balsamea* (L.) Mill.), and white spruce (*Picea glauca* (Moench) Voss) regeneration in mixedwood stands on mesic sites. Three yellow birch-softwood uneven-aged stands were selected in the Province of Quebec (Canada) to evaluate the impact of a range of post-harvest environmental conditions on the abundance of tree species, and to detect interactions between species during the first three growing seasons following partial cutting. Single-tree selection cutting (25% of basal area removed), shelterwood seed-cutting (50% of basal area removed), and group selection cutting (gaps of 625 m²) were compared to a control treatment; pre-established regeneration was removed in all treatments. General results show that the abundance and height growth of the new cohort of regeneration depends on the availability of viable seeds, soil water content, light availability, interspecific competition, and browsing pressure. Specifically, single-tree selection cutting or seed-cutting combined with soil disturbance increases the abundance of yellow birch (70 000 seedlings/ha), while regeneration of maples is more abundant after canopy harvesting on an undisturbed seedbed (80 000 seedlings/ha). For softwood species, the establishment and survival are low during the first years following harvesting (< 5 000 seedlings/ha). At the end of the study, regeneration of hardwood species dominated the vertical structure of the new cohort and was the most developed in group selection cutting.

Keywords: single-tree selection cutting, group selection cutting, shelterwood, regeneration, early growth, seedbed, competition, browsing, *Betula alleghaniensis*, *Acer saccharum*, *Acer rubrum*, *Betula papyrifera*, *Thuja occidentalis*, *Abies Balsamea*, *Picea glauca*

Résumé

L'effet de trois procédés de régénération sur la dynamique d'établissement et la croissance initiale de la régénération de bouleau jaune (*Betula alleghaniensis* Britton), d'érable à sucre (*Acer saccharum* Marsh.), d'érable rouge (*Acer rubrum* L.), de bouleau blanc (*Betula papyrifera* Marsh.), de thuya occidental (*Thuja occidentalis* L.), de sapin baumier (*Abies balsamea* (L.) Mill.) et d'épinette blanche (*Picea glauca* (Moench) Voss) a été étudié dans des peuplements mixtes sur station mésique. Trois bétulaies jaunes résineuses inéquienues ont été sélectionnées dans la province de Québec (Canada), afin de déterminer l'impact d'une gamme de conditions de croissance après la coupe sur l'abondance de nouveaux semis des essences commerciales et de clarifier les interactions entre les essences durant les trois premières saisons de croissance suivant la récolte. Pour y arriver, des coupes de jardinage par pied d'arbre (25 % de la surface terrière récoltée) et par trouées (trouées de 625 m²), ainsi qu'une coupe d'ensemencement (50 % de la surface terrière récoltée) ont été comparées à des peuplements témoins et la régénération préétablie a été enlevée dans tous les traitements. En général, les résultats démontrent que l'abondance et la croissance en hauteur de la nouvelle cohorte de régénération dépendent de la disponibilité de graines viables, de l'humidité du substrat, de la disponibilité de la lumière, de la compétition interspécifique et du broutement. Plus précisément, les coupes partielles par pied d'arbre et l'exposition du sol minéral augmentent l'abondance du bouleau jaune (70 000 semis/ha), tandis que la régénération des érables est plus abondante après une coupe partielle sur un substrat non perturbé (80 000 semis/ha). Quant aux résineux, l'établissement et la survie sont faibles durant les premières années suivant les coupes partielles (< 5 000 semis/ha). À la fin de l'étude, la régénération des feuillus dominait la structure verticale de la nouvelle cohorte et était la plus développée dans la coupe de jardinage par trouées.

Mots clés: jardinage par pied d'arbre, jardinage par trouées, coupe progressive, régénération, croissance initiale, lit de germination, compétition, broutement, *Betula alleghaniensis*, *Acer saccharum*, *Acer rubrum*, *Betula papyrifera*, *Thuja occidentalis*, *Abies Balsamea*, *Picea glauca*

Introduction

To achieve sustainable use of mixedwood forests, we have to insure adequate regeneration and maintain stand structure and dynamics (Hunter 1999; Côté et al. 2003; Prévost et al. 2003). Mixedwood ecosystem dynamics are poorly known (Collins et al. 1979) and difficult to mimic, considering the individual ecological characteristics of the multiple species which are involved (Oliver and Larson 1996; Prévost et al. 2003; Dubois et al. 2006). After disturbance, many species share the forest floor space, and fast-growing species often invade the growing space, which results in a low density of less competitive vegetation (Oliver and Larson 1996; Heitzman et al. 1999; Lamy et al. 1999). Thus, a better understanding of factors governing establishment and early growth of individual species and interactions between them will allow the adaptation of management practices that minimize ecological impacts on the composition of successional strata.

Species composition of a new cohort is affected by many biotic and abiotic factors. Among these are (i) the availability of viable seeds, (ii) the biophysical environment of establishment and early growth, (iii) interspecific competition for resources, and (iv) preferential seed and seedling predation. Seed availability is conditioned by the number and distribution of seed trees (Cornett et al. 1997; Greene and Johnson 1998; Rooney et al. 2002) and by the frequency of seed production. Depending on the species, good seed crops occur at variable intervals, but the frequency for most northeastern North American tree species ranges from 2 to 7 years (Godman and Mattson 1976; Burns and Honkala 1990). Vegetative reproduction is also used by some species, such as red maple (*Acer rubrum* L.) and northern white-cedar (*Thuja occidentalis* L.) (Johnston 1990; Walters and Yawney 1990).

Mixedwood stands may be managed under many silvicultural systems, depending on the desired species composition and stand structure (Anderson et al. 1990; Oliver and Larson 1996; Smith et al. 1997). One approach uses low intensity cutting treatments, such as single-tree selection cutting, which promotes the establishment of shade-tolerant species (Smith et al. 1997; Nyland 2002; Raymond et al. 2003) by providing partial shelter of the forest floor, high soil moisture, and seed tree proximity. In contrast, a seed-cutting is a common first stage of a shelterwood regeneration system, which creates a higher range of

light and temperature conditions to allow the establishment of less shade-tolerant species (Wedeles et al. 1995; Smith et al. 1997; Asselin et al. 2001). Yet another approach is group selection cutting, which is frequently used to promote a greater diversity of species with different shade tolerance (Brewer and Merritt 1978; Runkle 1981; Raymond et al. 2006). In this system, the centre of large gaps offers growing conditions similar to small clearcuts, while the gap edge shades the forest floor (Anderson et al. 1990). Full sunlight conditions in large canopy openings induce high mortality of mid-tolerant and shade-tolerant species mainly due to drought-related death of germinants, but intolerant fast-growing species will establish and dominate (Smith et al. 1997; Dubois et al. 2006). In all canopy treatments, seedbed receptivity may be improved by soil scarification, either with specialized machines or imposed unintentionally during tree skidding.

In addition to physical environmental conditions, rodents and herbivores influence the composition and recruitment of the understory through differential consumption of seeds (Jensen 1982; Côté et al. 2003; Raymond et al. 2003) and by exerting browsing pressure (Frelich and Lorimer 1985; Tilghman 1989; Strole and Anderson 1992). Predation gives a competitive advantage for the germination of unconsumed seed species (Côté et al. 2003) and the growth of distasteful species, which contain high concentrations of tannins and terpenes (Borgmann et al. 1998; Samson et al. 2002). However, the impact of predation on species composition is a function of local population levels. For example, where herbivore populations are low and food is abundant, consequences on stand development will be limited (e.g., Grigal and Ohmann 1975). Fungal pathogens of seeds and seedlings also can influence the composition of the new cohorts (Burns and Honkala 1990).

The present study examined the establishment dynamics and the species composition of regeneration over a range of cutting intensities and environmental conditions, to guide silvicultural practices and determine the short-term regeneration success of canopy treatments in mixedwood stands. To achieve this objective, we established an experiment in the balsam fir-yellow birch domain, an ecosystem that is heavily used by the Quebec forest industry (Archambault et al. 1997; Dubois et al. 2006), and which is part of the distribution range of snowshoe hare (*Lepus americanus* Erxleben), white-tailed deer (*Odocoileus virginianus* Zimmerman), and moose (*Alces alces* Gray) (Godbout 1998; MRNFP 2003).

We examined the combined influence of partial harvesting intensities, environmental factors, seed abundance, seedbed disturbance, and browsing exclusion treatments on the abundance of individual species during three growing seasons. We pursued the following objectives: (i) to determine the impact of canopy treatment and seedbed type on environmental factors influencing the establishment of the post-cutting regeneration; and (ii) to understand the interactions among species in the dynamics of establishment and vertical stratification.

Methods

Study site

The study was conducted in the Outaouais Region of western Quebec, 120 km northwest of Fort-Coulonge ($46^{\circ}51'N$, $77^{\circ}23'W$) from 2003 to 2007. The site was located in the Balsam fir-Yellow birch bioclimatic domain, Ecological Region 4b-M (Gosselin et al. 1998). The climate is humid-continental, with a mean annual temperature ($\pm SD$) of $2.6 \pm 0.4^{\circ}\text{C}$ and total annual precipitation of $1037 \pm 115 \text{ mm}$ (1971-2000; *data from BioSIM*, Régnière 1996). In 2005-2006 on the study area, the frost-free period was 144 consecutive days, with a total of 223 days without frost.

Three contiguous uneven-aged stands were selected on the basis of a mixed composition dominated by yellow birch (*Betula alleghaniensis* Britton), which was growing on moderately well-drained sites. The thin organic layer (9 cm) is developed on a 50-100 cm deep mineral soil, with a sandy-loam to loamy-sand texture in the podzolic B-horizon. The pH ($\pm SD$) of organic and mineral layers were 3.3 ± 0.5 and 4.0 ± 0.3 respectively. Selected stands had not experienced recent harvesting (the last partial cut was in 1963 for all stands). There was no major perturbation reported, although the balsam fir component was probably affected by the two most recent spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks (Morin 1998). Mean stand basal area ranged from 21.2 to 26.5 m^2/ha (diameter at breast height $\geq 9.1 \text{ cm}$). Dominant canopy species included: yellow birch, 32% of basal area; white-cedar, 25%; red and sugar maple (*Acer saccharum* Marsh.), 24%; white spruce (*Picea glauca* (Moench) Voss), 7%; paper birch (*Betula papyrifera* Marsh.), 7%; and balsam fir (*Abies balsamea* (L.) Mill.), 5%. Horizontal stand structure was heterogeneous

with an intimate mix of species and aggregations of white-cedar, while the vertical structure was irregular, including multiple layers. The understory was composed of mountain maple (*Acer spicatum* Lamb.) and squashberry viburnum (*Viburnum edule* (Michx.) Raf.) (both combined = 35.6% cover), together with red and sugar maple, white-cedar, yellow birch, balsam fir, and spruce (Table 6). In 2003, other commercial tree species that were observed in the regeneration stratum included American beech (*Fagus grandifolia* Ehrh.) and eastern white pine (*Pinus strobus* L.).

Table 6. Abundance and stocking of seedlings (diameter at breast height < 1.1 cm) for commercial tree species before harvesting and removal of pre-established regeneration and three growing seasons following canopy treatments, excluding the control.

Tree species	Before harvesting (2003)		Three growing seasons after harvesting	
	Abundance (seedlings/ha)	Stocking (%)	Abundance (seedlings/ha)	Stocking (%)
Paper birch	0	0.0	2 422	20.2
Yellow birch	31 042	37.5	53 385	73.9
Red and sugar maple	135 115	72.9	80 651	96.9
Balsam fir	16 875	47.9	443	10.4
Spruce spp.	3 958	18.8	313	7.0
White-cedar	34 792	58.3	1 224	12.5
Other species ^a	208	2.1	729	9.4
Hardwood	166 326	87.9	137 168	96.9
Softwood	55 664	85.4	1 999	30.2
All species	221 990	100.0	139 167	96.9

^a ‘Other species’ includes:

Before harvesting: American beech, eastern white-pine

After harvesting: American beech, eastern white-pine, trembling aspen, pin cherry, red oak, black ash

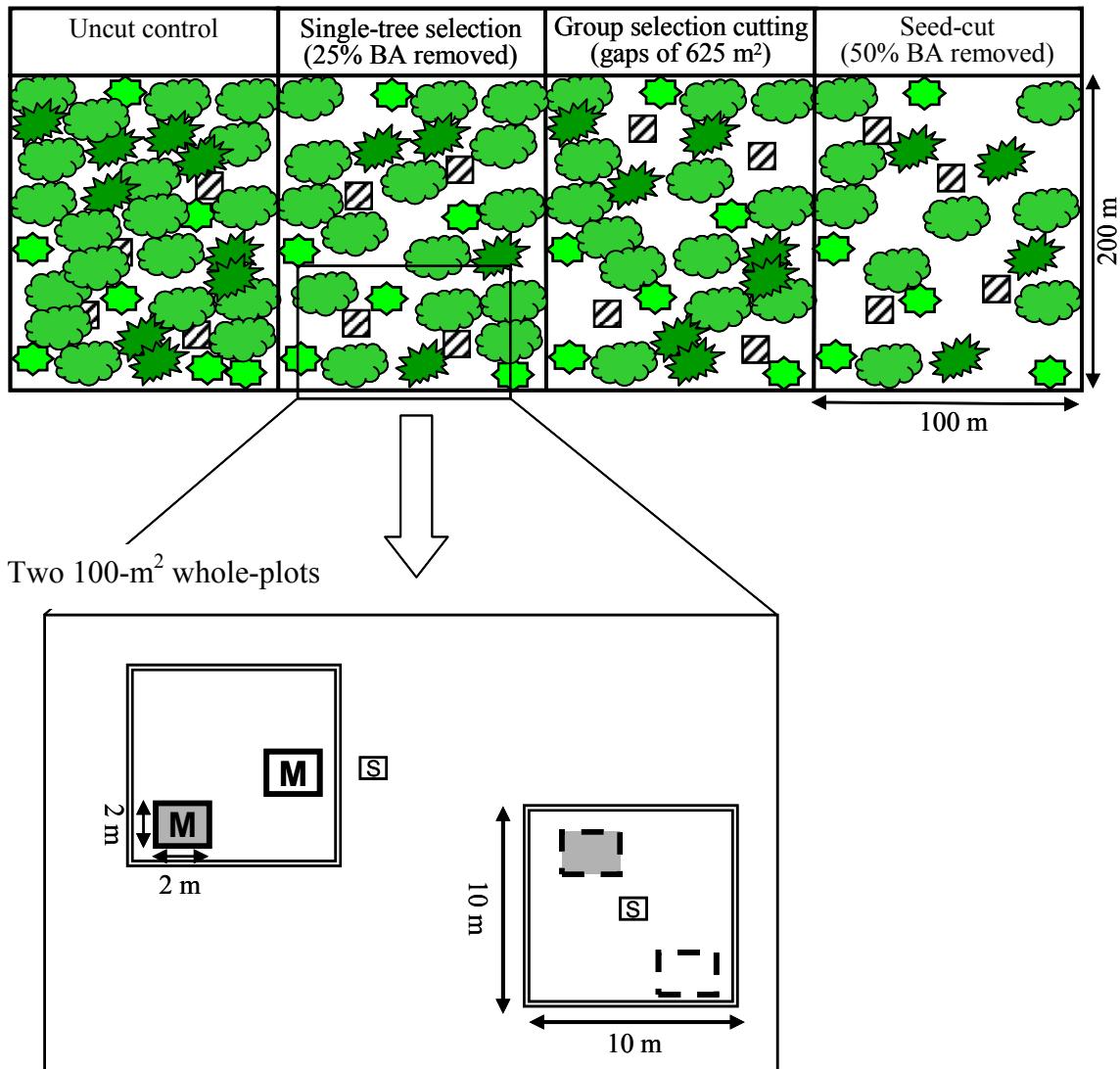
The study area was located in the northern part of the white-tailed deer range, in a region where moose are also present. In 2004, large mammal population densities were estimated as: no deer recorded; about 3.4 moose/10 km² (Lamontagne and Lefort 2004), and about 6 hares/10 km² (Godbout 1998). The density of hare is low, while that of moose is high compared to other administrative regions of the province (MRNF 2004). Occasional and

random browsing was observed on regeneration at the time when sites were selected. Little information is available on small mammal populations in the study area.

Design and data collection

Four rectangular 8-ha blocks were established in 2003, and partially harvested in June of the following year (Figure 7a). To compare the post-harvest regeneration of different cutting intensities, each block was divided into four 2-ha canopy treatments: (i) control without harvesting; (ii) 25% single-tree selection cutting (20% marking of basal area, and 5% for losses and operational purposes); (iii) 50% seed-cutting (40% marking, and 10% for losses and operational purposes); and (iv) group selection cutting, with five square gaps of 625 m². The number of gaps in the group selection cutting was set for experimental purposes; our harvest rate was more intensive than operational group selection system (*see* Nyland 2002). The seed-cutting is a common first stage of a shelterwood regeneration system, aimed at opening the canopy while retaining seed trees and partial cover during the establishment of a new regeneration cohort (Smith et al. 1997). In single-tree selection cutting and the seed-cutting, harvesting was done across all diameter classes, thereby maintaining species size-class proportions. In the group selection cutting, all trees were cut in the gaps, while the adjacent residual canopy remained intact. Gaps were located at a distance ≥ 35 m from one another. Felling was done with a single-grip harvester and whole-trees were hauled by cable skidder.

(a) One 8-ha block including four 2-ha canopy treatments

**Figure 7.** Example of one 8-ha block including four 2-ha canopy treatments, and two 100-m² whole-plots including two 4-m² subplots with or without exclosure.

Note: In 100-m² whole-plot (double lines); solid square, 4-m² subplot without exclosure; dash square, 4-m² subplot with exclosure; white square, undisturbed seedbed; gray square, disturbed seedbed; M, subplots with environmental monitoring (soil moisture, soil temperature); S, seed traps.

The experimental design is a split-plot with repeated measures. It includes four square 100-m² whole-plots per canopy treatment ($n = 64$; Figure 7a). Whole-plot location guidelines were: (i) ≥ 10 m from the block edges; (ii) semi-randomly distributed in the single-tree selection cutting, seed-cutting, and control treatment; (iii) in gap centres in the group selection cutting; and (iv) avoidance of humid depressions. Basal area by species was inventoried with a prism (basal area factor=2) around the center of each whole-plot. Each whole-plot includes two square 4-m² subplots (Figure 7b). In half of the whole-plots, subplots had browsing control treatments that were created by erecting animal exclosures. Exclosures were 1-m high, and constructed with a wood frame covered by metal screening (hexagonal mesh apertures of 8 cm²). The bottom of the screen was flattened on the ground to prevent intrusions by digging rodents. The screen covered the top in 2004 only. In all whole-plots, the surface organic horizon of one subplot was disturbed manually with a rake after harvesting (July 2004) to expose the superficial mineral horizon (Ae), while soil was left undisturbed in the other. All subplots were left to natural seeding. In each subplot, the pre-established regeneration of all woody species, including shrubs, was cut just after the harvesting to minimize there influence during the periods of germination and establishment of the post-harvest regeneration. Exclosure and seedbed treatments were assigned randomly among experimental units.

Regeneration measurements were carried out at the end of August 2005 and 2006. Regeneration of all tree species was counted yearly by 5-cm height classes in all 4-m² subplots. Browsing on each seedling was also monitored by percentage of the total foliage consumed (0 = absence of browsing; 1 = 1-25%; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%) and by herbivore (deer, moose, hare). Natural seed rain for all species was monitored with 64 1-m² seed traps covered with galvanized screen (square mesh of 1 cm²; Hughes et al. 1987). Each seed trap was paired with a whole-plot and was placed into or near this whole-plot (Figure 7b). Trap material was collected on an annual basis in May 2005, 2006, and 2007. Material was sieved (6.4-mm and 2.8-mm opening) and seed lots without vegetal debris were weighed (mean weight: 6.1 g (2005); 4.7 g (2006); and 28.0 g (2007)). In 2007, subsamples of seed lots were used for germination tests (5.0 g) and the number of germinants was extrapolated to seed lot weight. Seeds were sterilized with 1.5% H₂O₂ to limit fungal contamination during germination tests. These tests were conducted in growth

chambers for 28 days. Seeds were exposed to a day/night cycle of 12 hours with controlled temperature of 30°C/20°C and humidity saturation (90-100%). The number of emerging germinants was counted by species every two days to obtain the total number of viable seeds likely to produce well-formed germinants.

Total light availability under the forest canopy, expressed as a percentage of total photosynthetic photon flux density (%PPFD), was estimated on cloudy days in July 2004. We used numerical hemispherical photographs of the forest canopy taken from a point 1.5 m above the centre of each whole-plot (Rooney et al. 2002). The photographs were analyzed with the Gap Light Analyser (GLA) (Fraser et al. 1999).

Two blocks were randomly chosen for detailed monitoring of selected environmental factors. An exploratory analysis was performed to evaluate the differences of water availability and temperature among canopy treatments, including the control. Seedbed properties were monitored in the uppermost 10 cm (Raymond et al. 2003); two pairs of subplots without exclosures (1 disturbed and 1 undisturbed) were randomly selected from each canopy treatment, including the control (Figure 7b). In 2005 (June, July, and August) and 2006 (May, June, July, and August), soil water content in the uppermost 10 cm was monitored (16 records subplot/month) via time-domain reflectrometry (Field Scout TDR 100, Spectrum Technologies Inc., East-Plainfield, IL). Soil temperature was recorded at 2-hour intervals at a depth of 6 cm with 16 data-loggers (WatchDog Model 100, Spectrum Technology Inc.) from May 2004 to October 2006.

Statistical analyses

Mixed model analyses of variance (PROC MIXED, SAS 9.1, SAS Institute Inc., Cary, NC, USA) were conducted to examine the effects of canopy treatments, browsing control treatments, seedbed types, and time on regeneration and soil responses. Response variables included (i) annual abundance of viable seeds by species, (ii) annual seedling abundance by species, (iii) volumetric soil water content, (iv) mean monthly soil temperature, (v) total light availability (%PPFD), and (vi) the area of competition-free soil (e.g., the percentage of soil surface available for establishment of tree species). Natural log-transformation with an optimized constant was performed on seed and seedling abundance and on soil moisture

data to correct for heterogeneity of variance among treatments (Quinn and Keough 2002). The remaining variables were not transformed.

In ANOVA models, canopy treatments, seedbed types, enclosure treatments, and time, together with their interactions, were considered fixed effects, while blocks and replicates were random effects. Each block included two identical whole-plots (replicates) that were analyzed as nested factors. After initial ANOVAs, some covariance parameters (random effects) and nonsignificant four-way interactions were eliminated to improve fitting and robustness of the model (Voss 1999). Degrees of freedom were calculated using Satterthwaite's method. Orthogonal contrasts were developed to investigate significant differences (Mize and Schultz 1985). Correlation between the abundance of seedlings and cover of competitive species (including shrubs, herbaceous, and ferns) were performed. Descriptive statistics were used for the percentage of total foliage consumed.

Finally, mixed analyses of variance were tried to compare the height distribution of seedlings of individual tree species in each canopy treatment at the end of the study (PROC MIXED, SAS 9.1, SAS Institute Inc., Cary, NC, USA). Normality of data and homogeneity of variances were examined to ensure compliance with the primary statistical assumptions. Our data did not comply with these assumptions, and transformations did little to improve the overall model. Consequently, a chi-square test using exact p-values was used to examine which classes were over or under represented for the species included in the analysis (PROC FREQ, SAS 9.1, SAS Institute Inc., Cary, NC, USA). The distribution of each species by 10-cm height class and canopy treatment was compared to the overall expected distribution of all studied species (Snedecor and Cochran 1967). This statistical analysis provided information about the vertical structure of the regeneration cohort with the overall distribution used as a reference.

Results

Seed rain

Viable seed production, rather than total seed production, was monitored. The factor Year was significant for all species either simply as a main effect or in interaction with the

canopy treatments, including the control (Table 7). Regardless of canopy treatment, the best seed crop was produced in 2006 for all species that were monitored (Figure 8). In that year, yellow and paper birch produced > 500 viable seeds/ m^2 in all canopy treatments, including the control. Mean basal area of mature trees around the seed traps was 6.5 and 3.0 m^2/ha for yellow and paper birch, respectively. Softwood species produced < 160 viable seeds/ m^2 . There were about 0.5 viable seed/ m^2 for balsam fir (mean basal area of mature trees around seed traps of 0.4 m^2/ha), 6 viable seeds/ m^2 for spruce (1.0 m^2/ha), and 158 viable seeds/ m^2 for white-cedar (4.8 m^2/ha). No viable seed of maples was found and only a few seeds were collected in seed traps, despite there being 3.4 m^2/ha of red maple and 2.1 m^2/ha of sugar maple around seed traps after cutting.

For paper birch, the Canopy treatment \times Year interaction shows a progressive increase in the abundance of viable seeds from 2004 to 2006 for all canopy treatments, including the control (Figure 8a). There was no difference between canopy treatments when seeds were very abundant, while there were more viable seeds in the control treatment than in harvesting treatments in 2004 and 2005. Viable seeds of yellow birch were most abundant in the control treatment and least abundant in gaps of group selection cutting (Figure 8b). Yellow birch had moderate seed production in 2004 and good production in 2006 (Figure 8c).

Canopy treatments (including the control) had no impact on seed abundance of softwood species (Table 7). In 2004 and 2005, there was < 1 viable seed/ m^2 for all softwood species (Figure 8d); 2004 had a better seed crop than 2005 for spruce, while the reverse situation occurred for white-cedar. Because spruce germinants are difficult to identify to species, they were pooled.

Table 7. ANOVAs of the effects of canopy treatments on the abundance of viable seeds by species over 3 seed crops.

Source of variation	dfn ^a	Hardwood				Softwood					
		paper birch		yellow birch		balsam fir		spruce spp.		white-cedar	
		dfd ^b	p-Value ^c	dfd	p-Value	dfd	p-Value	dfd	p-Value	dfd	p-Value
Canopy treatment (C)	3	60	0.010	36	0.002	33	0.305	12	0.627	42.8	0.964
UC vs. S25, S50, and GAP ^d	(1)	---	---	36	0.009	---	---	---	---	---	---
GAP vs. S25 and S50	(1)	---	---	36	0.003	---	---	---	---	---	---
S25 vs. S50	(1)	---	---	36	0.474	---	---	---	---	---	---
Year (Y)	2	120	<0.001	36	<0.001	33	<0.001	168	<0.001	29.2	<0.001
2006 vs. 2004 and 2005	(1)	---	---	36	<0.001	33	<0.001	168	<0.001	29.2	<0.001
2004 vs. 2005	(1)	---	---	36	<0.001	33	0.706	168	0.022	29.2	0.037
C × Y	6	120	0.002	36	0.307	33	0.496	168	0.128	29.2	0.931
Y × (UC vs. S25, S50, and GAP)	(1)	120	0.005	---	---	---	---	---	---	---	---
Y × (GAP vs. S25 and S50)	(1)	120	0.050	---	---	---	---	---	---	---	---
Y × (S25 vs. S50)	(1)	120	0.905	---	---	---	---	---	---	---	---

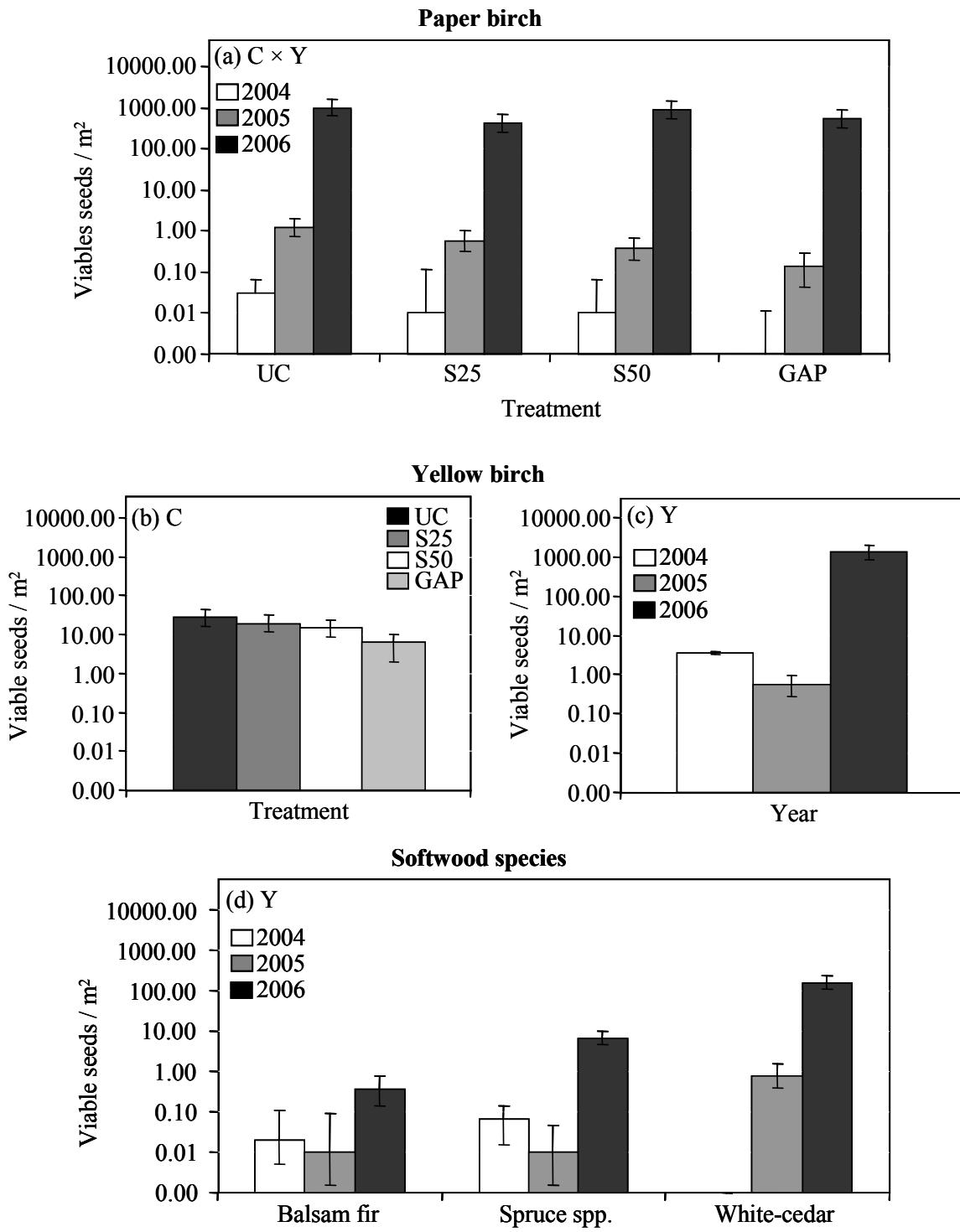
Note: Orthogonal contrasts performed for significant main effects and interactions between sources of variance.

^a Numerator degrees of freedom.

^b Denominator degrees of freedom.

^c Natural log-transformation of seed abundance ($y = \ln(\text{viable seeds} + 0.1)$).

^d UC, uncut control; S25, single-tree selection cutting (25% basal area removed); S50, seed-cutting (50% basal area removed); GAP, group selection cutting.



Note: Logarithmic scales are used.

Figure 8. Abundance of viable seeds in significant interactions and simple main effects including canopy treatments and time (see Table 7). Error bars show 95% confidence intervals. Same legend as Table 7.

Detailed monitoring of environmental factors

Canopy treatment also affects environmental conditions such as soil water content, soil temperature, and light availability. The control treatment had the lowest soil water content and soil temperature compared to harvesting treatments (Table 8; Figures 9a and 9b). Soil water content was the same for single-tree selection cutting, seed-cutting, and group selection cutting, while soil temperature and light transmission were higher in the group selection than in the other canopy treatments (Figures 9b and 9c). Light availability above the shrub layer depended on canopy treatment ($F_{3,12} = 134.36$; $p < 0.001$). Control treatment, single-tree selection cutting, and seed-cutting did not differ with respect to the percentage of total light (GAP vs. Control+S25+S50, $p < 0.001$; Control vs. S25+S50, $p = 0.083$; S25 vs. S50, $p = 0.290$).

Monthly soil moisture patterns differed greatly between the two years within all canopy treatments, including the control (Table 8; Figure 10a). 2005 growing season was particularly dry, with a sharp decline in soil water content between June and July/August. In 2006, soil water content was more stable throughout the growing season. In mesic sites with mineral soils, precipitation during the growing season directly influenced water availability. Over the period May 1 to August 31, the summer of 2005 was drier (299.7 mm of precipitation) than the summer of 2006 (450.5 mm) (*data from BioSIM*, Régnière 1996). During the drought of July and August 2005, more moisture was retained by the uppermost 10 cm of soil in the disturbed versus the undisturbed seedbeds. Mean soil temperature was the same in July across the two growing seasons, but higher in June and August 2005, compared to 2006 (Figure 10b).

Table 8. ANOVAs of the effects of canopy treatments and seedbed types on the monthly soil water content and soil temperature over 2 growing seasons.

Source of variance	dfn ^a	Soil water content		Soil temperature	
		dfd ^b	p-Value ^c	dfd	p-Value
Canopy treatment (C)	3	11.6	0.003	9.1	0.006
UC vs. S25, S50, GAP ^d	(1)	8.4	<0.001	9.1	0.025
GAP vs. S25 and S50	(1)	8.4	0.320	9.1	0.003
S25 vs. S50	(1)	8.4	0.069	9.1	0.297
Seedbed type(S)	1	6	0.071	6.4	0.274
C × S	3	6	0.062	6.4	0.314
Year (Y)	1	24.3	<0.001	7.6	<0.001
Month (M(Y))	5	24.3	<0.001	7.6	<0.001
June (2005 vs. 2006)	(1)	---	---	7.6	0.003
July (2005 vs. 2006)	(1)	---	---	7.6	0.337
August (2005 vs. 2006)	(1)	---	---	7.6	<0.001
C × Y	3	24.3	0.331	7.6	0.997
C × M(Y)	15	24.3	0.304	7.6	0.516
S × Y	1	1704	0.151	8	0.624
S × M(Y)	5	1704	0.005	8	0.710
S × May	(1)	1704	0.036	---	---
S × June (2005 vs. 2006)	(1)	1704	<0.001	---	---
S × July (2005 vs. 2006)	(1)	1704	<0.001	---	---
S × August (2005 vs. 2006)	(1)	1704	<0.001	---	---
C × S × Y	3	1704	0.921	8	0.862
C × S × M(Y)	15	1704	0.247	8	0.277

Note: Orthogonal contrasts performed for significant main effects and interactions between sources of variance.

a, b, d Same legend as Table 7.

^c Natural log-transformation of soil water content ($y = \ln(\text{soil water content} + 0.1)$).

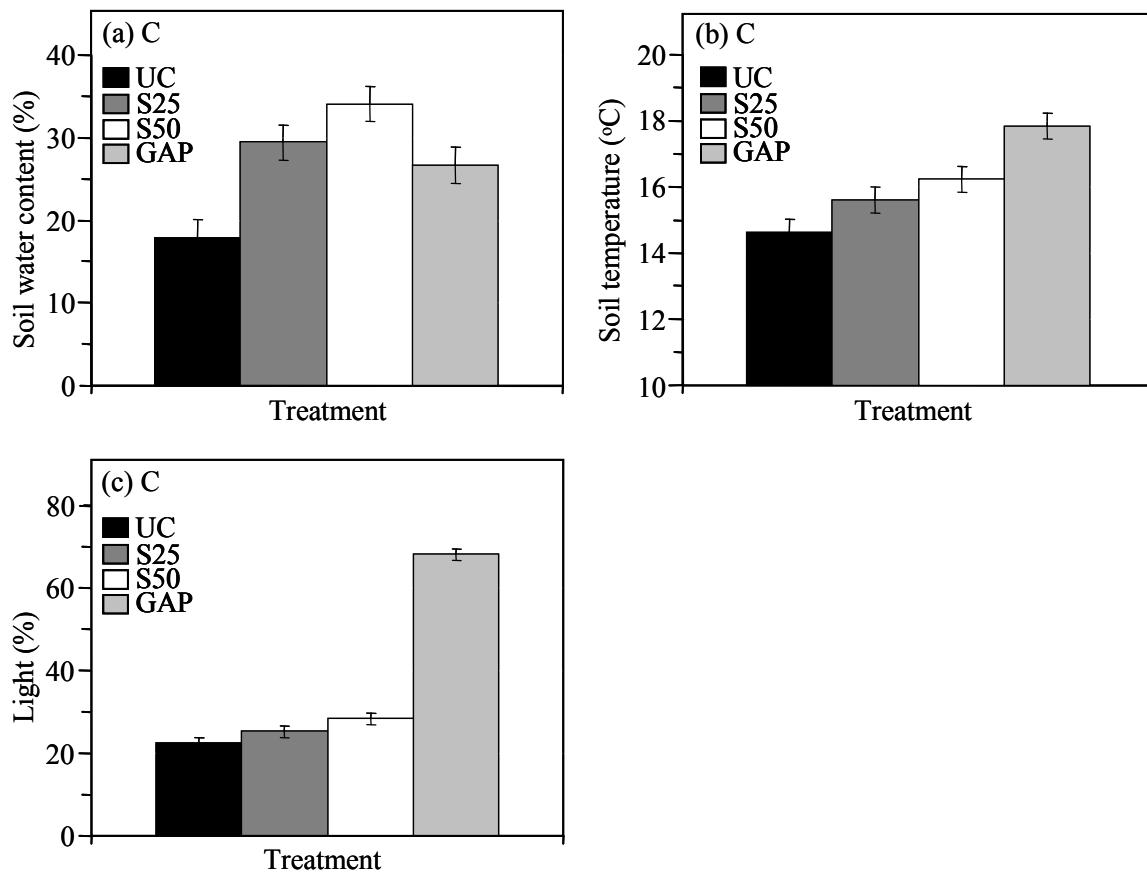


Figure 9. Soil water content, soil temperature, and light availability by canopy treatment over two years (*see* Table 8). Error bars show 95% confidence intervals. Same legend as Table 7.

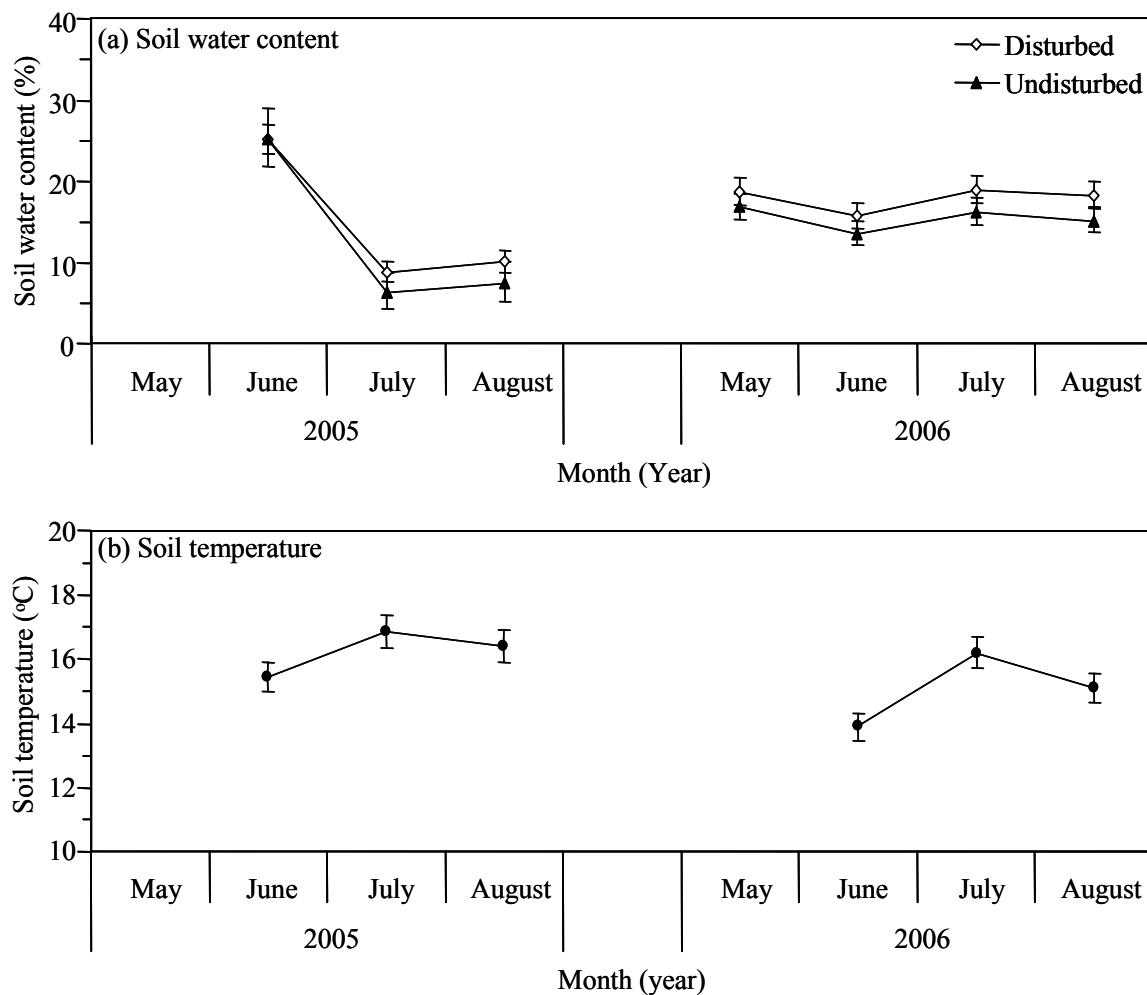


Figure 10. Monthly changes in soil water content and soil temperature over two growing seasons (see Table 8). Error bars show 95% confidence intervals.

Abundance of regeneration

Before harvesting, the stockings of hardwood and softwood regeneration were in the same range (Table 7). After the removal of pre-established regeneration and three growing seasons after harvesting, only one third of subplots contained new post-harvest softwood regeneration, while almost all subplots had new hardwood regeneration. Abundance and stocking of paper and yellow birch increased, but maple abundance decreased without diminishing stocking. Maple regeneration after cutting was mostly (about 60%) composed of red maple from vegetative reproduction. Balsam fir, white-cedar, and spruce densities were less abundant after compared to before harvesting, decreasing by 96% (Table 7). There were also marginal establishment of new tree species which were absent before cutting: trembling aspen (*Populus tremuloides* Michx.), pin cherry (*Prunus pensylvanica* L.), red oak (*Quercus rubra* L.), and black ash (*Faxinus nigra* Marsh.).

All hardwood species were influenced by the two-way interaction between Canopy treatment and Seedbed type (Table 9; Figures 11a, 11c, and 11e). Soil disturbance had a positive impact on birch in the harvesting treatments, relative to the control (Figures 11a and 11c). For paper birch, the highest abundance of seedlings was monitored in 2006 on disturbed seedbeds, in particular in the seed-cutting treatment (Figure 11b). However, the abundance of maples was higher on undisturbed soil within the seed-cutting and single-tree selection treatment than either under control treatment and group cutting treatment combined with an undisturbed seedbed or under other canopy treatments combined with a disturbed seedbed (Figure 11e). Total abundance of maple seedlings increased with time since cutting (Figure 11f).

The interaction Canopy treatment \times Exclosure treatment \times Year was significant for yellow birch only (Table 9), and contrasts show differences between the control and harvesting treatments for both exclosure levels and years (Figure 11d). Harvesting always allowed the establishment of more yellow birch seedlings and the total abundance was the highest in 2005, while protection against herbivores was beneficial for both years.

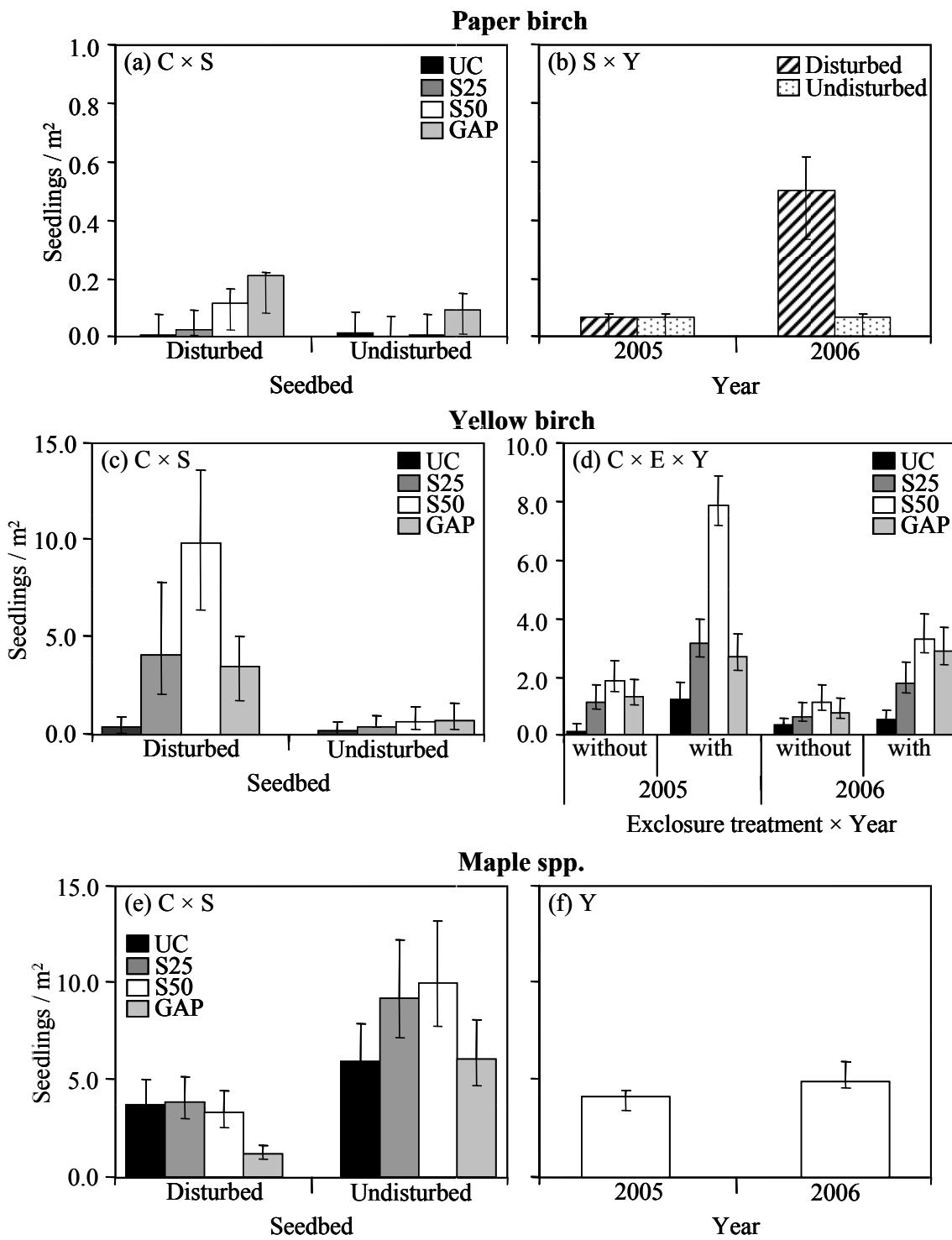
Table 9. ANOVAs of the effects of canopy treatments on abundance of hardwood seedlings by species over 2 years.

Source of variance	dfn ^a	paper birch		yellow birch		maple spp.	
		dfd ^b	p-Value ^c	dfd	p-Value	dfd	p-Value
Canopy treatment(C)	3	12	0.110	12	0.004	58.9	0.011
Exclosure (E)	1	46	0.600	44	< 0.001	58.9	0.725
C × E	3	46	0.388	44	0.943	58.9	0.942
Seedbed (S)	1	80.3	< 0.001	56	< 0.001	60.4	< 0.001
C × S	3	80.3	0.023	56	< 0.001	60.4	0.005
S × (UC vs. S25, S50, GAP) ^d	(1)	80.3	0.018	56	< 0.001	60.4	0.004
S × (GAP vs. S25 and S50)	(1)	80.3	0.553	56	0.027	60.4	0.031
S × (S25 vs. S50)	(1)	80.3	0.052	56	0.193	60.4	0.438
E × S	1	80.3	0.059	56	0.059	60.4	0.783
C × E × S	3	80.3	0.534	56	0.302	60.4	0.190
Year (Y)	1	80.3	< 0.001	115	< 0.001	59.4	0.004
C × Y	3	80.3	0.076	115	0.178	59.4	0.098
E × Y	1	80.3	0.311	115	0.154	59.4	0.085
C × E × Y	3	80.3	0.121	115	0.012	59.4	0.713
Y × E(UC vs. S25, S50, GAP)	(1)	---	---	115	0.007	---	---
Y × E(GAP vs. S25 and S50)	(1)	---	---	115	0.059	---	---
Y × E(S25 vs. S50)	(1)	---	---	115	0.433	---	---
S × Y	1	80.3	< 0.001	115	0.423	59.4	0.083
C × S × Y	3	80.3	0.063	115	0.804	59.4	0.237
E × S × Y	1	80.3	0.066	115	0.123	59.4	0.764

Note: Orthogonal contrasts performed for significant main effects and interactions between sources of variance.

^{a, b, d} Same legend as Table 7.

^c Natural log-transformation of seedling abundance ($y = \ln(\text{seedlings} + 1)$).



Note: Scales are adapted to species abundance.

Figure 11. Abundance of hardwood species regeneration in significant simple main effects and interactions including canopy treatments, seedbed types, exclosure treatment, and time (see Table 9). Error bars show 95% confidence intervals. Same legend as Table 7.

The abundance of spruce seedlings was the highest in the seed-cutting (Table 10; Figure 12a), while the abundance of white-cedar regeneration in 2006 was reduced in the harvesting treatments, compared to the control treatment (Figure 12c). Time since harvesting increased the abundance of white-cedar seedlings in the control (Figure 12c), but the opposite response was observed for balsam fir across all canopy treatments, including the control (Figure 12d). Animal exclosures increased spruce abundance (Figure 12b). No effect of seedbed type was significant for conifer species (Table 10).

Table 10. ANOVAs of the effects of canopy treatments on abundance of softwood seedlings by species over 2 years.

Source of variance	dfn ^a	balsam fir		spruce spp.		white-cedar	
		dfd ^b	p-Value ^c	dfd	p-Value	dfd	p-Value
Canopy treatment(C)	3	112	0.882	122	0.016	56	0.090
UC vs. S25, S50, GAP ^d	(1)	---	---	122	0.096	---	---
GAP vs. S25 and S50	(1)	---	---	122	0.290	---	---
S25 vs. S50	(1)	---	---	122	0.010	---	---
Exclosure (E)	1	112	0.982	122	0.004	56	0.810
C × E	3	112	0.107	122	0.053	56	0.669
Seedbed (S)	1	112	0.238	122	0.327	171	0.349
C × S	3	112	0.220	122	0.090	171	0.157
E × S	1	112	0.194	122	0.326	171	0.590
C × E × S	3	112	0.112	122	0.170	171	0.905
Year (Y)	1	115	0.029	58.9	0.681	171	0.035
C × Y	3	115	0.368	58.9	0.721	171	0.031
Y × (UC vs. S25, S50, GAP)	(1)	---	---	---	---	171	0.033
Y × (GAP vs. S25 and S50)	(1)	---	---	---	---	171	0.134
Y × (S25 vs. S50)	(1)	---	---	---	---	171	0.136
E × Y	1	115	0.665	58.9	0.510	171	0.734
C × E × Y	3	115	0.743	58.9	0.804	171	0.174
S × Y	1	115	0.061	58.9	0.088	171	0.206
C × S × Y	3	115	0.469	58.9	0.068	171	0.610
E × S × Y	1	115	0.606	58.9	0.088	171	0.722

Note: Orthogonal contrasts performed for significant main effects and interactions between sources of variance.

^{a, b, d} Same legend as Table 7.

^c Natural log-transformation of seedling abundance ($y = \ln(\text{seedlings} + 1)$).

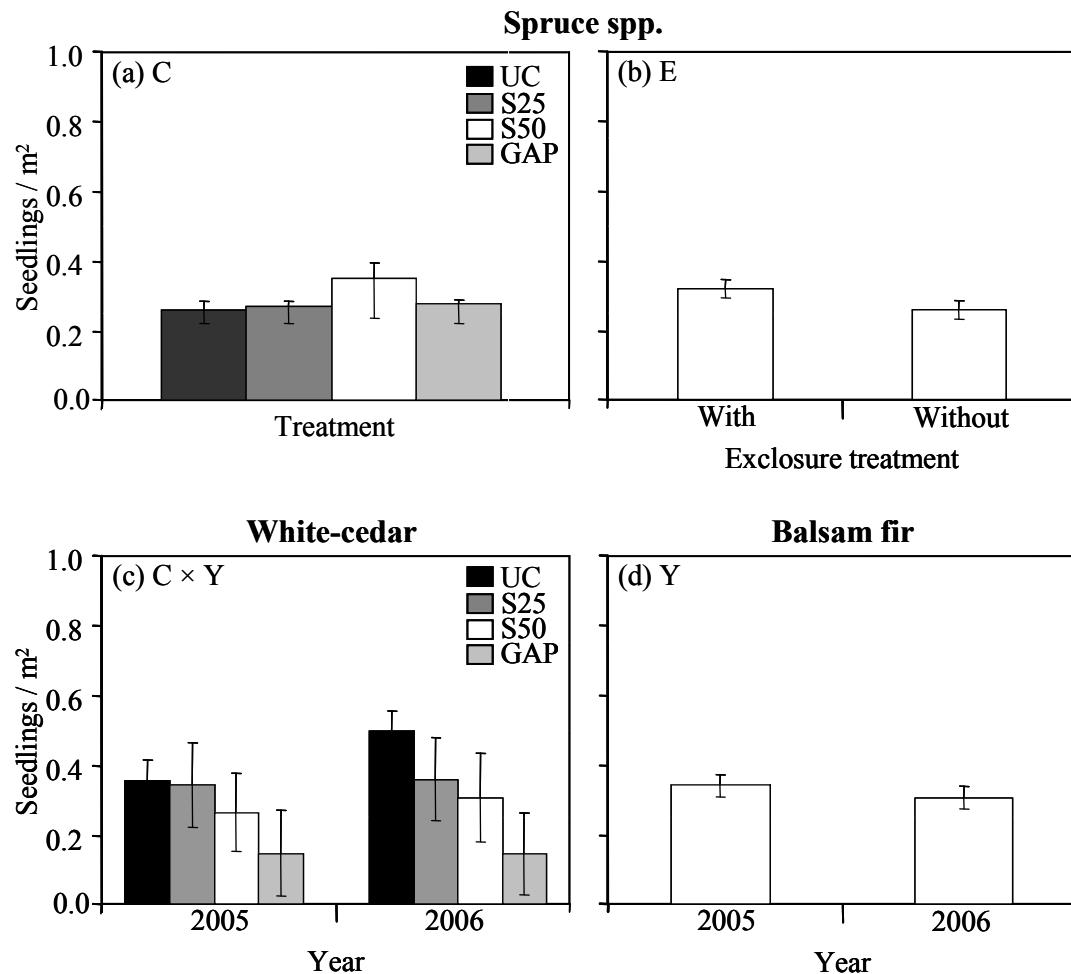


Figure 12. Abundance of softwood species regeneration in significant simple main effects and interactions including canopy treatments, exclosure treatment, and time (see Table 10). Error bars show 95% confidence intervals. Same legend as Table 7.

Height distribution

Three growing seasons after harvesting, the general distribution of all newly established species and canopy treatments reveals that half of the seedlings were smaller than 10 cm, and 13.4% were taller than 40 cm. Table 11 shows which classes are over represented or under represented for the species included in the analysis. The total number of seedlings monitored varied greatly among species and canopy treatments and has to be considered in the interpretation of results (Figure 13). Total number of softwood seedlings was low. Spruce seedlings were absent from the control treatment, while there were no white-cedar seedlings recorded in the group selection cutting.

The tallest class (> 40 cm) was entirely composed of hardwood species, while balsam fir was the only softwood species with few seedlings taller than 31 cm (Figure 13). All white-cedar seedlings were smaller than 21 cm and over represented in the shortest class (1-10 cm) compared to the general distribution of all species and canopy treatments combined (Table 11). Paper birch and ‘other species’ were under represented in the shortest class. In the control treatment, there were no seedlings in the tallest class and few seedlings taller than 20 cm (Figure 13). There were more seedlings of yellow birch, maples, and white-cedar in the shortest class, compared to the general distribution of all species and canopy treatments combined (Table 11). Seedlings in the tallest class were over represented in the group selection cutting, followed by seed-cutting and single-tree selection cutting.

Table 11. Height distribution of individual species in each canopy treatment (expected, or average distribution of all species and canopy treatments combined, shown as a percentage).

Height class		1-10 cm	11-20 cm	21-30 cm	31-40 cm	>40 cm
General distribution of all species and canopy treatments combined	n-value ^a	49.3%	20.9%	9.5%	6.9%	13.4%
Paper birch	UC ^b	4		—	—	—
	S25	7	+	—	—	—
	S50	46	—			+
	GAP	40	—		+	+
Yellow birch	UC	32	+	—	—	—
	S25	685		+		
	S50	653				
	GAP	612	—	+	+	+
Maple spp.	UC	1010	+			—
	S25	1262				—
	S50	1131				
	GAP	704	—	+		+
Balsam fir	UC	6		+	—	—
	S25	5		—	+	—
	S50	6	+		—	—
	GAP	6	—	+	+	—
Spruce spp.	UC	0	—	—	—	—
	S25	2	+	—	—	—
	S50	7			—	—
	GAP	3		+	—	—
White-cedar	UC	64	+	—	—	—
	S25	36	+	—	—	—
	S50	11	+	—	—	—
	GAP	2	—	—	—	—
Other species	UC	2	+	—	—	—
	S25	20	—			+
	S50	198	—		+	+
	GAP	69	—	—		+

Note: + or – indicates a very significant difference superior or inferior to the general distribution by height class and canopy treatment ($\chi^2=6.63$, $p < 0.010$).

^a n-value show the total number of seedlings found in each canopy treatment.

^b Same legend as Table 7.

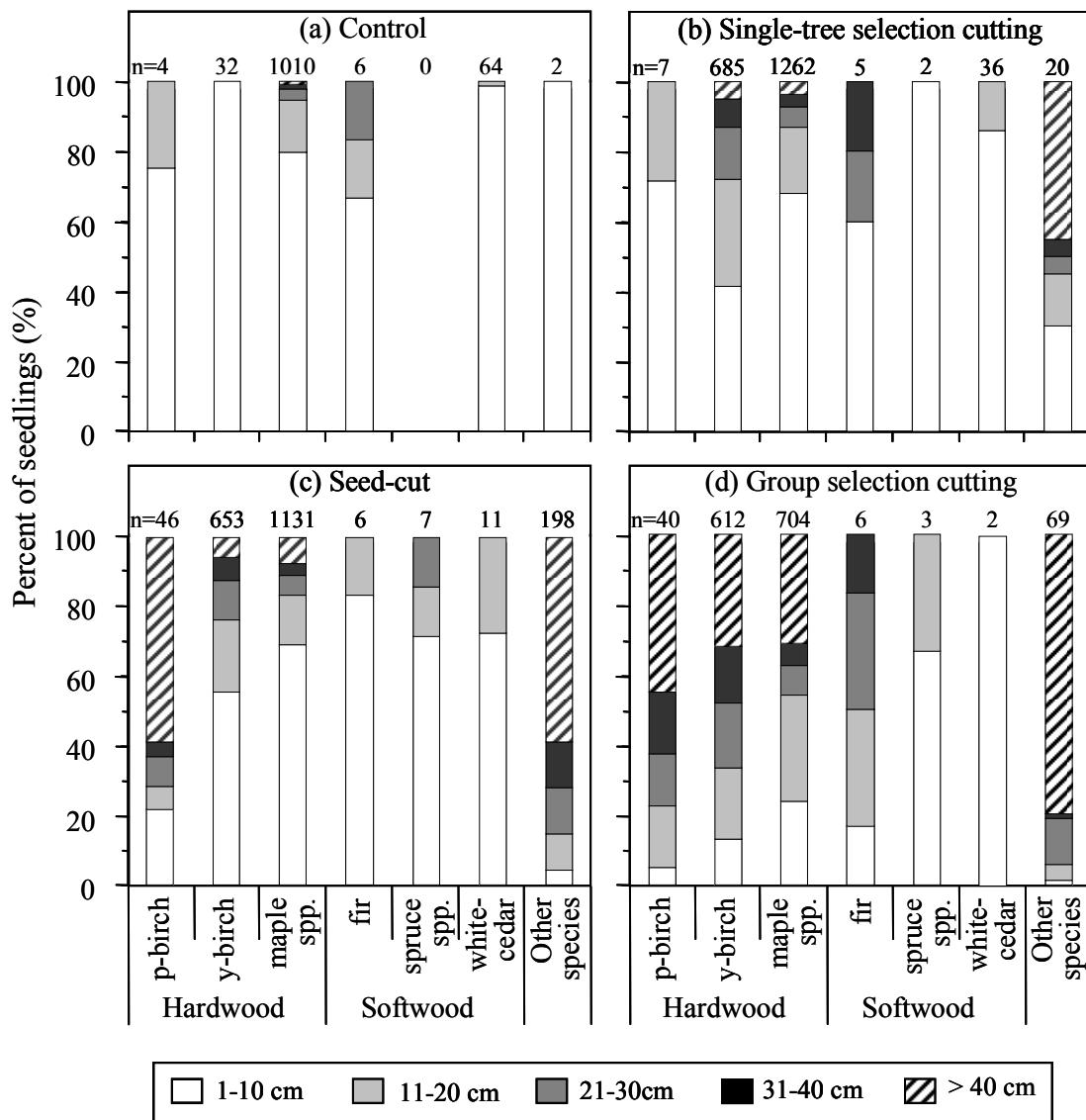


Figure 13. Distribution of seedlings by height class in each canopy treatments including control 3 growing seasons after harvesting.

Note: n-values show the mean number of seedlings found in each canopy treatment in 2006. ‘Other species’ includes: trembling aspen, American beech, mountain maple, eastern white pine, pin cherry, red oak, and black ash.

Interspecific competition and browsing pressure

At the end of the study, the abundance of conifer seedlings was negatively correlated with competitive species cover composed of shrubs, herbaceous, and ferns (*data not shown*; $r = -0.235$, $p = 0.007$), while the abundance of hardwood species was not affected ($r = -0.021$, $p = 0.815$). The area of competition-free soil available for establishment of tree species was influenced only by canopy treatments (*data not shown*; $F_{3,56} = 37.17$, $p < 0.001$), while exclosure treatments, seedbed type, and interactions were nonsignificant. The percent of disturbed and undisturbed subplot area that was occupied by shrub, herbaceous, and fern species was 10.2% in the control, 19.4% in the single-tree selection, 21.4% in the seed-cutting, and 71.1% in the group selection.

No browsing marks that would have been caused by deer were observed, while moose consumed neither softwood species nor hardwood seedlings smaller than 20 cm during the course of the study. About 6.1% of unprotected hardwood species taller than 20 cm were browsed by moose. In 2006, ‘other species’ (9.8% of seedlings taller than 20 cm browsed), red and sugar maple (4.5%), and yellow and paper birch (3.9%) suffered the greatest browsing pressure. Browsing was mostly observed in seed-cutting and group selection cutting (83.3% of occurrences), with mainly 1–25% of the total foliage consumed.

Discussion

Only three growing seasons after partial harvesting, vertical stratification in the new regeneration cohort was already apparent (Figure 13). Hardwood species are more abundant than softwood species in all canopy treatments including the control (Figures 11 and 12) and dominate the height distribution. Regardless of the canopy treatment and seedbed type, the abundance of softwood seedlings is always $< 5\,000$ seedlings/ha. Softwood seedlings are part of the lowest stratum of regeneration because they have a slower growth rate than mid-tolerant and intolerant hardwood species. Depending on the canopy treatment in mixedwood stands, variable growth rates of species can significantly affect structural attributes and contribute to the stratification of the emerging community (Hibbs 1983; Wang and Nyland 1993). Silviculturists must know how their treatments modify environmental conditions, together with the consequences of these modifications on the

abundance and development of species that they want to manage (Fowells and Means 1990).

Before harvesting, our study area was fully stocked with commercial tree species, but we removed this regeneration during the establishment of the experiment design. Three growing seasons later, a part of the forest floor was still vacant (Table 6). Moreover, at the end of the study, softwood species were present only on one-third of the harvested area, and they did not recover their pre-harvesting density. According to the literature, there is generally little regeneration of conifers established immediately following logging compared to that of hardwood species (Heitzman et al. 1999; Raymond et al. 2003). The results therefore do not reflect exactly the impact of harvesting at an operational scale, where advance regeneration was not systematically eliminated. In fact, if the management objective is to promote shade-tolerant species using a regeneration strategy based on pre-established regeneration, such as balsam fir, white-cedar, and sugar maple (Anderson et al. 1990; Godman et al. 1990), it would be better to protect and release pre-established seedlings rather than only established post-harvest regeneration.

Harvesting treatments strongly promoted hardwood regeneration of mid-tolerant species (yellow birch, red maple, red oak, and black ash) and established new shade-intolerant species (paper birch, trembling aspen, and pin cherry) (Table 6; Figure 11). Their abundance is greatly variable among canopy treatments and they are the tallest in group selection cutting, followed by seed-cutting and single-tree selection cutting (Figure 13). However, the composition and vertical stratification of the succession stratum are variable among canopy treatments, likely the consequence of variations in environmental conditions created by harvesting. The residual canopy plays an important role in natural seeding, shading the forest floor, moderating extreme temperatures, limiting invasion by competitive vegetation, and keeping soil moisture at an acceptable level for establishment and early growth (Figures 9 and 10).

Availability of viable seeds

The availability of viable seeds is a strong driver of seedling abundance. Seed availability is strongly linked to the quantity and proximity of seed trees. After cutting, there were more

seed trees of hardwood species compared to softwood species and the abundance of viable seeds and new seedlings roughly corresponded to basal area of seed trees (Figures 8, 11, and 12). Based on mature trees, white spruce was clearly the dominant spruce species, while red (*Picea rubens* Sarg.) and black spruce (*Picea mariana* (Mill.) BSP) were rarely found in the study area. Thus, seeds and seedlings of spruce should be mostly white.

Dispersal distance is greater for birches (up to 1 km) than for maples and softwood species (< 100 m) (Anderson et al. 1990; Burns and Honkala 1990). Maples and balsam fir have the shortest dispersal distance and the lowest basal area of seed trees, which partially explains the few seeds caught by traps and the low density of post-harvest seedlings (Figures 8 and 12d). High dispersal capacity should be combined with high seed production to compensate for low seed availability immediately around seed trees (Ribbens et al. 1994). Production is also variable between species and years. According to the literature, seed production is greater for birches than conifers and maples (paper birch > yellow birch > white-cedar > spruces > balsam fir > maples), while the frequency of good seed crops is variable, depending on biotic and abiotic factors (frequency of good seed crops: paper birch > red maple > yellow birch ≈ white spruce > balsam fir > white-cedar > sugar maple) (Fowells 1965; Godman and Mattson 1976; Anderson et al. 1990; Burns and Honkala 1990; Perala and Alm 1990). The interval between good seed crops is 2 to 3 years for birches, red maple, and spruces and can be up to 4 years for balsam fir, 5 years for white-cedar, and 7 years for sugar maple. Consequently, in order to maximize the availability of seed through time and space, it is preferable to keep a continuous number of seed trees close to the area requiring regeneration, which was not the case in group selection cutting, given the low abundance of maple and white-cedar seedlings (Figures 11e and 12c). This is especially important for species with low seed productivity and short dispersal distances, e.g., softwood species and sugar maple. Some species have a seed bank standing during few years in the forest floor and producing new seedlings even if seed crop is very poor (e.g. paper and white birch).

Lack of viable seeds for red and sugar maple can also be explained by samara length, which ranges from 12 to 25 mm in red maple and from 20 to 27 mm in sugar maple (Godman et al. 1990; Farrar 1996), and which could hardly go through the grid covering the seed traps (1-cm² mesh). Moreover, germination of red maple seeds occurs mostly 2 to 6 days after

liberation (Walters and Yawney 1990); thus, germinants emerged in the traps rather than in the growth chamber. During the study, sugar maple did not have good seed crops, but red maple did in 2004 and 2006 (*personal observation*). In addition, red maple stumps sprout vigorously after harvesting (Walters and Yawney 1990), contributing to the high abundance of seedlings and the stocking close to 100% in canopy treatments excluding the control, even if seeds have a short distance of dispersal (Table 6). Asexual reproduction also explains that maple was over represented in the largest height class compared to the general distribution of all species and canopy treatments combined (Table 11; Figure 13). Height growth of sprouts is higher than sexual regeneration because they benefit from an established root system (Walters and Yawney 1990). When sprouts compete for water and nutrients, they have an advantage on newly established seedlings (seed origin). Moreover, mortality of sprouts is rare due to their low vulnerability to drought and high soil temperatures in the uppermost 10 cm, which results in an increase of maple abundance with time since cutting (Figure 11f).

Environmental conditions after canopy treatments

As expected, post-cutting environmental factors have a variable impact on the abundance of regeneration, depending on a species' needs. Drought and high ground-surface temperatures are the principle causes of mortality for newly germinated seedlings in most species that have been studied; consequently, soil moisture is essential for their establishment and early survival (Anderson et al. 1990; Burns and Honkala 1990; Cornett et al. 2000a). Thus, the centre of gaps in group selection cutting, where soil temperature and light availability are the highest, is likely not the best environment for the establishment of all the studied species (Figures 11 and 12). However, group selection cutting offers the best conditions for height growth of all species present (Figure 13).

Reduction of the overstory density, combined with disturbed soil, is best for the establishment of birches, even if availability of viable seeds is higher in the control treatment (Figures 11a and 11c). This can be explained by the fact that disturbance, through the removal of the humus and exposure of the mineral soil, slightly increased available water in the uppermost 10 cm during a drought period, while the partial shading moderated

extreme temperatures and light availability close to ground level. In other words, the reduction in the density of the number of viable seeds is compensated by an increase in seedbed receptivity. According to Anderson et al. (1990) and Chapter 1, these growing conditions could also improve the establishment of spruces and white-cedar, but the low abundance of viable seeds did not allow us to confirm that fact. If enough soil moisture is available, balsam fir can germinate on disturbed and undisturbed soils under a wide range of light intensities (Anderson et al. 1990; Frank 1990). According to Greene and Johnson (1998) and Zarnovican (2003), the establishment of balsam fir seedlings may also be greater than white-cedar and spruce, because seeds are heavier (balsam fir: 7.6 mg; white spruce: 2.3 mg; white-cedar: 1.2 mg) (Burns et Honkala 1990; Farrar 1996; Simard 1999). Thus, despite important differences in seed rain of balsam fir, spruce, and white-cedar, the number of established seedlings was almost the same.

Interspecific competition

During their first years, seedlings of softwood species suffer high mortality caused by drought, early and late frost, and hardwood litterfall (Anderson et al. 1990; Frank 1990; Simard et al. 2003). This likely explains the stability or decrease in the abundance of seedlings with time since cutting, even if there was a supply of viable new seeds (Figure 12). It may also be true for yellow birch, depending on light conditions, soil moisture, and competitive species (Erdmann 1990). Seedlings and sprouts of maples suffer little mortality caused by suppression (Godman et al. 1990; Walters and Yawney 1990). Hardwood and competitive species will also limit the establishment of softwood species and cause considerable mortality by using resources and by rapidly invading growing space. Fast-growing vegetation will also limit the development of the regeneration of more slow-growing, shade-tolerant species even if they can survive for a few years when overtapped. On the other hand, early growth is largely determined by the amount and character of overhead competition, with most species requiring nearly full sunlight for optimum growth (Marquis et al. 1964; Logan 1969; Anderson et al. 1990; *see Chapter 1*).

There can be many desirable seedlings three years after cutting, but interspecific competition was high. Abundance of competition is proportional to the percentage of

canopy opening, with the highest invasion in group selection cutting. High light availability and free growing space encourages a proliferation of pioneer species (paper birch, trembling aspen, and pin cherry) and competitive vegetation, including shrubs, herbs, and ferns. Competitive species cover was an important factor limiting regeneration of conifer species (negative correlation). In the study area, most competition after harvesting came from red raspberry (*Rubus idaeus* L.), squashberry viburnum, mountain maple, spinulose shield-fern (*Dryopteris spinulosa* Watt), and carex (*Carex* spp.). Therefore, the conservation of a partial canopy during seedling establishment is preferable to reduce losses attributable to interspecific competition (White et al. 1985; Erdmann 1990; Johnston 1990). If advance regeneration had not been removed, it would also have been competing and limiting abundance of new seedlings.

Browsing and predation pressure

At the end of the study, 70.2% of seedlings were smaller than 20 cm (Table 11); the preferred food for deer and moose is above that height (Beals et al. 1960; Saunders and Puettmann 1999a). Accordingly, most seedlings were not browsed after three growing seasons. Furthermore, browsing impact depends on local herbivore populations and the abundance of food. In our study area, deer were scarce and the density of hare was low. Density of moose was high, but understory vegetation taller than 20 cm, mostly composed of mountain maple, squashberry viburnum, and red maple, was abundant, which likely limited the browsing pressure on seedlings monitored in the experimental plots. Consequently, browsing was not a driving factor for composition and stratification of the regeneration cohort, but the situation is often reported to be temporary and different in other regions with higher herbivore populations (Heitzman et al. 1999; Côté et al. 2004). However, the high abundance of skid trails in group selection cutting and seed-cutting promoted the abundance of food by soil disturbance, made movement easier for large mammals, and increased accessibility to seedlings (Johnston 1972). Hence, there was a higher occurrence of moose browsing in harvested plots with higher cutting intensity, compared to the control treatment and single-tree selection.

Hare browsing on newly established seedlings was difficult to detect, because hare can entirely consume new seedlings. This herbivore limited the abundance of yellow birch and spruce seedlings, as demonstrated by significance of protection against herbivores (Figures 11d and 12b). Indeed, hares were responsible for browsing half of the 3-year-old yellow birch seedlings that were present on a study site in Quebec (Gastaldello 2005), while they were not reported to browse spruce.

Seed predation could also be problematic for maples, yellow birch, spruces, and balsam fir (Anderson et al. 1990; Godman et al. 1990; Frank 1990; OMNR 2000). Small mammals, birds, squirrels, and insects consume almost all tree seeds, but seed predation is uncommon for some species, such as white-cedar (Johnston 1990; Bartlett et al. 1991; Simard et al. 2003). More research is required regarding the possible roles of parasites and pathogens in reducing the viability of seeds before and after seed dispersal (Farmer 1997).

Management considerations

The challenge in mixedwood stand silviculture is to deal with many species with different ecological characteristics. As we have demonstrated, adequate conditions for establishment of post-harvest regeneration are not the same for all desirable species. Stands are heterogeneous and application of treatments should also be flexible and varied with respect to their intensity and dimensions of the gaps that they create. In the absence of pre-established regeneration, the best treatment to regenerate multiple species with different life history characteristics and habitat requirements in the studied ecosystem is probably to harvest somewhere between 25% and 50% of the basal area by selecting individual trees and small groups, paired with a passive or active site preparation (Nyland 2002). Too small canopy opening will not favor the establishment of mid-tolerant and intolerant species, while a cutting intensity higher than 50% or with large gaps will increase the interspecific competition with shade-intolerant species and competitive vegetation, thereby putting softwood species and sugar maple at a disadvantage. Special care should be provided to maintain a sufficient number of seed trees for the long-term establishment of seedlings, and to protect and promote the softwood advanced regeneration.

If shade-tolerant seedlings are pre-established, either naturally over a long period of time since cutting or operationally through the imposition of low intensity cuts, a partial canopy removal creating larger gaps or a final removal cutting in a shelterwood system would release established seedlings and maximize their height growth.

Conclusion

Three growing seasons after partial harvesting and removal of pre-established regeneration, the new cohort was at the end of the invasion stage (*see* Oliver and Larson 1996). Generally, seedling establishment needs an abundance of viable seeds, partial shelter of the forest floor, a disturbed seedbed, and limited abundance of fast-growing species. In early establishment dynamics, hardwood species dominated abundance, stocking, and height distribution, but softwood seedlings may survive under suppression and continue their establishment and development. Specifically, yellow birch was the studied species that was best adapted to establish under partial harvesting combined with a disturbed seedbed, while the abundance of maple was the highest without soil disturbance. The abundance of softwood species regeneration was low although good conditions for their establishment were not observed in this study. In the following years, interspecific competition for resources, vertical stratification, and mortality within the new cohort will continue and mixedwood stand composition will evolve. Long-term studies should be conducted to confirm the final composition of the post-harvest stand and to predict volume and productivity by individual species. More studies are also needed to evaluate the role of pre-established regeneration in the succession stratum after harvesting.

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Chapitre III

**Height and diameter growth of northern white-cedar
(*Thuja occidentalis* L.) seedlings, layers, and small
saplings in mixedwood stands under partial cutting
management**

Abstract

Northern white-cedar (*Thuja occidentalis* L.) is often considered as a very slow growing species and its presence in the regeneration stratum offers no guarantee of successful stand succession. The objective of this retrospective study was to quantify the development of white-cedar seedlings and saplings from sexual or asexual origin in mesic mixedwood stands managed by partial cutting. Three sites were selected; two in Quebec, Canada (Outaouais Region (OR) and Papineau-Labelle wildlife reserve (PL)), and one in Maine, United States (Penobscot Experimental Forest (PEF)), to model relationships between age, height and diameter increment, available light, and partial cutting. White-cedar seedlings and layers have established in all stands, while white-cedar stems recruited scarcely over 30 cm high. Stems taller than 130 cm were present almost exclusively on the site with the lowest white tailed-deer (*Odocoileus virginianus* Zimmerman) density. Consequently, height and diameter increment were modelled only for sites with less than 6 deer/km² (OR and PL). Time needed to reach 30 cm is about the same at all study sites (6-7 years for layers and 11-13 years for seedlings), but predicted height growth is best on the PL site allowing stems to reach 130 cm high about 10 years earlier (14 vs. 24 years for layers and 20 vs. 32 years for seedlings). Height growth increases with indirect transmitted light ($6.2\% \leq$ indirect light $\leq 36.0\%$) following a quadratic form. An increase of 10% of indirect light, between 15 and 25% of light, results in a height increment of about 5 cm/yr. Partial canopy opening increased diameter increment at the soil level; 75.8% of stems showed a diameter increment significantly higher than before cutting and this response persisted for at least 10 years. Results suggest that white-cedar regeneration growth is slow, but can be encouraged by partial harvests.

Keywords: height growth, diameter growth, partial cutting, light availability, regeneration, browsing, eastern white cedar, *Thuja occidentalis*, *Odocoileus virginianus*

Résumé

Le thuya occidental (*Thuja occidentalis* L.) est souvent considéré comme une essence à croissance très lente et sa présence dans la strate de régénération n'est pas garante de son maintien dans le peuplement. Cette étude rétrospective vise à quantifier le développement des semis et des petites gaules de thuya d'origine sexuée et asexuée dans les peuplements mixtes sur station mésique. Trois sites expérimentaux ont été choisis au Québec, Canada (dans la région de l'Outaouais (OR) et la réserve faunique Papineau-Labelle (PL)) et au Maine, États-Unis (Penobscot Experimental Forest (PEF)) pour modéliser les relations entre l'âge, l'accroissement en hauteur et en diamètre, la disponibilité de la lumière et les coupes partielles. Les semis et les marcottes de thuya se sont établis dans tous les peuplements, mais peu de tiges sont recrutées à plus de 30 cm de hauteur et les tiges plus grandes que 130 cm se retrouvent presque exclusivement sur le site ayant la plus faible densité de cerf de Virginie (*Odocoileus virginianus* Zimmerman). Conséquemment, l'accroissement en hauteur et en diamètre a été modélisé seulement sur les sites ayant moins de 6 cerfs/km², soit OR et PL. Le temps nécessaire pour atteindre 30 cm est semblable sur les deux sites étudiés (6-7 ans pour les marcottes et 11-13 ans pour les semis). La croissance subséquente en hauteur prédictive est meilleure à PL ce qui permet aux tiges d'atteindre 130 cm de hauteur environ 10 ans plus tôt (14 vs 24 ans pour les marcottes et 20 vs 32 ans pour les semis). La croissance en hauteur augmente suivant une forme quadratique avec la lumière transmise indirecte ($6,2\% \leq \text{indirect light} \leq 36,0\%$). Une augmentation de 10 % de celle-ci, entre 15 et 25 % d'intensité, résulte en un accroissement en hauteur d'environ 5 cm/an. Quant à la coupe partielle, elle augmente l'accroissement diamétral au niveau du sol. Après une ouverture du couvert, 75,8 % des tiges présentent un accroissement diamétral significativement plus grand qu'avant la coupe et cette réaction persiste durant au moins 10 ans. Les résultats démontrent que la régénération de thuya croît lentement, mais qu'elle peut être encouragée par des coupes partielles.

Mots clés: thuya occidental, croissance en hauteur, croissance diamétrale, coupe partielle, disponibilité de la lumière, régénération, broutement, *Thuja occidentalis*, *Odocoileus virginianus*

Introduction

Northern white-cedar (*Thuja occidentalis* L.) is a commercially valuable species present in the eastern half of Canada and the northeastern part of the United States (Johnston 1990). It occurs in many forest types, including the Acadian Forest complex and the boreal forest. Throughout its native range, white-cedar forms pure stands on wet and dry sites, but growth is best on mesic mineral soils (Curtis 1946; Nelson 1951; Johnston 1990), where it shares the growing space with many other tree species (Johnston 1990). In mixedwood stands on mesic sites, frequently associated species are yellow birch (*Betula alleghaniensis* Britt), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), and northern conifers, including balsam fir (*Abies balsamea* (L.) Mill.), white (*Picea glauca* (Moench) Voss) and red (*Picea rubens* Sarg.) spruce, and eastern hemlock (*Tsuga canadensis* (L.) Carrière). Depending on the silvics and growing rate of each species, vertical stratification and self-thinning take place in the regeneration cohort (Oliver and Larson 1996; Smith et al. 1997). In this competition for space and resources, white-cedar seedlings and saplings are frequently disadvantaged and overtapped (see Chapter 2).

White-cedar regenerates equally well from asexual reproduction (layering) and sexual reproduction (seed origin) (Johnston 1990; Miller 1992). On wet sites, layering accounts for more than fifty percent of white-cedar stems (Verme and Johnston 1986; Johnston 1990; Bergeron 2000), but sexual reproduction seems to dominate on mesic sites (Scott and Murphy 1987; Chimner and Hart 1996; Bergeron 2000). Key elements for the establishment and early survival of white-cedar sexual regeneration (seedlings) are partial shading and constant humidity of the forest floor, together with proximity of white-cedar seed trees, and availability of receptive seedbeds such as disturbed soil (see Chapter 1) and decayed wood (Simard et al. 1999). However, layering is possible where any part of a branch or stem is in contact with a sufficiently moist substrate (Curtis 1946; Johnston 1990). A minimum threshold for soil moisture has yet to be established, while other environmental factors do not seem to affect the success of this regeneration mode (Kneeshaw and Bergeron 1998). For many tree species, the commercial value of stems from asexual origin (layers) has been questioned, because a poorer form and lower productivity has often been attributed to layers compared to seedlings (Jarvis and Cayford

1961; Doucet 1987; Anderson et al. 1990). Nevertheless, as shown by Doucet (1987), black spruce layers may be as valuable as seedlings for wood productivity at the stand level.

A high abundance of white-cedar regeneration at an early stage offers no guarantee of successful stand succession. Seedling mortality remains high during the first years (DeLong et al. 1997; Simard et al. 2003) and only 4% of established white-cedar seedlings reach a height of 25 cm (Scott and Murphy 1987). Mortality of established seedlings (height > 30 cm) and small saplings is also high (*see* Chapter 4). Moreover, their development can be hampered by browsing damage incurred by white-tailed deer (*Odocoileus virginianus* Zimmerman), moose (*Alces alces* Gray) or snowshoe hare (*Lepus americanus* Erxleben) (Johnston 1972, 1990).

Ecosystem-based management aims to mimic natural disturbances and maintain the vertical and horizontal structure. In mixedwood stands, natural disturbances are mostly sporadic gaps that are created by the mortality of individual stems or a small group of trees (Seymour et al. 2002). Thus, partial cutting techniques can be used, such as single-tree selection cutting, group selection cutting, and shelterwood cuts (Smith et al. 1997). Until now, many studies have examined the short-term impact of partial cutting on the composition, abundance, and stocking of natural regeneration in mixedwood stands (e.g. Brissette 1996; Archambault et al. 2003; *see* Chapters 1 and 2), especially in relation to the biophysical environment created by canopy gaps. The focus of such studies is often the establishment of the new cohort and the proportion of the site occupied by each species. However, few studies have analysed the growth response of pre-established white-cedar seedlings and saplings, which may play a crucial role in stand renewal (Scott and Murphy 1987; Johnston 1990; Hofmeyer 2008).

Although shade-tolerant white-cedar seedlings and saplings can stay quiescent in an overtopped position for many decades, partial cutting can release them and change their development pattern (Scott and Murphy 1987; Johnston 1990). In fact, light availability at the forest floor level is often considered to be a primary driver of regeneration growth (Pacala et al. 1994; Finzi and Canham 2000; Mitchell 2001; Moores et al. 2007), but regional climate, soil fertility and moisture status, stem origin, and browsing pressure may also have to be considered.

To be able to predict stem productivity, to evaluate white-cedar yield, and to schedule forest interventions, a better understanding of development patterns of seedlings, saplings, and layers is necessary. The main objective of this retrospective study was to quantify the height and diameter growth of white-cedar regeneration from sexual and asexual origin in mixedwood stands. We modelled the effects of time and light availability on the height increment of individual white-cedar stems from zero to 200 cm tall. In addition, we determined the diameter growth response of pre-established seedlings and layers (≥ 3 -years-old) to partial harvesting, over a 10-year period. Implications of observed responses are discussed with regards to concerns about mixedwood stand management.

Methods

Study site

The study encompassed a wide territory, which included a significant portion of the geographic range of white-cedar and a variety of deer and hare densities. Three sites throughout the native range of white-cedar were selected: the first site is located in the Outaouais Region of western Quebec, Canada (hereafter called OR; $46^{\circ}34'N$, $77^{\circ}27'W$); the second site was in the Papineau-Labelle wildlife reserve of western Quebec, Canada (hereafter called PL; $46^{\circ}10'N$, $75^{\circ}20'W$); and the third site was on the Penobscot Experimental Forest in Maine, United States (hereafter called PEF; $44^{\circ}52'N$, $68^{\circ}38'W$).

During the summer of 2005, eight mixedwood stands with a significant white-cedar component, that had been partially cut between 1971 and 1983 using diameter-limit cutting, were selected on the OR and PL sites (four on each site), while eight stands were selected on the PEF. Stand selection guidelines were: (i) partially cut before 1985; (ii) stand composition representative of stands growing on mesic sites; and (iii) mean basal area of white-cedar ranged from 10% to 66% (diameter at breast height ≥ 9.1 cm). Diameter-limit cuts that were used on the OR and PL sites were realized in an operational context, while the PEF had been established by the United States Forest Service in 1950 for stand-level silvicultural experiments (Brissette 1996). The PEF includes ten treatments replicated twice, but we focus on data that were collected from four partial harvest treatments. Treatments include selection cutting with 5-, 10-, and 20-year cutting cycles and fixed

diameter-limit cutting with a harvest interval of about 20 years, based on stand volume increment (Brissette 1996). Harvest intensity in the selection treatments is a function of the cutting cycle and structural goal (Marquis 1978; Guldin 1991; *see* Chapter 4). Fixed diameter-limit cutting is a partial cutting using species-specific size thresholds, above which merchantable trees are cut (*see* Kenefic and Nyland 2005). Even if frequency and intensity of partial harvesting were different on the three sites, all these treatments tend to maintain an irregular to uneven-aged stand structure, establish a new cohort of trees, and release regeneration at each entry. Partial harvesting is common in mixedwood stands and it has been suggested that such treatments create a biophysical environment favorable for successful regeneration and recruitment of white-cedar (Schaffer 1996; Hofmeyer 2008; Chapter 1). However, white-cedar sustainability is not the focus of silviculture treatments on the PEF (Kenefic et al. 2005).

The PEF is generally warmer than the two Quebec sites and has a longer growing season, while the OR site is the coldest (Table 12). For the three sites, soil texture in the B-horizon ranges from silt-loam to sandy-loam, with good to poor drainage. Mean stand basal area ranged from 23.5 to 37.2 m²/ha. Dominant canopy species included mixed northern conifers (white-cedar, balsam fir, and white and red spruce), while hemlock is present only on the PL and PEF sites. White-cedar was about 8% of the total basal area on the PEF site. The most common hardwoods are birches (yellow and/or paper (*Betula papyrifera* Marsh.)) and maples (red and/or sugar). Horizontal stand structures were heterogeneous with an intimate mix of species and aggregations of white-cedar, while vertical structures were irregular to uneven-aged as a result of past cutting and natural disturbances. There was no major natural perturbation reported, although the fir component was probably affected by the two most recent spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks (Morin 1998). The understory was mostly composed of balsam fir, maples, white-cedar, yellow birch, and hemlock. The mean cover of shrubs, mainly mountain maple (*Acer spicatum* Lamb.) and squashberry viburnum (*Viburnum edule* (Michx.) Raf.), was 41-60%, which may limit the growth of tree species.

Table 12. Ecological description of the three study sites. OR site, Outaouais Region; PL site, Papineau-Labelle wildlife reserve; PEF site, Penobscot Experimental Forest.

Study site	OR site	PL site	PEF site
Climate^a			
Bioclimatic domain or Forest region	Balsam fir-Yellow birch	Sugar maple-Yellow birch	Acadian Forest
Elevation (m)	400	320	75
Mean annual temperature (°C)	2.55 ± 0.42	2.83 ± 0.45	6.68 ± 0.34
Total annual precipitation (mm)	1037 ± 115	1138 ± 115	1066 ± 137
Mean annual snowfall (cm)	336 ± 63	357 ± 72	289 ± 78
Growing season (days)	147 ± 16	157 ± 17	183 ± 15
Soil			
Texture of B-horizon	Loamy-sand - sandy-loam	Loam — loamy-sand	Silt-loam — sandy-loam
Sand (%)	70.2	61.8	35.6
Loam (%)	21.4	27.2	37.2
Silt (%)	8.4	11.0	27.2
pH			
Humus	3.25 ± 0.47	3.15 ± 0.46	3.28 ± 0.31
B-horizon	3.95 ± 0.29	3.95 ± 0.49	4.45 ± 0.53
Organic layer (cm)	9	7	9
Depth of soil (cm)	50-100	50-100	50-100
Drainage	Good	Good	Good to poor
Composition of the overstory^b			
Total basal area (m ² /ha)	34.5	37.2	23.5
Main softwood species	<ul style="list-style-type: none"> • White-cedar (30%) • Balsam fir (13%) • White spruce (4%) 	<ul style="list-style-type: none"> • White-cedar (29%) • Balsam fir (16%) • Hemlock (12%) 	<ul style="list-style-type: none"> • Hemlock (31%) • Red/white spruce (23%) • Balsam fir (22%)
Main hardwood species	<ul style="list-style-type: none"> • Yellow birch (23%) • Red maple (11%) • Sugar maple (3%) 	<ul style="list-style-type: none"> • Yellow birch (15%) • Sugar maple (6%) • Red maple (6%) 	<ul style="list-style-type: none"> • Red maple (9%) • Paper birch (3%)
Composition of the understory^c			
Mean density of seedlings (seedlings / ha)	50 139	49 491	30 189
Main softwood species	<ul style="list-style-type: none"> • White-cedar (17%) • Balsam fir (16%) • White spruce (2%) 	<ul style="list-style-type: none"> • Balsam fir (31%) • White-cedar (7%) • Hemlock (3%) 	<ul style="list-style-type: none"> • Balsam fir (43%) • Hemlock (20%) • White-cedar (12%)
Main hardwood species	<ul style="list-style-type: none"> • Sugar maple (28%) • Yellow birch (20%) • Red maple (16%) 	<ul style="list-style-type: none"> • Yellow birch (20%) • Sugar maple (17%) • Red maple (17%) 	<ul style="list-style-type: none"> • Paper birch (8%) • Red maple (8%)
Herbivore densities (nb/km²)^d			
Deer	0.0	5.5	6.2
Hare	0.6	0.6	15.2
Moose	0.3	0.1	0.3

^a Monitored between 1971-2000 (± SD) (*data from BioSIM*, Régnière 1996).

^b All trees with DBH ≥ 1.1 cm; percent of total basal area occupied by each species.

^c All seedlings taller than 5 cm with DBH < 1.1 cm (percent of all seedlings of merchantable species)

^d Estimated from hunting surveys in 2004-2005 (Lamontagne and Lefort 2004; MDIFW 2007; MRNF 2007a).

In looking at the abundance of white-cedar regeneration on each site, we observed that there were twice as many seedlings on the OR site than on the PL site and the PEF (Figure 14). All sites had the same abundance of white-cedar seedlings smaller than 15 cm, but the PL and PEF sites had fewer seedlings in the remaining height classes. Moreover, seedlings taller than 100 cm were absent from sample plots on the PL and PEF sites. Some seedlings taller than 30 cm were found on both sites (PL and PEF), while no seedlings taller than 60 cm were found on the PEF. Height distribution of white-cedar regeneration allowed further analyses on the PL site, while the PEF site was not used to analyse seedling and sapling development of white-cedar. Thus, the latter site was included for comparison and interpretation of the results.

The study was located within the natural range of white-tail deer, where moose and hare are also present (Table 12). It is difficult to get precise information about herbivore densities, because estimated densities of hare, moose, and deer are based on hunting surveys instead of direct inventories (Huot et al. 2002). Consequently, herbivore densities should be interpreted as relative rather than absolute values. In 2004-2005, deer were absent from the OR site, while the density of deer was high on the PL site and highest on the PEF. At the time when the sites were selected, little browsing was observed on white-cedar regeneration on the OR site, while deer browsing was frequently observed on the PL site and the PEF.

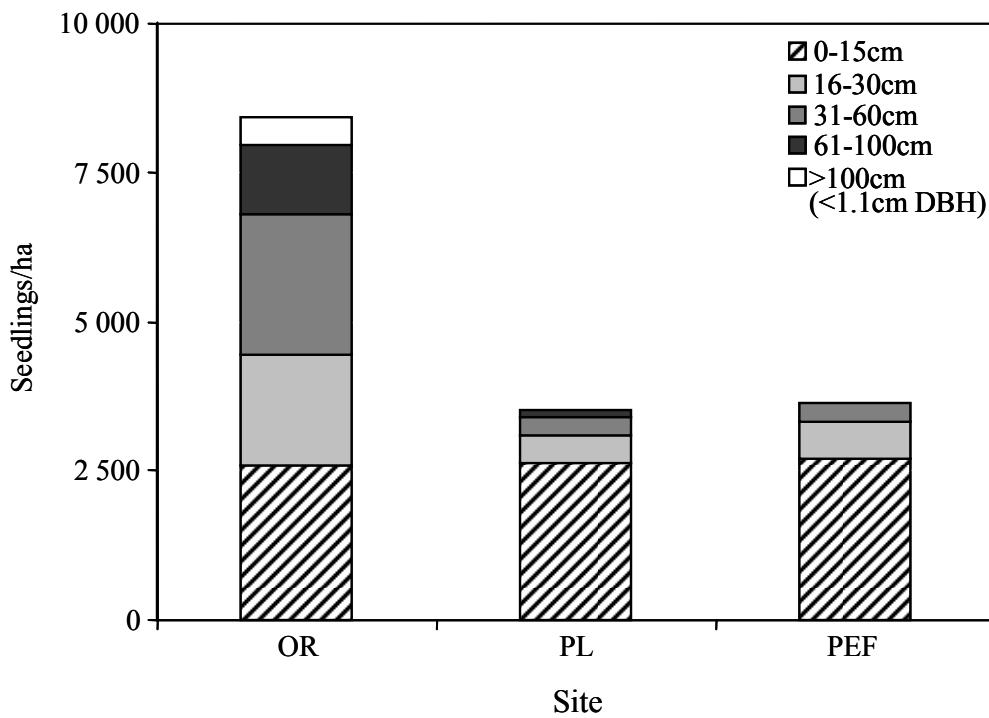


Figure 14. Abundance and height distribution of white-cedar regeneration on three sites selected throughout the distributional range of white-cedar. OR site, Outaouais Region (Quebec, Canada); PL site, Papineau-Labelle wildlife reserve (Quebec, Canada); PEF site, Penobscot Experimental Forest (Maine, United-States).

Design and data collection

Within each selected stand on the OR and PL sites ($n = 8$), nine circular plots of 400-m^2 were established ($n = 72$). Inside each plot, all merchantable living trees with a diameter at breast height (DBH) $\geq 9.1\text{ cm}$ were tallied by species, DBH, vigour, and quality. Monitoring of environmental conditions, including characterisation of soil, seedbed, and each vegetation stratum, was also done in one-third of randomly chosen plots.

Saplings were measured within a 100-m^2 circular subplot centred within each of the 400-m^2 plots. They were tallied by species and DBH classes ($2 = 1.1\text{-}3.0\text{ cm}$; $4 = 3.1\text{-}5\text{ cm}$; $6 = 5.1\text{-}7.0\text{ cm}$; $8 = 7.1\text{-}9.0\text{ cm}$). Regeneration monitoring was done in three circular 4-m^2 subplots equally spaced on the circumference of the 100-m^2 subplots. Regeneration of all tree species was counted by 5-cm height classes. Browsing on each seedling was also monitored by an approximate percentage of the total foliage consumed ($0 = \text{absence of browsing}$; $1 = 1\text{-}25\%$; $2 = 26\text{-}50\%$; $3 = 51\text{-}75\%$; $4 = 76\text{-}100\%$).

Two seedlings (sexual origin) or layers (asexual origin) of white-cedar (hereafter called stems) taller than 130 cm on the OR site and taller than 30 cm on the PL site were selected and numbered for more detailed analysis of development ($n = 144$). These stems were the closest to the centre of the 400-m^2 plot, when they were present. Very few stems taller than 130 cm were available (on the fringe of inventory plots) on the PL site, so we had to lower the height criterion to 30 cm. No stem taller than 30 cm was found on the PEF at the time when the stems were selected. Ground level and north side were marked on each stem. Diameter at the soil level and total height were measured. For each selected stem, root excavation was conducted for determination of the regeneration origin (Paquin et al. 1999), because curvature at the base of the stem is not a good indicator. When the buried layer connection was still connected to the parent tree, the asexual origin of the stem was indisputable. As a layer grows older and becomes independent, the unused connection may be broken by rot, decay or mechanically during harvesting (Stanek 1961), thereby preventing a precise determination of its asexual origin in the field (Doucet 1987). Laboratory analyses are then required (see below). In all cases, whole stems including shoot, branches, foliage, and roots were collected for precise analyses of growth.

In order to characterise the micro-environment, direct, indirect, and total light availability, which were expressed as a percentage of photosynthetic photon flux density (%PPFD) for each stem, were estimated on cloudy days in July 2005. We used hemispherical numerical photographs of the forest canopy taken from a point 150 cm above the soil level after stem harvesting. The photographs were analysed with the Gap Light Analyser (Fraser et al. 1999).

Stem analysis

Harvested stems were sectioned and cross-sectional discs were sampled at 10-cm intervals from the soil level to top height. Discs were dried and sanded, and rings were counted with a microscope. If there were more than 10 years difference between two successive discs, rings were counted on supplementary cross-sectional discs taken from the middle of the section. Twenty-five percent of the discs were counted twice, with a mean difference of 0.61 year between the two counts. For advance regeneration (\geq 3-years-old at the time of partial cutting; $n = 58$), discs collected at the soil level were analysed in detail with a tree-ring measuring system (TA Uni-slide System, Velmex Inc., Bloomfield, NY, USA; precision = \pm 0.1 mm) to separately measure growth for four perpendicular radii corresponding to the cardinal points. Butt rot was present on two discs where only two radii were used to measure growth. Annual growth was averaged for each disc and multiplied by 2 to get diameter increment. The 2005 growing season was incomplete, and therefore, excluded from the diameter growth analysis.

Each root (diameter \geq 1.0 cm) that was attached to the base of the stem was sectioned for microscopic examination. As the analysis has been successfully performed with black spruce (*Picea mariana* (Mill.) B.S.P), we tried to differentiate initial morphology of root and branch (Stanek 1961; Paquin et al. 1999). This examination was unsuccessful in clearly identifying regeneration origin because initial morphology of roots was indistinguishable from branches with a microscope. Thus, differentiation between both regeneration origins was determined from height growth in the first year. Annual height increment in the first year is always less than 5 cm for a seedling grown under natural conditions (Simard 1999; Chapter 2) or in the greenhouse (Habeck 1958; Harry et al. 1987). Stems with a superior

height growth were presumed to be layers, resulting from the contribution from the parent tree. We tested this value with stems that were still connected to the parent tree, and all of them had grown more than 5 cm in the first year.

Statistical analyses

A height growth model was constructed to determine the time needed to reach a given height. Age zero was fixed at the height of the soil level. We tested the hypothesis that growth rate was influenced by site, regeneration origin, and period (before or after partial cutting). History of browsing pressure for each stem was unknown and we could not include this effect in the modelling using retrospective data. Analysis was performed using the NLMIXED procedure (SAS 9.1, SAS Institute Inc., Cary, NC, USA). The independent variable was the height of the disc, while the dependent variable was the age of the disc. Categorical variables in the model, computed as fixed effects, included site (OR vs. PL) and regeneration origin (sexual vs. asexual). As three to 20 discs were used from each stem, the analyses were conducted to take into account multiple measurements on the stem using a random effect. Stands and plots were also random effects. Only significant variables were included in the model. A power function (Equation 1) was used for all combination of site and regeneration origin, except for sexual regeneration on the PL site for which a distinct model was required (Equation 2). Assumptions of normality, homoscedasticity, and independence were respected, and no transformation of the dependent variable was applied. Adjusted correlation coefficients were computed using a linear regression (PROC REG; SAS 9.1) of predicted values in function of observed values.

$$\text{Equation 1: } T = (a_1 I_1 + a_2 I_2 + a_3 I_3) \times H^{(b_1 I_1 + b_2 I_2 + b_3 I_3)}$$

$$I_1 = \begin{cases} 1, & \text{if site = OR and regeneration type = sexual} \\ 0, & \text{otherwise} \end{cases}$$

$$\text{where } I_2 = \begin{cases} 1, & \text{if site = OR and regeneration type = asexual} \\ 0, & \text{otherwise} \end{cases}$$

$$I_3 = \begin{cases} 1, & \text{if site = PL and regeneration type = asexual} \\ 0, & \text{otherwise} \end{cases}$$

Equation 2: $T = a_1 I_1 \times H^{b_1 I_1}$
 where $I_1 = \begin{cases} 1, & \text{if site = PL and regeneration type = sexual} \\ 0, & \text{otherwise} \end{cases}$

Terms in the model were defined as follows: T = age of the disc (year); H = height of the disc (cm); a_i and b_i are parameters to be estimated.

Mean height increment for the three last complete growing seasons (2002-2004) was also modelled as a function of the percentage of full sunlight. Correlations were used to choose among direct, indirect, and total light for the modelling. Using the GLM procedure (SAS 9.1), we tested site (OR vs. PL), regeneration origin (sexual vs. asexual), total height of the stem in 2001 (continuous variable), and percentage of total foliage consumed (4 classes; measured in 2005) as variables. The backward elimination method was used for selection of fixed effects. Site was the only significant variable retained in addition to available light to affect height increment (*see Results*). Assumptions of normality, variance homogeneity, and independence were respected, and no transformation of the dependent variable was applied. The following quadratic model form was used:

Equation 3: $HI = a + b \times L + c \times L^2 + d \times S$

where HI = mean height increment of the three last complete growing seasons (cm); L = available light (%PPFD); S = site (binary variable); a , b , c , and d are parameters to be estimated.

Diameter growth response to partial cutting was evaluated at the level of individual stems to determine if the pre-established regeneration respond to the canopy opening. We identified the moment at which growth became significantly greater than before treatment and how long this response persisted over a 10-year period. For the analysis, three-year windows (for both pre- and post-cutting) were used instead of a single year, because this method filters out the variability in diameter growth due to annual changes in temperature and precipitation (Lorimer and Frelich 1989; Nowacki and Abrams 1997). Because the exact month of the year when the partial harvest took place was unknown, the year of cutting (year = 0) was not included in the diameter growth analysis. After cutting (years = 1 to 10), the moving average method was used to find differences generated by adding and

dropping only one year at the time (Wei 2006). This method is frequently used in dendrochronology to search for release of stems following disturbance of the canopy (Nowacki and Abrams 1997; Black and Abrams 2003; Royama et al. 2005). Models were constructed for each individual seedling and post-cutting period to compare the eight post-cutting periods with the pre-cutting period (mean diameter increment of years -3 to -1). The MIXED procedure (SAS 9.1) was used. Random effects (stand and plot) and fixed effect (site, regeneration origin, total height of the stem before cutting) were included in analyses. No adjustment was required because only two means were compared by stem in each ANOVA. Assumptions of normality and independence of residuals, and variance homogeneity were respected and no transformation was needed. A significant difference between estimates ($\alpha = 0.05$) indicates a positive or negative difference compared to the pre-cutting period.

Results

The following results are derived only from the OR and PL sites, because no stem data were available from the PEF. Table 13 describes the characteristics of 144 stems used in the stem analyses. Only stems older than 3-years-old at the soil level at the moment of the partial cutting were considered pre-established. Before partial cutting, 58 stems were pre-established; 84.5% of these stems were on the OR site and were generally older and larger than those on the PL site (Table 13). The fact that 86 sampled stems were not present on both sites before partial cutting reveals that establishment of new white-cedar seedlings and layers had occurred following partial cutting. In 2005, the proportion of stems potentially of asexual origin was almost the same on both sites with 13.9% and 11.1% on the OR and PL sites, respectively. The means for height, diameter, and age of stems were higher on the OR site relative to the PL site, but their ranges overlapped. On the OR site, 9.7% of stems presented browsing marks in 2005, while 47.2% of stems were browsed on the PL site.

Table 13. Descriptive characteristics of white-cedar stems at the moment of the partial cutting done between 1971 and 1983, and when they were harvested during the current study. OR site, Outaouais Region; PL site, Papineau-Labelle wildlife reserve.

(a) Before partial cutting (pre-established stems \geq 3-years-old)

Variable	OR site					PL site						
	N ^a	Mean	\pm	SD ^b	Minimum	Maximum	N	Mean	\pm	SD	Minimum	Maximum
Number of stems (Asexual origin)	49 (4)						9 (0)					
Height (cm)		26.0	\pm	17.0	3.6	79.6		8.8	\pm	5.9	2.5	21.7
Diameter (cm) ^c		3.4	\pm	2.1	0.4	10.0		1.0	\pm	0.9	0.3	3.1
Age (year) ^c		13.2	\pm	6.9	3.0	34.0		5.3	\pm	2.6	3.0	9.0

(b) In 2005 (all stems)

Variable	OR site					PL site						
	N	Mean	\pm	SD	Minimum	Maximum	N	Mean	\pm	SD	Minimum	Maximum
Number of stems (Asexual origin)	72 (10)						72 (8)					
Height (cm)		181.3	\pm	29.9	132.0	281.0		81.4	\pm	44.9	34.2	277.0
Diameter (cm) ^c		26.9	\pm	7.2	15.2	47.6		10.0	\pm	5.1	3.1	22.0
Age (year) ^c		40.6	\pm	10.0	20.0	65.0		17.7	\pm	6.5	8.0	33.0
Browsing^d												
Unbrowsed	65						38					
1-25%	6						20					
26-50%	1						8					
51-75%	0						5					
76-100%	0						1					

^a Number of stems.

^b Standard deviation.

^c Diameter and age at the soil level.

^d Number of stems by percentage of foliage consumed (measured in 2005 only).

Height growth

Both site and regeneration origin were significant predictors of height growth, and were included in the model as binary variables, while period (before or after partial cutting) was not significant. Predicted height growth rate is the highest on the PL site, resulting in fewer years needed to reach a given height (Figure 15). For heights > 30 cm, the growth rate is about the same for seedlings and layers (the curves were almost parallel) on each site, but layers started with a greater height increment during the first years. Consequently, layers need fewer years than seedlings to reach the same size. The time needed to reach 30 cm is about the same on both sites ($\text{seedling}_{\text{PL}} = 11 \text{ yrs}$; $\text{seedling}_{\text{OR}} = 13 \text{ yrs}$; $\text{layer}_{\text{PL}} = 6 \text{ yrs}$; $\text{layer}_{\text{OR}} = 7 \text{ yrs}$), but the highest growth rate on the PL site allows stems to reach 130 cm about 10 years earlier compared to the OR site ($\text{seedling}_{\text{PL}} = 20 \text{ yrs}$; $\text{seedling}_{\text{OR}} = 32 \text{ yrs}$; $\text{layer}_{\text{PL}} = 14 \text{ yrs}$; $\text{layer}_{\text{OR}} = 24 \text{ yrs}$). Moreover, the shape of the curves shows that predicted height growth rate increases as white-cedar stems become older and larger for the range of height analyzed, especially on OR site.

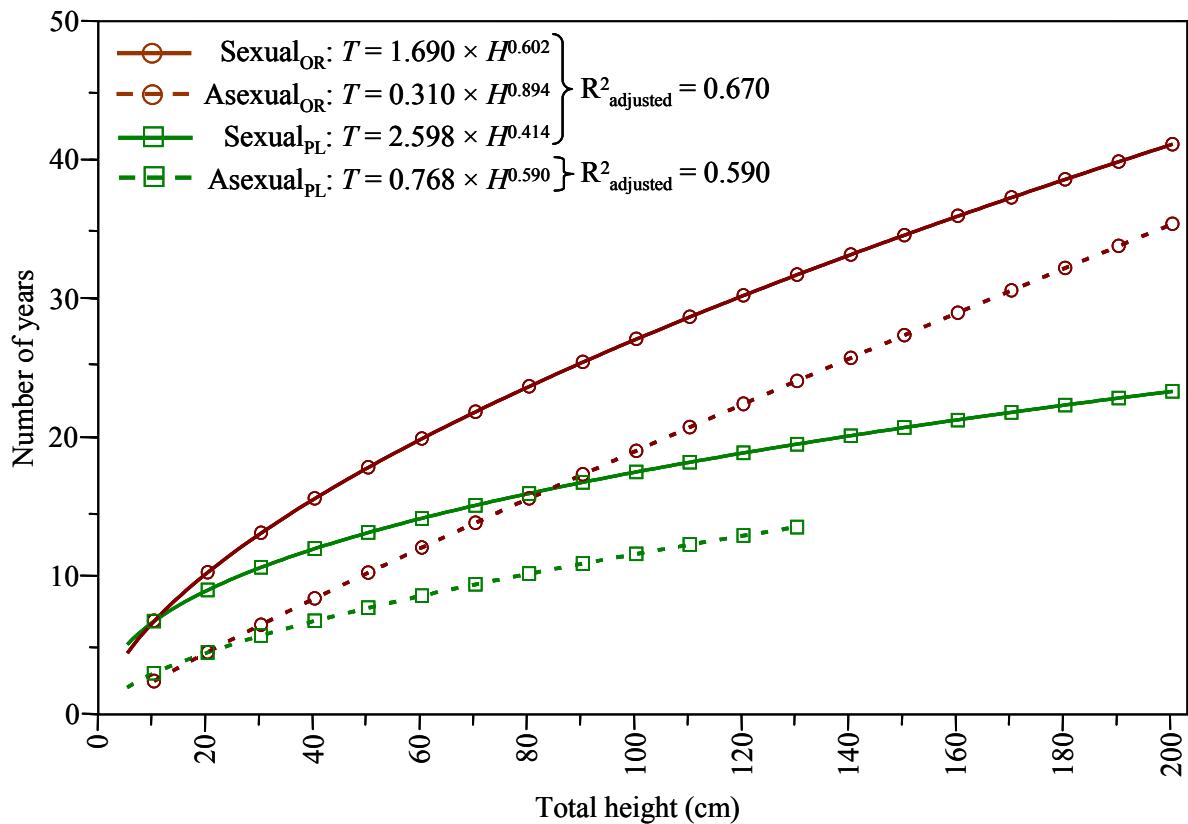


Figure 15. Time-height relationship calculated from Equations 1 and 2 on Outaouais Region (OR site) and Papineau-Labelle wildlife reserve (PL site).

Height-light relations

The mean height increment of the last three complete growing seasons was positively correlated with both indirect and total light availability (Table 14). However, indirect light is the most closely correlated with height increment. Among the variables tested in modelling, only site had a significant effect, while regeneration origin, total height in 2001, and browsing pressure did not significantly influence the height increment-indirect light relationship (Figure 16). Over the range of indirect light that we encountered ($6.2\% \leq$ indirect light $\leq 36.0\%$), there is an increase in predicted height increment when the percentage of indirect light increases on both sites, but height increment is always greater on the PL site. Between 6.2 and 16.2% of indirect light on PL, the increase of 10% indirect light results in an additional height increment of about 0.9 cm/yr. However, between 15 and 25% indirect light on both sites, the same increase results in an additional height increment of 5.3 cm/yr.

Table 14. Correlations between mean height increment of the three last complete growing seasons (2002 to 2004) and direct, indirect, and total light availability (% PPFD).

Light	Available light (%) (mean \pm SD ^a)	Pearson correlation coefficient (<i>r</i>)	Probability > <i>r</i>
Direct	18.94 ± 8.44	0.146	0.075
Indirect	17.19 ± 6.21	0.437	<0.001
Total	18.19 ± 6.57	0.314	<0.001

^a Standard deviation.

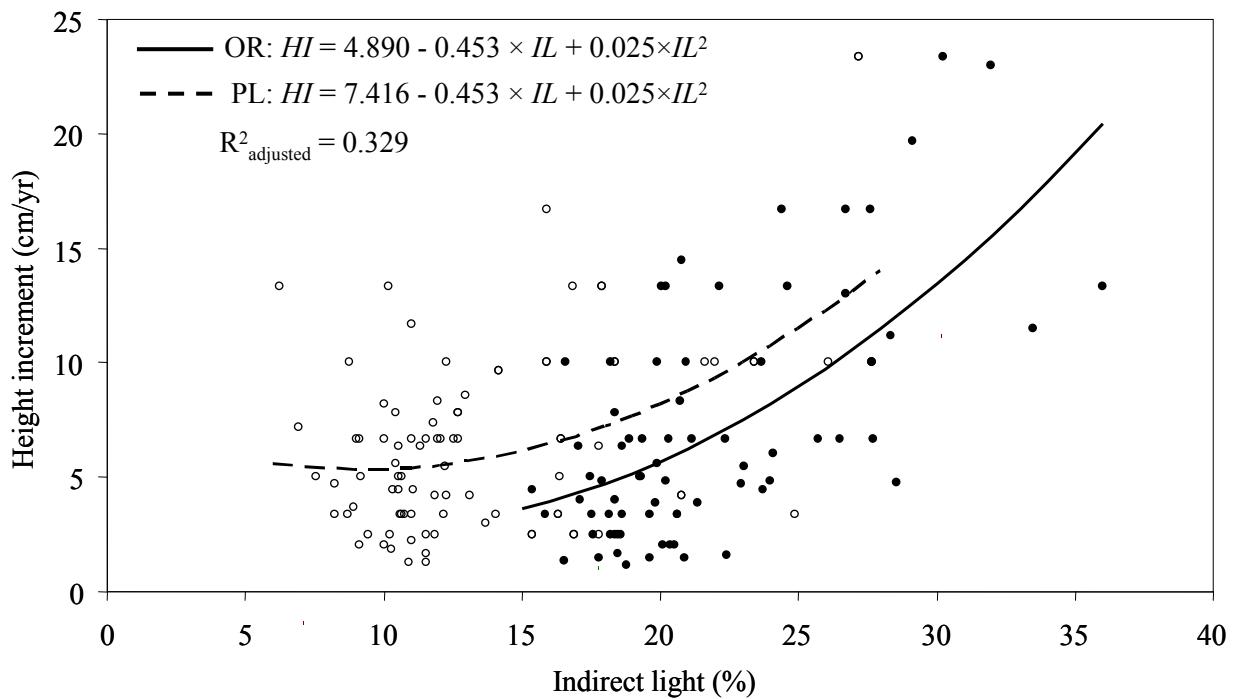


Figure 16. Height increment-indirect light relationship calculated from Equation 3. Solid line and closed circles = Outaouais Region (OR site); dashed line and open circles = Papineau-Labelle wildlife reserve (PL site).

Diameter growth

Before partial cutting, the mean annual diameter increment ranged from 2.5 to 3.0 mm/yr (mean slope = 0.06) and it progressively increased with time since cutting, up to 6.5 ± 3.3 mm/yr, 10 years after cutting (mean slope = 0.22; Figure 17). In the first post-cutting period (years 1 to 3), 43.1% of stems showed a significant increase in diameter increment in comparison with pre-cut levels (Figure 18). For subsequent 3-year periods (years 2 to 10), between 1.7% and 10.3% of stems had significantly higher diameter increments for the first time. After the first significant 3-year period, diameter increment of most stems remained higher than before cutting for the rest of the data sequence that we analysed. 19.0% of stems did not react to partial cutting, while 5.2% had at least one period of significant decrease in diameter increment, compared to the pre-cutting period. Site, stand, plot, regeneration origin, and total height at the moment of cutting had no significant impact on diameter growth response.

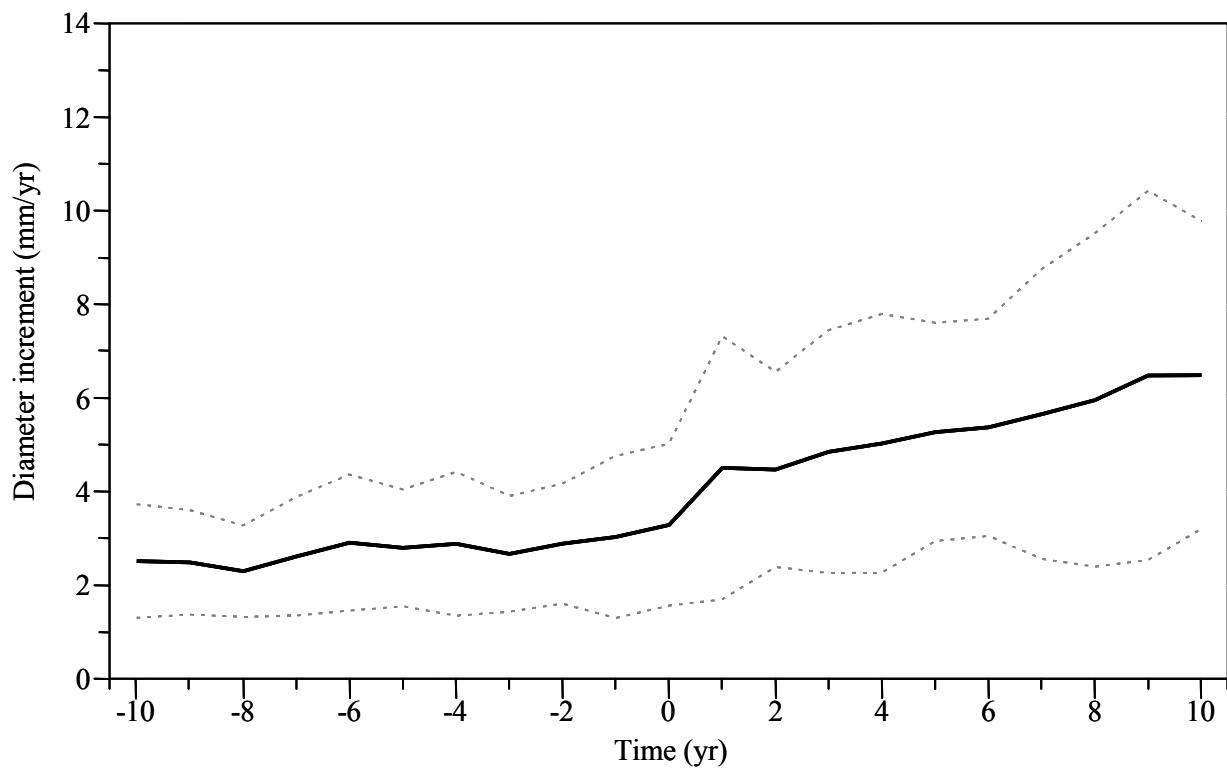


Figure 17. Mean annual diameter increment at the soil level for stems \geq 3-years-old when the partial cutting was imposed on both sites ($n = 58$). 0 = year of the partial cutting. Dashed lines indicate the standard error.

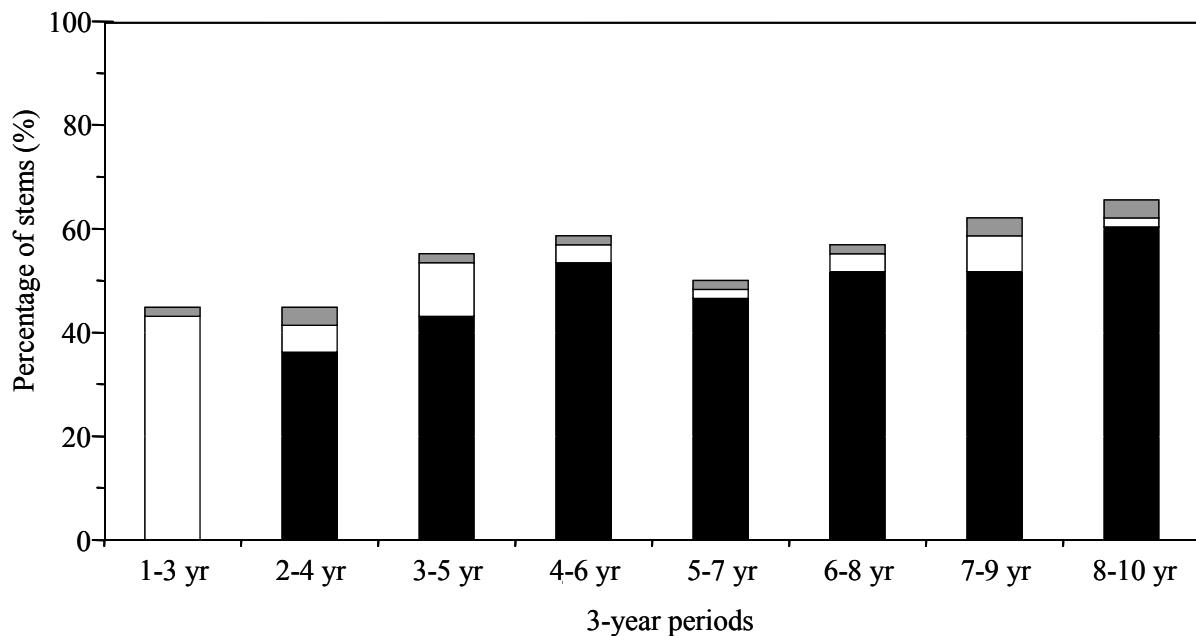


Figure 18. Distribution of stem responses showing a significant different diameter increment at the soil level, compared to the pre-cutting period (years -3 to -1); 0 = year of partial cutting; n = 58; $\alpha = 0.05$.

Note: Open bars = percentage of stems with a first period of significant positive difference; black bars = percentage of stems with a period of significant positive difference, which was not the first one (\geq one previous significant period); gray bars = percentage of stems with a period of significant decrease in comparison with pre-cutting growth.

Discussion

Impact of growing conditions

Despite the fact that partial cutting treatments differed in terms of frequency and intensity of harvesting, all study sites, including the PEF, had comparable abundances of seedlings shorter than 15 cm in 2005 (Figure 14). This result suggests that regeneration can take place under a variety of uneven-aged silvicultural treatments and environmental conditions. The shade-tolerance of seedlings and their capacity to limit height and diameter growth allow the formation of a seedling bank waiting for an opening in the canopy, in the same way as balsam fir (Morin et al. 2008). This white-cedar seedling bank theory agrees with Forester et al. (2008) who found many white-cedar seedlings < 22 cm in lowland white-cedar stands in Wisconsin. Thus, the insufficiency of white-cedar regeneration reported in mixedwood stands managed by partial cutting (Chimner et Hart 1996; Davis et al. 1998) would not seem to be associated with a lack of seedling establishment. In fact, white-cedar is not particularly difficult to regenerate through sexual reproduction, if there are seed trees in close proximity and the forest floor is disturbed, partially shaded, and constantly moist (*see* Chapter 1). More demographic research is required regarding the dynamic of establishment and mortality in a white-cedar seedling bank.

Up to a height of 30 cm, the difference in predicted height growth between the OR and PL sites is minor, and regional characteristics and available light do not seem to modify the growth rate (Figure 15). White-cedar seedlings need 11 to 13 years to reach 30 cm height. In practice, this means that on average 12 years must be added to age counts obtained on cores or discs taken at stump height (30 cm) in order to have a more precise estimation of tree age. This value is in the same range as balsam fir, white and black spruce, and hemlock in northeastern North America (between 5 and 15 years; Hatcher 1960; Anderson et al. 1990; Nienstaedt and Zasada 1990). Another 8 to 20 more years are needed for seedlings to reach 130 cm, a reference height often used for tree coring. As height growth begins at a very slow rate relative to that associated with hardwood species on mesic sites (Hannah 2004; Chapter 2), white-cedars are often overtapped in regeneration cohorts of mixedwood stands. However, height growth rate increases when white-cedar regeneration gets older

and larger in a way that differences appear gradually between sites. At a height of 50 cm, white-cedar seedlings and layers are predicted to grow 8.6 and 10.5 cm/yr, respectively, on the best site (Figure 15). Predicted height growth is close to the growth of red spruce on the PEF, which is 12 cm/yr, but lower than balsam fir growth (18 cm/yr; Moores et al. 2007) and hardwood species (Hofmeyer 2008). Consequently, white-cedar stems are generally smaller than associated tree species and they may stay overtopped for many decades. However, an extended period in suppression is not problematic for this shade-tolerant conifer (Johnston 1990; Fraver 2004; Hofmeyer 2008).

Browsing may be a predominant factor explaining the low recruitment of white-cedar seedlings to larger size classes (Cornett et al. 2000b; Rooney et al. 2002; Forester et al. 2008). Deer are the most important predators of white-cedar seedlings and saplings, especially in winter, and may cause mortality of stems by recurrent browsing (Côté et al. 2004; Hannah 2004). Hare density could decrease the abundance of white-cedar regeneration, but it is not a problem where food is abundant, which was the case in the study stands. Moose density was the same in all regions (Table 12). Like hare, moose browse white-cedar only when other food sources are scarce (Grigal and Ohmann 1975).

Browsing pressure may have a regionally variable impact on white-cedar regeneration, depending on the abundance of deer (e.g., Davis et al. 1998; Cornett et al. 2000b; Rooney et al. 2002). Thus, on the PL and PEF sites, where a high population of deer is present (Table 12), browsing may contribute to explain the lack of recruitment of white-cedar seedlings (Cornett et al. 2000b; Rooney et al. 2002; Forester et al. 2008). Deer mainly browse seedlings that are between 30 and 200 cm high (Beals et al. 1960; Saunders and Puettmann 1999a) and preferentially browse taller seedlings. In our study, this resulted in a low density of white-cedar seedlings in height classes > 15 cm for the two sites where deer densities were high (Figure 14; Chapter 4). No significant effect of browsing on height growth was detected on stems that were analysed (Figure 16), possibly because these stems experienced low browsing pressure. 95.8% of stems had less than 50% of total foliage consumed without recurrent browsing. The lack of older and taller seedlings on the PL and PEF sites could indicate that advance regeneration on these sites had grown to a size where heavy browsing would eliminate them. Browsing is frequent on the PEF; 90% of large

seedlings (> 30 cm high) and small saplings showed signs of browsing in 2005 (see Chapter 4). Unbrowsed large seedlings and small saplings were physically protected from browsing by unpalatable species (facilitation phenomenon, see Borgmann et al. 1998). Based on the time-height relationship, stems on the PL site, which have the highest growth rate, need fewer years to reach a height of 200 cm; thus, they are vulnerable to browsing over a shorter period than seedlings and layers on the OR site, if there were browsing pressure (Figure 15). Consequently, depending on region and regeneration origin, white-cedar seedlings and layers would be vulnerable to browsing damage for at least 23 years and up to 41 years.

For diameter growth, best conditions are generally created after partial harvesting of the overstory. Half of the pre-established white-cedar seedlings and layers have a quick (≤ 5 years) and consistent response to partial opening of the canopy. This result corroborates the idea found in the literature, that partial cutting releases pre-established regeneration and stimulates their growth (Smith et al. 1997; Moores et al. 2007; Hofmeyer 2008) by the redistribution of environmental resources. This response to favorable changes in growing conditions has been reported by Heitzman et al. (1997) and Fraver (2004) for white-cedar. However, partial harvesting does not create uniform growing conditions and space, leaving sometimes the local density of the overstory unchanged. This punctual intervention did not release all overtapped stems and growth of some seedlings and layers may have been disadvantaged by taller stems in their immediate neighbourhoods (Paquin and Doucet 1992a). This fact may explain why about 25% of stems did not react positively to the partial cuts (Figure 18). Another possible explanation is that pre-established stems of faster-growing tree species, such as birches, red maple, and balsam fir, together with the shrub stratum were also present at the moment of partial cutting and benefit more from the released growing space. It is also possible that some white-cedar seedlings and layers were not vigorous enough to react to the opening, because insects, diseases, and recurrent browsing may weaken them (Rose et al. 2000; Côté et al. 2004).

Available light had a positive influence on height growth (Figure 16) and the best effects for given levels of indirect light are found on the PL site. Observed levels of modelled height growth are in accordance with those of Logan (1969), experimented in a controlled

environment, where a rise of almost 6 cm/yr is predicted for white-cedar seedlings (> 30 cm high) when light passes from 13 to 25%. However, small seedlings generally intercepted a lower percentage of light due to their overtapped position, which partially explains their increasing growth rate when the seedlings get larger. Moreover, indirect light is the most closely correlated with height increment of white-cedar stems, while direct light has the lowest impact. This result limits the effect of gap size, shape, and exposition on growth rate compared to direct light, because indirect light can penetrate through the canopy surrounding gaps (Canham 1988). When direct light is the driving factor, the configuration of gap is important to maximise direct radiation and catch the narrow range of incidence angles (Canham et al. 1990). Moreover, white-cedar seedlings and saplings are regularly observed at the edges of gaps (Verme and Johnston 1986; Scott and Murphy 1987) where direct light is limited.

Growing conditions are also important to consider in the development patterns of seedlings. Those conditions seem effectively to contribute to explain a part of the differences noted between sites because the highest height growth was observed on the PL site located in the Sugar maple-Yellow birch bioclimatic domain. This domain is characterized by higher mean temperatures, a longer growing season, and more abundant total annual precipitation in comparison with the OR site, which is located farther to the northwest (Gosselin et al. 1998; Gosselin et al. 2000). Further studies are thus needed to determine the effect of environmental factors on white-cedar development.

Impact of regeneration origin

The percentage of layers versus seedlings found on the OR and PL sites is comparable to proportions reported in the literature from mesic sites (Scott and Murphy 1987; Bergeron 2000). During the early stage, seedlings are smaller than layers of the same age (Figure 15; Lussier et al. 1992). The asexual reproduction mode may have the advantage of an increased survival and establishment success in comparison to the high mortality and slow growth rates of the early establishment phase of seedlings of white-cedar (Simard et al. 2003; RNC 2008; Chapter 1). The establishment phase lasts until a height of 30 cm is

attained (Baldwin 1977), which takes about 12 years for white-cedar seedlings, while layers are about 5 years younger at the same height (Figure 15).

After this establishment phase, layers and seedlings have similar height growth and both react to partial cutting with higher diameter increment at the soil level. Moreover, the lack of influence of possible regeneration origin on the height increment-indirect light relationship suggests that established seedlings and layers have the same growth rate when growing under same light conditions (Figure 16). This result indicates that seedlings and layers have almost the same shade-tolerance, which differs from the interpretations of Curtis (1946) and Schaffer (1996), who asserted that layers are more shade-tolerant than seedlings. Consequently, the initial differences in growth rate that have been attributed to stem origin have no long-term impact on growth and productivity, as has been demonstrated for black spruce (Paquin and Doucet 1992a, 1992b).

All the results obtained for seedlings and layers separately must be taken with caution because an arbitrary threshold of 5 cm growth in the first year was used to distinguish between seedlings and layers, when connection with the parent broken. The method for identification of regeneration origin needs improvement. However, this threshold value agrees with all layers found with unbroken connections, which represented one-third of stems classified as layers and they do have a height growth superior to 5 cm in the first year. Furthermore, it is corroborated by studies in natural conditions and greenhouses, which have shown that height growth of white-cedar is always lower than 5 cm in the first year (Habeck 1958; Harry et al. 1987; Simard 1999; Chapter 1). However, this identification method is not infallible. Two other methods should then be explored: i) as is the case with black spruce, the initial anatomy of branches and roots may differ and a microscopic study of discs could distinguish both organs (Stanek 1961) and ii) an analysis for genetic identification of stems could allow the association between layers and parent trees as clones (Prat et al. 2006; White et al. 2007). Both of these methods need complex laboratory analyses and have not been proved for white-cedar. Moreover, the first method has proven to be inappropriate in practice for species which develop adventitious roots, such as black spruce and balsam fir (Parent et al. 2000). White-cedar also develops adventitious roots (Curtis 1946).

Conclusion

Even though deer densities varied widely, small white-cedar regeneration abundance (≤ 15 cm) was comparable on three different sites, which were located in contrasting climatic regions and experiencing different partial cutting treatments. However, recruitment above 30 cm high was limited in the presence of high deer densities, which may result in low abundance of saplings. Seedling and layer growth was slow, requiring 24 to 32 years for seedlings and 14 to 20 years for layers to reach a height of 130 cm. Seedlings and layers were nevertheless able to respond quickly and consistently to partial cuts. This response has been observed for stems differing in origin and initial height growth. Time to reach 30 cm was about the same on two study sites, but predicted height growth of taller seedlings varies regionally depending on growing conditions, which influenced the number of years needed to reach 130 cm (10 years earlier on PL site). Moreover, height growth is proportional to indirect light for stems taller than 30 cm, which means that stems may take advantage of conditions associated with gap formation and partial cutting. In further studies, we have to compare height and diameter increment and size of the response to partial opening with associated species to better understand dynamics of mixedwood stands on mesic sites.

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Chapitre IV

**Northern white-cedar (*Thuja occidentalis* L.)
regeneration dynamics on the Penobscot Experimental
Forest in Maine: 40-year results**

Abstract

The objective of this study was to assess the long-term dynamics of northern white-cedar (*Thuja occidentalis* L.) seedling and sapling growth and mortality on the Penobscot Experimental Forest (PEF) in Maine, United States. Data collected between 1965 and 2005 in four twice-replicated partial cutting treatments were analysed. White-cedar seedlings established in all treatments despite relatively high white tailed-deer (*Odocoileus virginianus* Zimmerman) population densities. However, while it appears that regeneration cohorts of associated softwoods increased in size over time, the white-cedar cohort did not. Ingrowth of white-cedar from the seedling to sapling stage ($1,3 \text{ cm} \leq \text{DBH} \leq 11,4 \text{ cm}$) was lower than the combined rates of sapling mortality and recruitment to the pole stage; sapling density of this species in 2005 was $> 80\%$ less than it was at the start of the measurement period. Sapling mortality was high and recruitment to larger size classes was low, though mortality decreased and recruitment increased as sapling size increased. Browsing is prolific; 90% of white-cedar seedlings and small saplings showed signs of browsing in 2005. Overall, white-cedar saplings growth was slow, with an estimated 100 years needed to grow from small sapling to merchantable size in the study stands. Efforts to release white-cedar saplings through precommercial treatment and control of browsing pressure are recommended for area with high deer densities.

Keywords: regeneration, partial cutting, recruitment, browsing, mortality, height growth, diameter growth, eastern white cedar, *Thuja occidentalis*, *Odocoileus virginianus*

Résumé

Cette étude à long terme vise la compréhension de la dynamique de croissance et de mortalité des semis et des gaules de thuya occidental (*Thuja occidentalis* L.) dans une forêt expérimentale au Maine, États-Unis (Penobscot Experimental Forest) ayant une densité de cerfs de Virginie (*Odocoileus virginianus* Zimmerman) relativement forte. Le dispositif est constitué de quatre traitements de coupe partielle répliqués deux fois et mesurés régulièrement entre 1965 et 2005. Même si toutes les cohortes de régénération établies dans les traitements comportent du thuya, les semis des essences résineuses associées ont crû en hauteur avec le temps, tandis que ceux de thuya sont généralement demeurés plus petits que 30 cm. Conséquemment, la densité de tiges de thuya ($1,3 \text{ cm} \leq \text{DHP} \leq 11,4 \text{ cm}$) a diminué de 80 % par rapport à celle au début des mesurages. Le recrutement des tiges de thuya à partir des stades semis et gaulis a été inférieur aux taux combinés de mortalité et de recrutement au stade perchis. La mortalité des gaules est élevée surtout chez les petites tiges ($1,3 \text{ cm} \leq \text{DHP} \leq 4,6 \text{ cm}$), tandis que le taux de passage aux classes diamétrales supérieures est faible et augmente progressivement avec le diamètre des tiges. La croissance diamétrale des gaules est lente et une tige de thuya prend environ 100 ans pour passer de 1,3 cm à 11,4 cm au DHP. Le broutement constitue également un problème et 90 % des semis et des petites gaules de thuya présentaient des signes en 2005. Dans les régions ayant une forte densité de cerfs, des efforts sont recommandés pour libérer les gaules de thuya grâce à une éclaircie précommerciale et pour contrôler le broutement.

Mots clés: régénération, coupe partielle, recrutement, broutement, mortalité, croissance en hauteur, croissance diamétrale, *Thuja occidentalis*, *Odocoileus virginianus*

Introduction

Northern white-cedar (*Thuja occidentalis* L.) is a commercial species present between the 44th and 48th parallels (Johnston 1990) in many forest types of northeastern United States and southeastern Canada, including the Acadian Forest. White-cedar grows in pure stands on wet and dry sites, but growth is best on mesic sites in the southern portion of its range, where it shares growing space with many other tree species (Johnston 1990). In mixedwood stands, natural reproduction is generally prolific after natural disturbances and harvesting activities (Smith et al. 1997), but species differ in silvics and reproduction strategies. Consequently, the silviculture system and timing of entry may favor one species over another (Seymour 1995). Key elements for white-cedar seedling establishment and early survival are: partial shading and constant humidity of the forest floor, proximity of white-cedar seed trees, and availability of receptive seedbeds such as disturbed soil or decayed wood (see Chapter 1). However, these favorable microsites are largely colonized by other mid- and shade-tolerant tree species having faster growth rate (e.g. balsam fir (*Abies balsamea* (L.) Mill.), red spruce (*Picea rubens* Sarg.), eastern hemlock (*Tsuga canadensis* (L.) Carrière), and yellow birch (*Betula alleghaniensis* Britt.)) (see Chapter 2). This leads to competition for growing space and resources, followed by stratification and self-thinning of the regeneration cohort (Oliver and Larson 1996; Smith et al. 1997).

Natural dynamics of Acadian Forest mixedwood stands are based on sporadic partial disturbances, mostly gaps created by mortality of individual stems or a small group of trees (Seymour et al. 2002). Stand-replacing perturbations, such as fire and catastrophic windthrow, are less frequent than in naturally even-aged, single-species stands (Wein and Moore 1977, 1979). Consequently, the establishment of regeneration is local and periodic instead of being continuous or mostly at the beginning of the rotation. Successful management of mixedwood stands is difficult, because the evolution of tree cohorts is difficult to predict compared to single-cohort systems (Moores et al. 2007). Silvicultural systems inspired by natural disturbances in mixedwood stands emphasize diversity of species and development of cohorts (Seymour and Hunter 1992). At the stand scale, a growing interest in ecosystem-based management brings into question current silvicultural practices and how they can maintain ecological values and functions of ecosystems (Guldin

1996; Puettmann and Ammer 2007). The white-cedar component is often small in mixedwood stands, but important to maintain natural dynamics, conserve wildlife habitats and food resources, and sustain the forest industry.

Many studies have investigated the impact of partial harvesting on the abundance and stocking of natural regeneration in mixedwood stands (e.g. Brissette 1996; Archambault et al. 2003; Chapters 1 and 2). The focus of such studies is often the composition of the newly established cohort and the proportion of the site occupied by each species. However, few studies have analysed the stratification of regeneration cohorts that occurs due to differential height and diameter increments among species, or the rates of recruitment and causes of mortality of individual saplings over the long term. This information is essential to understand the evolution of a population of trees and better assess long-term sustainability of species and stand structure (Kenefic et al. 2005). Long-term experiments, including repeated measurement and monitoring of individual stems, offer a great opportunity to better understand the dynamics of mixedwood stands (Sendak et al. 2006; Kenefic et al. *in revision*).

In addition to interspecific competition, white-cedar seedlings and saplings may be disfavored by preferential browsing pressure. Many cases of browsing damage by white-tailed deer (*Odocoileus virginianus* Zimmerman), and to a lesser extent by snowshoe hare (*Lepus americanus* Erxleben), have been reported as compromising white-cedar regeneration (Johnston 1972, 1990; Davis et al. 1998). This pressure, added to harvesting treatments, can have a long-term effect on the composition of mixedwood stands (Frelich and Lorimer 1985; Cornett et al. 2000b), depending on herbivore population levels (see Chapter 3).

Our objective was to examine the dynamics of white-cedar regeneration in managed mixedwood stands in the southern portion of the Acadian Forest. To achieve this objective, we analyzed the height class distribution of white-cedar seedlings and saplings over time in a number of partially cut stands, and compared this distribution to those of associated softwoods (i.e. balsam fir, spruce species, and eastern hemlock). In addition, we determined rates of white-cedar recruitment, diameter growth, and mortality (as well as causes of mortality) from remeasurements of individual saplings made over a 30-year period.

Implications of observed dynamics are discussed in light of concerns about white-cedar sustainability.

Methods

Study site

This study uses 40 years of data collected by the U.S. Forest Service, Northern Research Station, as part of their stand-level silvicultural experiment at the Penobscot Experimental Forest (hereafter called ‘PEF’). The PEF was established by the Forest Service in 1950 in Bradley and Eddington, Maine ($44^{\circ}52'N$, $68^{\circ}38'W$; Brissette 1996). Though the history of the PEF prior to the Forest Service study is not well documented, it is known to have experienced repeated partial cutting (Safford et al. 1969; Kenefic et al. 2006). In 1950, the area used for the silvicultural experiment was softwood-dominated and irregular to uneven-aged as a result of past cutting and natural disturbances (Sendak et al. 2003). The climate on the PEF is cool and humid with a mean annual temperature ($\pm SD$) of $6.7 \pm 0.3^{\circ}\text{C}$ (1971–2000) (*data from BioSIM*, Régnière 1996). The normal annual precipitation is $1\,066 \pm 137$ mm; almost 50 percent of precipitation falls between May and October, and annual snowfall averages 289 ± 78 cm. The growing season is about 183 ± 15 days.

Average elevation of the PEF is less than 75 m above the sea level (Brissette 1996). Soils are the result of glacial influences and are variable in terms of texture, drainage, and depth of organic layer (Brissette 1996). The stands used in the present study have an organic layer of generally less than 16 cm developed on a 50 to 100-cm deep glacial till. Soil texture in the B-horizon ranges from silt-loam to sandy-loam with good to poor drainage (Safford et al. 1969). The pH ($\pm SD$) of organic and mineral layers were 3.3 ± 0.3 and 4.5 ± 0.5 respectively.

The PEF is part of the Acadian Forest where mixed northern conifers, including balsam fir, spruces (mostly red and white (*Picea glauca* (Moench) Voss)), eastern hemlock, white-cedar, and eastern white pine (*Pinus strobus* L.), are abundant. The most common hardwoods are red maple (*Acer rubrum* L.), paper birch (*Betula papyrifera* Marsh), gray birch (*Betula populifolia* Marsh.), quaking aspen (*Populus tremuloides* Michx.), bigtooth

aspen (*Populus grandidentata* Michx.), sugar maple (*Acer saccharum* Marsh.), yellow birch, American beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus americana* L.), and northern red oak (*Quercus rubra* L.) (Sendak et al. 2003). The mixture of species varies according to soil conditions and harvesting treatments. Understory tree species composition generally reflects the overstory and is softwood dominated. In mixedwood stands, arrangement of seedlings is determined by canopy composition, biophysical environment, interspecific competition, and browsing pressure.

It is difficult to get precise information about herbivore densities, because there have been no hare, moose (*Alces alces* Gray), or deer surveys on the PEF. However, scientific literature from the Lake States and hunting surveys in Maine indicate an increase in deer and hare populations during the last century (Grigal and Ohmann 1975; Chimner and Hart 1996; Rooney et al. 2002). According to the Maine Department of Inland Fisheries and Wildlife (MDIFW), deer populations tripled between 1960 and 2000 while hare populations increased by 1.5 times, and moose abundance remained low. In 2008, there were between 5.8 to 9.7 deer/km², about 15.2 hare/km², and 0.3 moose/km² in the region where the PEF is located (MDIFW 2007).

Design and data collection

The 240-ha experiment on the PEF includes even- and uneven-aged silvicultural systems and exploitative cutting. The long-term study includes ten treatments replicated twice and randomly assigned to experimental units (hereafter called ‘compartments’) of about 10 ha (Brissette 1996; Kenefic et al. 2006). In this paper, we focus on data from four of the partial harvest treatments; partial harvesting is common in mixedwood stands and it has been suggested that such treatments create a biophysical environment favorable for the successful regeneration and recruitment of white-cedar (Schaffer 1996; Hofmeyer 2008; Chapter 1). Treatments include: selection cutting with 5-, 10-, and 20-year cutting cycles and fixed diameter-limit cutting with a harvest interval of about 20 years based on stand volume increment (Brissette 1996). All of these treatments tend to maintain an irregular to uneven-aged stand structure, establish a new cohort of trees, and release regeneration at each entry (Kenefic et al. 2005). Harvest intensity in the selection treatments is a function

of cutting cycle and a structural goal defined using the BDq method (where B is the residual basal area, D is the retained diameter class, and q is the negative exponential constant between diameter classes; Marquis 1978; Guldin 1991). The q-factor is 1.96 on 5-cm diameter at breast height (DBH) classes and target residual basal area (for trees \geq 1.3 cm DBH) is 26.4 m²/ha, 23.0 m²/ha, and 18.4 m²/ha for the 5-, 10-, and 20-year cutting cycles, respectively (Seymour and Kenefic 1998). Fixed diameter-limit cutting is a commonly applied, exploitative form of partial cutting (*see* Kenefic and Nyland 2005). The treatment on the PEF uses species-specific size thresholds above which merchantable trees are cut, allowing long-lived species to reach larger DBH (*for thresholds used see* Brissette 1996). In all treatments, felling is done with chainsaws and logs are transported with rubber-tired skidders (Brissette 1996). Season of harvest varies but is usually fall or winter.

Each compartment includes between 13 and 23 continuous forest inventory (CFI) plots monitored every 5 years and before and after each stand entry (Brissette 1996). Treatments and inventories are not synchronized among compartments (*see* Brissette 1996; Sendak et al. 2003), i.e., replicates of the same treatment are harvested and measured in different years per staggered dates of initial treatment application. Plots were established on a systematic grid according to compartment area to inventory about 15 percent of the productive area (Brissette 1996; Kenefic et al. 2005). These plots consist of two concentric circles measuring 0.02 ha and 0.08 ha. All trees with DBH $>$ 11.4 cm are measured on the larger plot, while trees with 1.3 cm \leq DBH \leq 11.4 cm (saplings) are measured on the smaller plot (Brissette 1996). Monitoring may be done during the growing season, but time between two successive inventories is calculated accordingly. Since the 1970s, trees have been numbered and DBH and condition (live, dead, and harvested) are recorded at each inventory.

Regeneration monitoring has been done since 1964 on the same time interval as saplings and merchantable trees, using three 4.05-m² subplots on the circumference of the 0.02-ha plots (Brissette 1996). Seedlings are counted by species and height classes (1 = 15-30 cm; 2 = 31-60 cm; 3 = 61-137 cm; 4 = > 137 cm high with DBH $<$ 1.3 cm) and seedlings $<$ 15 cm are noted as present or absent in each subplot. Because young spruce seedlings are difficult to identify to species, they were pooled. However, based on saplings and larger trees, it is

clear that red spruce is the dominant spruce with white spruce occasionally present and black spruce (*Picea mariana* (Mill.) B.S.P.) rarely found (Brissette 1996). In 2005, browsing on each seedling was monitored by the percentage of foliage consumed (0 = absence of browsing; 1 = 1-25%; 2 = 26-50%; 3 = 51-75%; 4 = 76-100%).

Statistical analyses

Abundance of regeneration

The PEF experiment has a factorial design with repeated measures. Mixed analyses of variance (PROC MIXED, SAS 9.1, SAS Institute Inc., Cary, NC, USA) were used to examine the effects of treatments on seedling stocking and density over the 40-year measurement period. Normality of data and homogeneity of variances were examined to ensure compliance with the primary statistical assumptions. Because our data did not comply with these assumptions, various transformations and weighting approaches were attempted. These did little to improve the overall model; consequently descriptive statistics were used to illustrate changes in regeneration density over time.

Seedling height distribution

A chi-square test using exact p-values was used to compare the height distributions of fir, hemlock, spruce species, and white-cedar seedlings at five moments during the last 40 years on the PEF (PROC FREQ, SAS 9.1, SAS Institute Inc., Cary, NC, USA). Pine species and tamarack (*Larix laricina* (Du Roi) K. Koch) occur rarely and were not included in the analysis. Every 10 years from 1965 to 2005, the distribution of each species by height class was compared to the overall expected distribution based on the 40-year average for all softwood species (Snedecor and Cochran 1967). This statistical analysis gave information about stratification by height class among softwood species over the entire measurement period with the 40-year average used as a reference. If no inventory was available in a given compartment at a given year, the closest inventory was used (± 2 years from the target year). Because species-specific height-class distributions were undifferentiated among partial cutting treatments (data not shown), height distributions were computed for all treatments combined.

White-cedar sapling dynamics

A total of 204 white-cedar saplings were numbered and monitored between 1973 and 2005 in the studied area. For the purpose of this analysis, these saplings were classed into three groups based on their DBH: small ($1.3 \text{ cm} \leq \text{DBH} \leq 4.6 \text{ cm}$), medium ($4.7 \text{ cm} \leq \text{DBH} \leq 8.0 \text{ cm}$), and large ($8.1 \text{ cm} \leq \text{DBH} \leq 11.4 \text{ cm}$). Trees with a $\text{DBH} > 11.4 \text{ cm}$ are considered poletimber and were not included in this analysis. The 30-year period was split into three 10-year periods. During each period, a sapling may stay in the same group (DBH remaining between the bounds during the entire period), grow into the next group, or die. No sapling had sufficient diameter increment to grow through two groups during a 10-year period (i.e., a small sapling never grew to the large sapling group in 10 years). In addition, ingrowth into the small sapling class was counted at each period, as was the number of stems that recruited to the medium and large groups. The number of saplings at the beginning and end of each 10-year period and the distribution of saplings by DBH class were used to understand the evolution of the population. The low number of white-cedar saplings by compartment did not allow analysis of variance on these data.

Turning rates, inspired by the turning rate calculations used in Quebec to model the evolution of growing stock (MRN 1998), were calculated by sapling DBH class. The advantage of this method is that it shows the dynamics of a population of stems over a given period, thus elucidating increment and mortality (MRN 1998). Turning rates were calculated for each diameter class individually because increment and mortality rates varied according to sapling size. Periodic diameter increment (PDI) of individual saplings was calculated for all stems living during the entire 10-year period (equation 1).

$$\text{Equation 1: } PDI_i = (D_B - D_A)/(Y_B - Y_A) \times 10$$

where PDI_i = periodic diameter increment of period i (cm/10 years); D_B = diameter at the end of period i (cm); D_A = diameter at the beginning of period i (cm); Y_B = last year of period i ; Y_A = first year of period i . Years are corrected for month of monitoring.

Saplings that died during a given period were excluded from PDI calculation, but were classified as killed by cutting or undetermined causes and used to estimate mortality rates. Because growth increment and mortality were undifferentiated by time period, data were

pooled across the entire measurement period to increase the number of observations and the robustness of predictions for each diameter group.

Results

In the mid 1950s, all studied compartments had a canopy with mixedwood composition dominated by hemlock, fir, and spruces. On average, hemlock accounted for 31.0% of total basal area, fir for 20.7%, spruces for 20.5%, and white-cedar for 13.7%. About 40 years later, all compartments were still softwood-dominated, but the composition of the overstory was slightly different; it was still dominated by hemlock (31.0%), spruces (22.9%), fir (22.0%), but white-cedar was reduced by half to 6.7% (U.S. Forest Service, *unpublished data*).

The understory has also been dominated by conifers since the beginning of monitoring. In the mid 1960s, 83.6% of regeneration was softwood species: fir (47.2% of all seedlings), hemlock (24.9%), spruces (8.3%), and white-cedar (1.5%). After 40 years of partial cutting, the abundance of conifers slightly increased to 87.5%: hemlock, spruces, and white-cedar increased to 32.2%, 15.6%, and 3.4% respectively, while fir decreased to 35.7% (U.S. Forest Service, *unpublished data*).

During the 40-year measurement period, seedlings of fir, hemlock, and spruces < 15 cm were present in more than 80% of subplots, while white-cedar seedlings of this height class are present in about 25% of subplots. Fir seedlings taller than 15 cm were present on 66.8% of subplots, hemlock on 55.6%, spruces on 44.7%, and white-cedar on 10.5% (Table 15). All treatments had presence of all softwood species. Though density of seedlings on stocked plots (i.e., plots with ≥ 1 seedling) was similar for all studied species, lower stocking of white-cedar resulted in a mean density of fewer than 3 000 seedlings/ha. Mean densities of seedlings per hectare in the studied treatments are shown in Figure 19.

Table 15. Regeneration stocking (percentage of subplots with at least one seedling) by conifer species, treatment, and 10-year period, and mean density of plots stocked with seedlings > 15 cm with DBH < 1.3 cm.

(a) Balsam fir

Treatment ^a	Mean stocking over 40 years	Seedlings > 15 cm with DBH < 1.3 cm					Mean density of stocked plots (seedlings/m ² ± SD)	
		Year						
		1965	1975	1985	1995	2005		
S05	84%	59%	69%	73%	65%	65%	1.4 ± 1.0	
S10	88%	66%	74%	87%	81%	81%	2.8 ± 2.6	
S20	82%	38%	40%	81%	75%	74%	2.0 ± 1.9	
FDL	83%	58%	56%	74%	74%	51%	1.6 ± 1.1	

(b) Hemlock

Treatment	Mean stocking over 40 years	Seedlings > 15 cm with DBH < 1.3 cm					Mean density of stocked plots (seedlings/m ² ± SD)	
		Year						
		1965	1975	1985	1995	2005		
S05	90%	49%	63%	70%	70%	74%	2.2 ± 2.1	
S10	62%	24%	44%	53%	42%	37%	2.3 ± 1.9	
S20	85%	12%	41%	86%	85%	78%	2.9 ± 2.1	
FDL	79%	48%	54%	73%	67%	43%	1.5 ± 2.0	

(c) Spruces

Treatment	Mean stocking over 40 years	Seedlings > 15 cm with DBH < 1.3 cm					Mean density of stocked plots (seedlings/m ² ± SD)	
		Year						
		1965	1975	1985	1995	2005		
S05	70%	21%	43%	59%	57%	55%	2.0 ± 1.0	
S10	73%	20%	45%	66%	63%	49%	1.7 ± 2.7	
S20	71%	8%	32%	68%	64%	54%	1.2 ± 1.4	
FDL	58%	28%	38%	64%	43%	19%	0.8 ± 0.8	

(d) White-cedar

Treatment	Mean stocking over 40 years	Seedlings > 15 cm with DBH < 1.3 cm					Mean density of stocked plots (seedlings/m ² ± SD)	
		Year						
		1965	1975	1985	1995	2005		
S05	16%	5%	11%	14%	8%	8%	1.7 ± 1.8	
S10	28%	5%	10%	19%	14%	11%	1.8 ± 1.9	
S20	25%	3%	3%	14%	20%	13%	1.9 ± 2.0	
FDL	29%	7%	10%	15%	14%	6%	1.4 ± 1.1	

^a S05, selection cutting with 5-year cutting cycle; S10, selection cutting with 10-year cutting cycle; S20, selection cutting with 20-year cutting cycle; FDL, fixed diameter-limit cutting.

Seedling height distributions

The distribution of softwood seedlings by height class reveals that the proportion of fir, hemlock, and spruce seedlings in the shortest class (15-30 cm) in 1995 and 2005 was lower than the expected value ($p < 0.01$; based on the 40-year average for all softwood species) (Table 16; Figure 19). In other words, they were under represented. However, the proportion of these species in the two tallest classes (61-137 cm and > 137 cm with DBH < 1.3 cm) was greater than expected during the same periods ($p < 0.05$ or 0.01); they were over represented. The distribution of seedlings by height class for white-cedar is the opposite of other species; the proportion of seedlings in the shortest class was always greater than expected ($p < 0.05$ or 0.01) (Table 16), while the proportion in the 61-137 cm class was also always lower than expected ($p < 0.05$ or 0.01).

Between 1965 and 2005, the proportion of seedlings in the two tallest classes increased by 10.8 times for hemlock, 2.8 times for fir, 2.1 times for spruce, and stayed exactly the same for white-cedar. Moreover, only 1.4% of white-cedar seedlings were taller than 137 cm during the 40-year measurement period, compared to 7.8% of hemlock, 7.6% of fir, and 4.8% of spruces (Figure 19).

Table 16. Height distribution of individual species at each 10-year period (expected, or 40-year average distribution of all species combined, shown as a percentage).

	Height class	15-30 cm	31-60 cm	61-137 cm	> 137 cm with DBH < 1.3 cm
General distribution of all species and periods combined		54%	25%	16%	5%
1965	Balsam fir				
	Hemlock	++		--	
	Spruces				
	White-cedar	++	--	--	
1975	Balsam fir				
	Hemlock				
	Spruces				
	White-cedar	++		--	-
1985	Balsam fir				
	Hemlock				
	Spruces				
	White-cedar	++		--	
1995	Balsam fir	--		++	
	Hemlock	--		++	++
	Spruces	--	+	+	
	White-cedar	+		-	
2005	Balsam fir	--		++	++
	Hemlock	--		++	++
	Spruces	--		++	
	White-cedar	++		--	

Note: + or - indicates a significant difference superior or inferior to the general distribution ($\chi^2 = 3.84$, $p < 0.05$); ++ or -- indicates a very significant difference superior or inferior to the general distribution ($\chi^2 = 6.63$, $p < 0.01$).

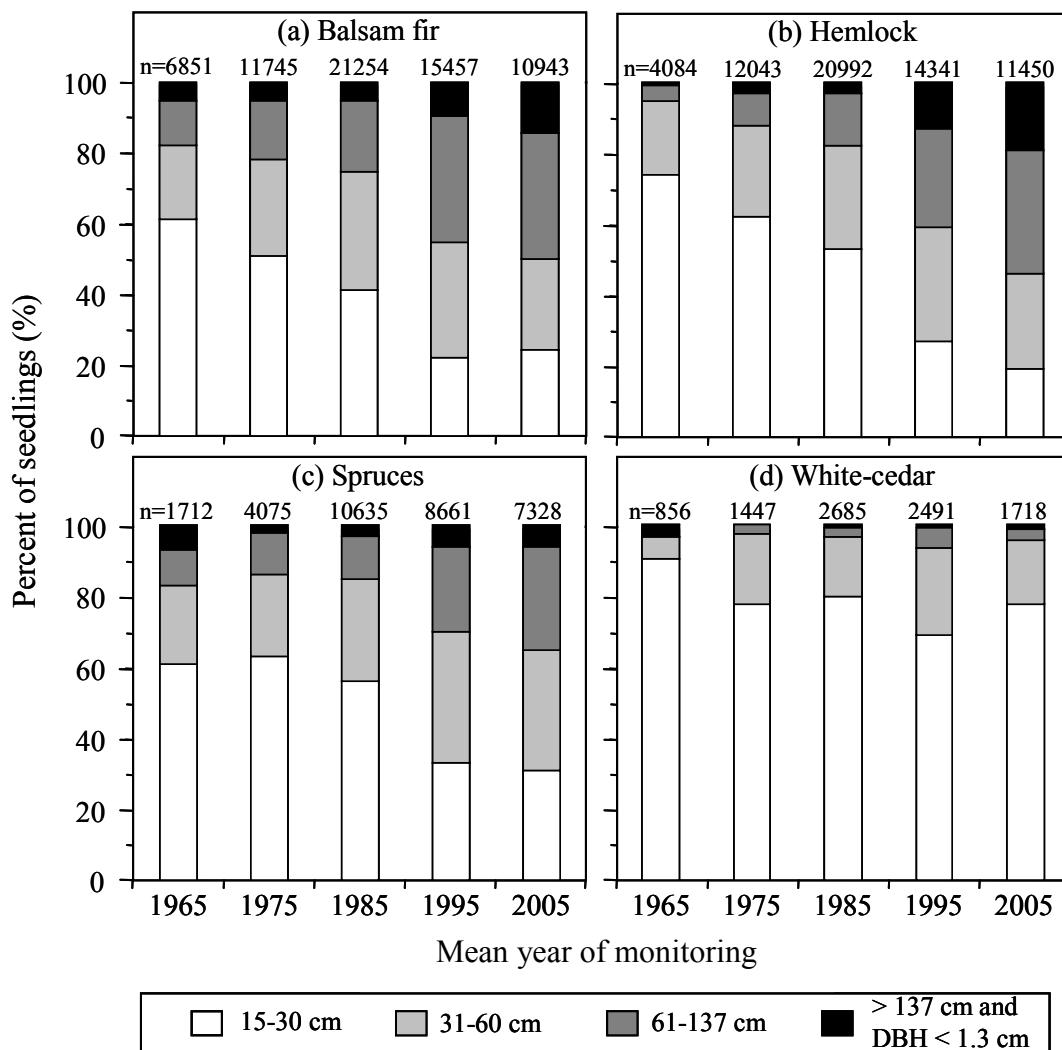


Figure 19. Distribution of seedlings by height class for balsam fir, hemlock, spruce species, and white-cedar.

Note: n-values show the mean number of seedlings by hectare found in all partial cutting treatments by 10-year period.

White-cedar sapling dynamics

There were 21 live, small ($1.3 \text{ cm} \leq \text{DBH} \leq 4.6 \text{ cm}$) white-cedar saplings on the sample plots at the beginning of the first numbered-tree measurement period (year = 1975) (Figure 20a). During the next 10 years, 15 of these saplings died and four recruited to the medium ($4.7 \text{ cm} \leq \text{DBH} \leq 8.0 \text{ cm}$) class. However, ingrowth from the seedling stage was only 10 saplings, so there were 12 live, small saplings at the end of the period. Between 1985 and 1995, ingrowth from the seedling stage was 9 saplings; density of small saplings increased during that period because only two died and three recruited to the medium class. During the last period (1995 to 2005), 12 small saplings died, one recruited to the medium class, and there were two ingrowth saplings; there were thus only three live, small saplings on the 138 sample plots in 2005.

The abundance of white-cedar saplings also decreased in the medium and large classes ($8.1 \text{ cm} \leq \text{DBH} \leq 11.4 \text{ cm}$) during the 30-year measurement period (Figures 20b and 20c). Recruitment from smaller classes was always less than the sum of the number of saplings growing into the next larger class and the number of saplings that died. Thus, density progressively decreased from 1975 to 2005. About 1/4 of saplings in the medium class grew to the large class during each 10-year period, while about 1/3 of large saplings grew to the poletimber class.

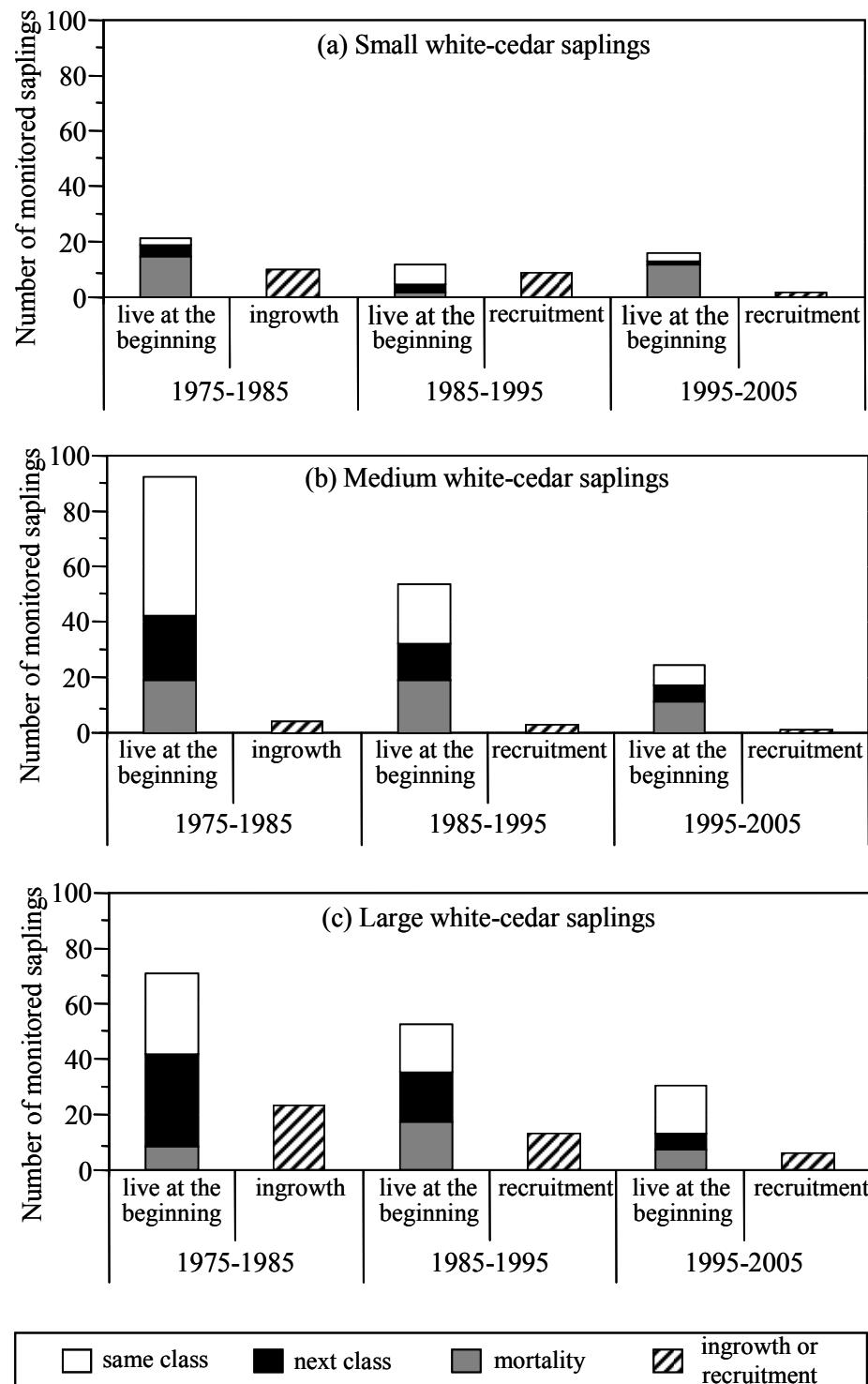


Figure 20. Dynamics of white-cedar saplings in 138 circular 0.02-ha plots over a 30-year period for small ($1.3 \text{ cm} \leq \text{DBH} \leq 4.6 \text{ cm}$), medium ($4.7 \text{ cm} \leq \text{DBH} \leq 8.0 \text{ cm}$), and large ($8.1 \text{ cm} \leq \text{DBH} \leq 11.4 \text{ cm}$) sapling size classes

Turning and mortality rates

Diameter increments of small, medium, and large saplings were 0.85, 0.94, and 1.63 cm/10yr, respectively (Table 17). Mortality rates were inversely proportional to the size of saplings: 58%, 29%, and 21% of small, medium, and large saplings, respectively. Harvesting operations accounted for 62.5% of large-sapling mortality, 32.7% of medium-sapling mortality, and 21% of small-sapling mortality. Other causes of mortality included browsing, self-thinning (mortality induced by competition for light and resources), desiccation, insects, and diseases. Monitoring in 2005 revealed that 92% of seedlings and small saplings > 30 cm tall were browsed. Most of them had more than 50% of their foliage consumed by deer, while 20% had more than 75% of their foliage consumed.

Diameter increment and mortality rate suggest that if we follow 100 small saplings for 10 years, 32 will still be in the small-sapling class, 10 will have grown to the medium class, and 58 will have died before the end of the period (Table 17). In the medium-sapling class, only 29 saplings will die during the 10-year period, allowing 52 to stay in the same class and 19 to grow to the large-sapling class. In the large-sapling class, higher diameter increment and lower mortality would allow 41 saplings to stay in the same class and 38 to grow to the poletimber, while 21 will die.

Table 17. Turning rates of white-cedar by sapling DBH class, including diameter increment and mortality rate, by 10-year period.

Sapling DBH class	Bounds (cm)		Increment (cm/10yr)	N ^a	Distribution by percentage				Total
	Min	Max			Same DBH class ^b	Next DBH class ^c	Mortality ^d		
Small	1.3	4.6	0.85	50	32	10	58	100	
Medium	4.7	8.0	0.94	167	52	19	29	100	
Large	8.1	11.4	1.63	152	41	38	21	100	

^a N show the total number of saplings used to calculated the increment in each sapling DBH class.

^b Saplings that stayed in the same DBH class.

^c Saplings that recruited to the next DBH class.

^d Saplings that died.

Discussion

There was a sharp decline in the abundance of white-cedar saplings between 1975 and 2005. Statistical analysis was not applied to these data because the low abundance of this secondary species did not allow sufficient degrees of freedom for mixed analysis of variance, or enough observations for growth modeling. Nevertheless, a reduction of 81.3% is as revealing as any significant statistical analysis. In 1975, there were 182 living white-cedar saplings on the measurement plots (65.9 stems/ha); there were only 34 (12.3 stems/ha) in 2005 (30 years later). The proportion of overstory basal area in white-cedar also declined by 50% in the study area since the early 1960s, while the number of merchantable trees was reduced by about 90% across the entire Forest Service study area since the early 1950s (U.S. Forest Service, *unpublished data*). The reduction of merchantable trees is partially due to logging activities (Brissette 1996), but also to low recruitment of saplings. These dynamics may compromise the sustainability of white-cedar and thus the maintenance of ecological values in ecosystem-based management where it is important to maintain each individual species. Conifer regeneration, including white-cedar, is sufficiently abundant to ensure renewal of stands across a range of partial harvest strategies (Brissette 1996), but survival and development of regeneration over the long-term must be assessed to ensure the sustainability of composition and structure, and ecosystem viability (Gauthier et al. 2008).

According to Brissette (1996), total softwood regeneration in the PEF partial cut treatments is profuse. Proximity of seed trees, receptivity of seedbeds, and moist environmental conditions all contributed to increases in the abundance of softwood regeneration over 40 years. White-cedar is a long-lived, shade-tolerant species noted to increase in frequency during succession in the mixedwood boreal forest (Bergeron and Dubuc 1989; Bergeron 2000). Regeneration of hemlock, spruce, fir, and white-cedar are favoured by uneven-aged systems on the PEF (Table 15; Figure 19). Hemlock, spruce, and fir are prolific, robust, and adapted to a broad range of site conditions (Brissette 1996), and are the most common species in the canopy, providing an abundant seed rain (Godman and Mattson 1976). These shade-tolerant seedlings are well adapted to establish on shady and moist forest floor and to colonize microsites warmed by increased available light after partial harvesting (Raymond

et al. 2000). Moreover, these conifer seedlings and saplings are more shade-tolerant than associated hardwood species (e.g. red maple, birches, aspens), and maintain height growth even under partial shading (Moores et al. 2007).

However, the success of regeneration depends not only on the establishment of seedlings, but also on the development and stratification of the new cohort (Grassi et al. 2003). Since 1985, the density of tall hemlock, fir, and spruce seedlings has been greater than the density of small ones (Table 16; Figure 19), creating the vertical stratification of the regeneration cohort and limiting the availability of light for suppressed stems (Oliver and Larson 1996; Smith et al. 1997). Seedlings of these species are getting larger, but white-cedar seedlings are not. They may be staying < 30 cm tall (waiting for an opening of the canopy), height growth may be limited by browsing, or they may be dying due to harvesting operations or other causes. Scott and Murphy (1987) found that 96% of white-cedar seedlings in their study did not reach a height of 25 cm or taller. Even if total abundance of white-cedar seedlings increased over 40 years, it is necessary to have new sapling ingrowth from the seedling stage to compensate for mortality and recruitment to the poletimber. To increase the density of saplings, ingrowth must be higher than turning and mortality rates. For white-cedar saplings, ingrowth is low and the mortality rate is high (Figure 20). This suggests that existing saplings that die (most of them) or grow to pole stage (few of them) are not replaced by seedlings growing into the sapling classes. This situation results in a white-cedar size structure biased toward merchantable stems and an imminent problem for white-cedar sustainability.

White-cedar saplings may tolerate browsing pressure for many years by mortgaging height and diameter growth, but if browsing persists over a long period, they will die. Repeated browsing is more difficult to tolerate for slow-growing species, as white-cedar, than for fast-growing species (Côté et al. 2004). Browsing is often considered to be the primary factor contributing to the decline of white-cedar regeneration in regions with high deer densities (Alverson et al. 1988; Heitzman et al. 1997; Cornett et al. 2000b). Field observations indicate that browsing of white-cedar seedlings is common on the PEF (U.S. Forest Service, *unpublished data*; Larouche, *unpublished data*). Saunders and Puettmann (1999) found higher susceptibility to browsing for seedlings between 30 cm and 130 cm

high in a study of eastern white pine in Minnesota; this may explain the higher abundance of unbrowsed white-cedar seedlings in the smallest height class compared to taller seedlings and saplings in the present study. The browsing pressure seems to be especially high on the PEF compared to the more northern regions of the Acadian Forest. It is possible to see more white-cedar regeneration in other parts of the region where deer populations are lower or topography is steep (*personal observation*). On the PEF, large saplings, mostly exempt from browsing pressure, are more often killed by cutting than medium and small saplings. Partial cutting generates damage to stems and roots of residual trees during logging and felling (Mitchell and Beese 2002). That may be an important problem for large saplings that are less flexible than small and medium saplings (Hannah 1988). Other possible causes of mortality may include: interspecific competition for resources and self-thinning, drought of humid sites, winter desiccation, and physical damage by trampling, snow, and tree fall. Insects, such as mites (*Oligonychus* spp.) and leafminers (*Argyresthia* spp.), and diseases may attack mature white-cedar and also cause mortality (Rose et al. 2000), but few scientific studies have evaluated the impact of insects and diseases on white-cedar seedlings and saplings.

Considering the mean PDI of saplings, a small sapling needs 39 years to reach the medium-sapling class (Table 17). It takes about the same amount of time for medium saplings to reach the large-sapling class, while large saplings grow 3.3 cm DBH in only 20 years. This suggests that a sapling needs about 94 years at breast height to become merchantable in the PEF partial cuts. This result is very similar to that of Hofmeyer (2008); they found through stem analysis that it took 96 years for white-cedar trees to grow from sapling to poletimber size in northern Maine. Similarly, results from Chapter 3 indicate that white-cedar stems of sexual origin need between 24 and 32 years to become 130 cm high in northern temperate forests without or with occasional browsing. That delay of recruitment to the pole stage is much higher than other associated tolerant softwood species (Hofmeyer 2008), and may be increased by preferential browsing pressure.

Calculation of turning rates and PDI allows the simulation of a population of saplings through the sapling stage. Three periods were combined to increase the number of observations because diameter increments did not differ between periods. However,

increment and mortality were different between sapling size classes, and we analysed them accordingly. The disadvantage of that method is the integration of all sites without consideration of the soil-vigour relationship (MRN 1998). Results should be projected carefully to other stands in the Acadian Forest.

With only two replicates of each treatment, the power to detect differences between treatments was low. Consistent with Brissette (1996), we found no major difference in the abundance and stocking of regeneration of each softwood species across the range of partial harvest treatments studied (Table 15). This contributes to the validity of our results for the pooled selection cutting variants and fixed diameter-limit treatment. However, the dynamics of young cohorts are likely influenced by silviculture system if harvest intensities vary greatly. Though it would be interesting to compare the vertical stratification of regeneration cohorts and increment and mortality of saplings with undisturbed and clearcut areas, such treatments on the PEF are markedly different in composition from the studied stands. Even-aged systems and natural disturbance dynamics should be studied further.

Management implications

White-cedar sustainability is not the focus of silvicultural treatments on the PEF (Kenefic et al. 2005). Irregular to uneven-aged stand structures will persist due to partial cutting, but the composition of future stands will probably be different from the current composition. There will be saplings and poles of hemlock, fir, and spruce, while white-cedar will be almost absent. It is not enough to maintain the stand structure and the vertical heterogeneity with multiple layers; the distribution of each individual species is also important to maintain.

This expected long-term change in composition creates an imbalance in the natural dynamics of the study stands and compromises the sustainability of the resource. It may be time to favor white-cedar through interventions such as keeping large, long-living white-cedar as seed trees; such trees are often cut due to internal decay (U.S. Forest Service, *unpublished silvicultural prescriptions*). In addition, control of the deer population would limit browsing. It may also be possible to add precommercial thinning to increase available growing space and resources by cutting competitive species and controlling stand species

composition (Brissette et al. 1999). White-cedar seedlings and saplings may grow faster under high sunlight conditions (up to 67% PPFD; *see* Chapters 1 and 3) or stay suppressed by stratification or be killed by self-thinning (Oliver and Larson 1996). Suppressed stems must survive in an overtopped position and maintain the capacity to react to canopy opening after many years in order to qualify for release (Schütz 2002); white-cedar demonstrates these characteristics after many years of suppression (Larouche et al. 2007; Hofmeyer 2008). Consequently, we recommend partial harvesting to encourage advance regeneration, browsing control to minimize seedling stress, and targeted release of white-cedar saplings in subsequent entries to promote height growth. Subsequent partial harvest entries present an ideal opportunity to make sure that the most difficult-to-recruit species receive the needed follow-up release to preserve their continued presence in mixedwood stands.

Conclusion

White-cedar seedlings have established in all partial cutting treatments studied on the PEF, even at relatively high deer population densities, but few have grown taller than 30 cm. Though it appears that the fir, spruce, and hemlock regeneration cohorts have increased in size over time, the white-cedar cohort has not. Consequently, there has been a progressive reduction in the density of white-cedar saplings. Ingrowth from the seedling to sapling stage has been lower than the combined rates of mortality and recruitment to the pole stage, and the number of white-cedar saplings is now > 80% less than it was at the beginning of the measurement period. Sapling mortality is high and recruitment to larger size classes is low, though mortality decreases and recruitment increases as sapling size increases. Browsing is prolific; 90% of seedlings and small saplings showed signs of browse in 2005. Overall, white-cedar sapling growth is slow, taking almost 100 years to grow from small sapling to merchantable size. Efforts to release white-cedar saplings and control browsing pressure are recommended. Future research should address the impacts of a broader range of silvicultural treatments, site characteristics, and browsing pressures on white-cedar dynamics, and further investigate the advantages and disadvantages of various silvicultural treatments for growth of white-cedar regeneration.

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Conclusion générale

Le thuya est une essence commerciale peu connue et les études existantes portant sur celui-ci se sont principalement déroulées dans les peuplements purs sur les stations humides et dans les régions ayant une forte densité de cerfs. Par contre, le thuya est ubiquiste, c'est-à-dire qu'il pousse sur tous les types et les qualités de station, toutes les classes de dépôt et de texture et toutes les positions topographiques en compagnie d'une multitude d'espèces. Ces conditions de croissance différentes permettent donc difficilement l'extrapolation des résultats existants.

Cette thèse portait spécifiquement sur la régénération du thuya poussant dans les peuplements mixtes sur stations mésiques. Son objectif principal était de déterminer les conditions permettant le succès de la régénération du thuya, en termes d'abondance, d'établissement et de croissance des semis et des gaules, après des coupes partielles. De manière générale, il est maintenant possible d'affirmer que les facteurs favorisant l'établissement de semis diffèrent de ceux permettant une meilleure croissance des semis et des gaules et qu'il y a des spécificités régionales. Les décisions d'aménagement doivent donc être prises en conséquence afin d'assurer le maintien de la composante de thuya dans les peuplements mixtes.

La synthèse des principaux résultats

Tous les peuplements étudiés comportent des semis de thuya plus petits que 15 cm, peu importe l'intensité et la fréquence des coupes partielles. C'est grâce à cette stratégie de banque de semis développée à long terme, qu'il n'est pas nécessaire d'établir de nouveaux semis de thuya à chaque intervention de récolte. L'établissement de nouveaux semis est toutefois favorisée par une ouverture par pied d'arbre d'environ 25 % de la surface terrière et un substrat minéral exposé. Le succès de régénération nécessite aussi la présence de semenciers assurant un apport de graines viables et une faible abondance de végétation compétitive afin de limiter la compétition interspécifique. Durant les trois premières années suivant la récolte, l'abondance de semis de thuya nouvellement installés est faible comparativement aux essences feuillues associées, mais elle est du même ordre de grandeur que celle des autres conifères. Le suivi à long terme dans les peuplements mixtes à

dominance résineuse démontre toutefois que l'abondance des semis dépend aussi de la composition de la canopée.

Bien que les semis de thuya plus petits que 15 cm soient généralement présents, leur croissance en hauteur est lente. Durant les trois premières saisons de croissance suivant la récolte, la croissance initiale du thuya est généralement inférieure à celle des feuillus et des conifères associés entraînant une stratification verticale de la nouvelle cohorte où les semis de thuya se retrouvent presque uniquement dans la classe de hauteur inférieure. Les semis de thuya nécessitent au moins 11 ans pour atteindre une hauteur de 30 cm, sans que la région ni la disponibilité de la lumière n'aient d'impact significatif. De plus, lorsque la densité de cerfs est élevée, peu de semis de thuya poussent au-delà de 30 cm de hauteur. Dans les régions étudiées où le cerf est abondant (> 5 cerfs/km²), la quantité de thuyas plus grands que 30 cm est fortement limitée. De plus, 90 % des semis et des petites gaules de thuya présentent des signes de broutement dans la région ayant la densité de cerfs la plus élevée. Il peut donc être nécessaire de contrôler le broutement pour assurer la présence de semis plus grands que 30 cm.

Même après cette phase d'établissement, la croissance en hauteur et en diamètre de la régénération de thuya demeure lente. Selon les conditions de croissance et la région, il faut de 14 à 32 ans à une marcotte ou un semis pour atteindre 130 cm de hauteur, tandis qu'il faut environ 100 ans à une gaule pour passer de 1,3 cm à 11,4 cm au diamètre à hauteur de poitrine. La croissance des arbres peut toutefois être influencée par la lumière disponible et les interventions sylvicoles. Qu'il s'agisse de semis plantés (> 40 cm de hauteur) ou de semis naturels (> 30 cm de hauteur), la croissance en hauteur augmente avec la disponibilité de la lumière. De plus, une coupe partielle peut augmenter significativement l'accroissement diamétral au niveau du sol des semis et des marcottes préétablis.

L'application des principaux résultats

À la lumière de ces résultats, il est préférable de travailler avec la régénération de thuya préétablie pour maintenir le thuya dans un peuplement aménagé. Les semis résineux s'établissent peu immédiatement après la récolte comparativement aux feuillus et ils subissent un fort taux de mortalité durant les premières années d'établissement. Qu'il

s’agisse de semis ou de marcottes, il est donc important de limiter les dommages à la régénération préétablie durant les interventions, afin d’assurer la contribution de celle-ci pour former le nouveau peuplement. Cette régénération, même si elle est opprimée durant plusieurs années, réagira positivement et rapidement à l’ouverture partielle du couvert. La plantation de thuya peut aussi donner de bons résultats en absence de régénération ou pour la réintroduction de cette essence. Dans un deuxième temps, une ouverture plus grande du couvert peut libérer les semis et les gaules et permettre une augmentation de la croissance. Idéalement, les semis préétablis doivent avoir terminé la phase d’établissement au moment de la libération, c’est-à-dire avoir une hauteur supérieure à 30 cm. En se basant sur les résultats obtenus, les semis de thuya doivent avoir au moins une dizaine d’années pour être considérés établis. L’intervalle de temps entre deux interventions doit alors être supérieure à 15 ans (en comptant un délai de régénération d’au moins 5 ans) et, plus elle est longue, plus la composante de thuya aura de chance d’être maintenue dans le peuplement. En somme, pour l’aménagement des peuplements mixtes, il serait préférable d’utiliser des procédés de régénération retirant le couvert par des interventions successives de faible intensité (p. ex. la coupe progressive irrégulière et le jardinage), plutôt que des coupes totales. Il serait alors possible de créer des conditions de croissance adéquates pour chaque étape de la régénération.

En outre, la dynamique de recrutement du thuya est fortement liée à la densité régionale de cerfs. Dans tous les peuplements mixtes étudiés, la basse régénération de thuya (semis < 15 cm) est présente, mais les semis plus grands que 15 cm sont moins abondants lorsque la densité de cerfs est élevée (> 5 cerfs/km²). En ce sens, lorsque le cerf est présent, la phase critique de la régénération est le recrutement des semis vers les classes de hauteur > 15 cm et vers le stade gaulis, plutôt que l’établissement de nouveaux semis. Afin de faciliter cette phase, certaines mesures peuvent être mises de l’avant. Par exemple, il pourrait être nécessaire d’exclure temporairement les cerfs de la zone à régénérer ou de conserver une forte densité de régénération pour protéger physiquement les thuyas contre le broutement (phénomène de facilitation). Par contre, cette dernière mesure risque d’engendrer une diminution du taux de croissance due à une limitation des ressources disponibles, principalement la lumière. La dynamique de régénération et de recrutement du

thuya doit être étudiée davantage dans les peuplements ayant des densités élevées de cerfs et dans les ravages.

Les perspectives de recherche

Cette étude a permis de développer de nouvelles connaissances sur la régénération du thuya après des coupes partielles sur une partie de son aire de distribution, mais de plus amples recherches seront nécessaires pour vérifier ces résultats dans d'autres régions, d'autres compositions et structures de peuplements, ainsi que d'autres stations forestières. Il est aussi nécessaire de faire plus de recherche pour quantifier l'utilisation du mode de reproduction asexué comparativement à celui sexué, surtout sur les stations mésiques. Pour y arriver, il sera nécessaire de raffiner les critères de distinction entre les semis et les marcottes.

Finalement, des études à long terme seront nécessaires pour définir les conditions et les taux de croissance de tiges individuelles à tous les stades de développement, ainsi que pour analyser le développement et la démographie d'un peuplement dont l'historique est connu. Il sera alors possible de confirmer la composition finale des peuplements mixtes aménagés et de prédire la productivité et le volume des essences secondaires.

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