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## RÉSUMÉ

Dans le nord-ouest du Québec, le thuya de l'Est atteint sa limite de répartition continue aux environs du 48<sup>e</sup> parallèle de latitude. Toutefois, quelques peuplements se trouvent jusqu'au 51<sup>e</sup> parallèle. La présence ou l'absence d'une espèce peut être expliquée par différents facteurs tels que le climat, les feux, les conditions édaphiques ou la compétition interspécifique. La présente étude tente d'établir quels facteurs influencent la limite de répartition nordique du thuya de l'Est au Québec.

Nous avons étudié l'effet du climat sur la croissance et la régénération du thuya à différentes latitudes. Nous avons également analysé la répartition du thuya selon la disponibilité de sites potentiels le long d'un gradient climatique. Finalement, nous avons tenté de comprendre la relation entre l'établissement du thuya et la dynamique des feux à la limite de sa répartition. Ces différentes analyses ont permis de constater que le climat n'avait qu'une influence partielle sur la répartition actuelle du thuya. Seule la régénération des sites marginaux était plus faible par rapport aux peuplements du sud. La régénération était toutefois présente dans ces sites isolés. De plus, le climat ne pouvait expliquer la baisse importante de l'abondance des peuplements rencontrée au centre du gradient latitudinal. Par ailleurs, la disponibilité de sites adéquats pour l'établissement du thuya ne semble pas être un facteur important puisque le thuya semble incapable de saturer tous les sites potentiellement disponibles au nord de sa répartition. Le feu apparaît avoir une grande influence sur la répartition du thuya. En effet, les peuplements trouvés au nord sont généralement plus âgés que les peuplements les entourant. Cela indique qu'ils n'ont pas brûlé en même temps que les autres peuplements lors du dernier feu, et se trouvent donc dans des endroits protégés. De plus, les peuplements marginaux étudiés se trouvaient tous à proximité de cours d'eau ou dans des endroits très humides, là où les feux sont moins probables.

Nous constatons donc que le feu, en association avec le climat, semble responsable de la limite de répartition actuelle du thuya de l'Est. En effet, le climat diminue le potentiel de régénération et les feux éliminent les arbres semenciers et limitent la dispersion des peuplements. Ainsi, la répartition du thuya de l'Est n'est pas en équilibre avec le climat en raison des feux trop fréquents. Dans une optique de changements climatiques, la migration de plusieurs espèces vivant en forêt boréale pourrait dépendre davantage de l'effet du climat sur les cycles de feu que de ses effets directs sur la biologie de l'espèce.

*Mots clés* : Thuya de l'Est, limite nordique, climat, reproduction, feu, facteurs édaphiques

## INTRODUCTION GÉNÉRALE

### **0.1 Objectif général : Analyser l'impact de facteurs potentiels pouvant contrôler la limite de répartition du thuya de l'est**

Les facteurs contrôlant la répartition des espèces sont des connaissances essentielles pour comprendre la dynamique des écosystèmes forestiers. Ces connaissances peuvent permettre, entre autre, de prévoir la réponse des écosystèmes ou des arbres aux changements climatiques et de mieux aménager le territoire de façon durable. En effet, un réchauffement climatique sans précédent en terme de vitesse et de magnitude est anticipé (GIEC 2007). Ce réchauffement pourrait avoir une importante répercussion sur la dynamique des écosystèmes. En effet, le climat peut influencer la physiologie, la phénologie (Kullman, 2007; Delbart *et al.*, 2008) et la croissance (Huang *et al.*, 2007; St-Germain et Krause, 2008) d'une espèce. Plusieurs études ont montré la migration ou l'extinction locale d'espèces en raison de changement climatique (Lloyd et Fastie, 2003; Parmesan, 2006; Kullman, 2007). Ainsi, le développement de modèle prédictif de la migration des espèces est très important afin de minimiser les conséquences potentiellement négatives des changements climatiques sur les écosystèmes forestiers.

Les modèles prédictifs actuels se basent principalement sur la niche réalisée des espèces (niche-based models) pour faire leur prédiction (Ressources naturelles Canada 2011). Ces modèles sont ainsi basés sur la présence ou l'absence d'espèces à certaines températures et supposent qu'avec le réchauffement climatique, ces espèces migreront pour s'établir à ces mêmes températures. Ces modèles ne tiennent pas compte du temps de réaction de l'espèce et de sa possibilité de dispersion. D'autres modèles tentent d'intégrer des données de type phénologique (process-based models) afin d'avoir un portrait plus réaliste pour chacune des espèces (Morin *et al.*, 2008).

La répartition d'une espèce est la résultante d'une combinaison complexe de facteurs. Certaines études s'accordent pour dire que le climat est un élément prépondérant dans la répartition des espèces à une grande échelle (Prentice *et al.*, 1992; Wang *et al.*, 2006). Toutefois, il semble que la limite nordique de la répartition des arbres ne soit pas uniquement contrôlée par le climat. Les perturbations naturelles, les conditions édaphiques et la compétition interspécifique peuvent aussi jouer un rôle important à une échelle plus régionale ou locale (Woodward, 1987; Richardson et Bond, 1991). L'importance de ces facteurs dépendraient de chacune des espèces. Ainsi, afin de prévoir correctement la réaction des espèces et de leur écosystème, il est essentiel d'étudier davantage les facteurs qui influencent la répartition d'une espèce pour que ces résultats soient intégrés dans les modèles de prédiction.

Peu d'études se sont penchées simultanément sur plusieurs facteurs explicatifs de la limite de répartition, préférant se concentrer sur une seule, généralement le climat. De plus, au Québec, aucune étude ne s'est réellement penchée sur l'étude d'une gamme de facteurs potentiels limitant la répartition du thuya de l'Est (*Thuja occidentalis* L.). Certaines études ont émis l'hypothèse d'une fréquence des feux trop grande (Heinselman, 1973) ou d'un climat peu propice (Tardif et Stevenson, 2001), mais l'importance relative de ces facteurs et de leurs interactions sur la répartition nordique du thuya de l'Est est méconnue.

## **0.2 L'effet de facteurs climatiques sur la répartition d'une espèce**

Le climat a souvent été suggéré comme étant un facteur contrôlant la répartition nordique des espèces (Richard, 1993; Carcaillet *et al.*, 2001). En effet, à la limite nordique de leur répartition, certaines espèces ont des populations de petite taille, une faible croissance et un faible taux de reproduction, conditions qui peuvent être attribuées au climat (Pigott et Huntley, 1981; Payette et Delwaide, 1994; Kullman, 2007). D'autre part, certaines études ont montré que la limite de répartition de certaines espèces d'arbres, notamment le sapin baumier (*Abies balsamea* L.) et thuya de l'Est, était située plus au nord lorsque les températures



étaient plus chaudes, ce qui suggère un effet du climat sur la répartition (Richard, 1993; Ali *et al.*, 2008).

### 0.2.1 Impact du climat sur la survie des arbres

Le climat peut affecter directement la survie des arbres en infligeant des blessures dues au froid, au feuillage et aux branches, ou par un nombre insuffisant de jours de croissance ou de précipitations (Woodward, 1987; Kullman, 1998). Sakai et Weiser (1973) ont d'ailleurs étudié l'effet de très basses températures sur la survie des branches et bourgeons. Ils ont démontré que plusieurs espèces boréales pouvaient tolérer des températures aussi froides que  $-80^{\circ}\text{C}$ . Il est néanmoins suggéré que l'effet du dessèchement hivernal pourrait avoir un impact plus important que le climat sur la survie des arbres (Hadley et Smith, 1983). Les variations de température et de précipitation peuvent également influencer le taux de croissance radiale d'une espèce pour une même latitude (Kozłowski *et al.*, 1991; Tardif et Bergeron, 1997; Tardif et Stevenson, 2001; Heinrichs *et al.*, 2007; Vila *et al.*, 2008) ou le long d'un gradient latitudinal (Pärn, 2003; St-Germain et Krause, 2008; Huang *et al.*, 2010).

### 0.2.2. Impact du climat sur le potentiel reproductif

L'expansion de l'aire de répartition d'une population d'arbres est reliée à sa régénération. Selon Caspersen et Sapruff (2005), la régénération d'une espèce dépend de la production de graines viables et de sites adéquats pour la germination. Toutefois, les conditions ambiantes doivent également être propices à la survie des semis. Les différentes étapes de la régénération peuvent être affectées par certains facteurs et mettre en péril la survie de l'espèce. Plusieurs études traitent de l'effet du climat à la limite nordique sur le processus reproductif des arbres en comparant la régénération à différentes latitudes (Pigott et Huntley, 1981; Flannigan et Woodward, 1993; Houle et Filion, 1993; Tremblay *et al.*, 2002; Messaoud *et al.*, 2007a). Ainsi, à la limite de répartition des arbres, le climat peut empêcher une forme de croissance érigée et la production de graines viables, essentielles pour la dispersion (Asselin et Payette, 2006). De plus, chez les peuplements d'érable rouge (*Acer rubrum* L.)

situés plus au nord, la production de samares est limitée possiblement en raison des épisodes de gel printanier, qui peut grandement diminuer le nombre de fleurs et de graines fertilisées (Tremblay *et al.*, 2002). Pour leur part, Pigott et Huntley (1981) ont montré que le tilleul à petites feuilles (*Tilia cordata* Mill.) ne pouvait se reproduire de façon sexuée à sa limite nordique. Ils se sont penchés spécifiquement sur les différentes phases de production d'une graine et ont démontré que le climat rigoureux limite l'allongement du tube pollinique et l'atteinte de l'ovule.

Le succès de germination des graines et la survie des semis sont aussi affectés par le climat. Pour certaines essences, dont le frêne blanc (*Fraxinus americana* L.), l'humidité constante est une variable des plus importantes pour la germination et la survie des semis (Simard *et al.*, 1998; Cornett *et al.*, 2000b; Messaoud et Houle, 2006). Ensuite, la température de l'air, par exemple le nombre de degrés-jours de croissance et le nombre de jour de gel printanier, semblent aussi jouer un rôle dans l'établissement des semis (Sirois, 2000; Tremblay *et al.*, 2002; Asselin *et al.*, 2003; Kullman, 2007). Les graines de pin rouge (*Pinus resinosa* Ait.), pour leur part, requièrent des températures de plus de 10°C pour germer (Flannigan et Woodward, 1993). De même, les semis de sapin baumier semblent être sensibles au climat puisque la densité de semis diminue au nord et ce même si la densité de sapins matures dans un peuplement y était plus élevée (Messaoud *et al.*, 2007a).

La reproduction sexuée peut être remplacée par un mode asexué en raison de contraintes environnementales. La reproduction végétative peut permettre à certaines espèces de se maintenir lors d'une perturbation ou d'une interruption dans leur cycle de reproduction. Le cycle reproductif peut être altéré notamment par une plus petite saison de croissance, par des températures froides ou par la fertilité du sol (Staneck, 1961). L'épinette noire (*Picea mariana* Mill.) et l'érable rouge se propagent majoritairement par reproduction asexuée à la limite nordique de leur répartition pour contrer le climat rigoureux (Payette, 1979; Tremblay *et al.*, 2002; Lloyd, 2005). Les peuplements d'épinette noire peuvent être composés de plus de 50% de clones à la limite des arbres, possiblement en raison du climat rigoureux qui empêche la germination des graines (Payette, 1979; Lloyd, 2005).

### **0.3 L'effet des facteurs édaphiques et topographiques sur la répartition d'une espèce**

La répartition d'une espèce peut être influencée par les conditions édaphiques environnantes. Une hypothèse soulevée pour expliquer la limite de répartition d'une espèce est la raréfaction d'habitats favorables qui peut être due à un changement dans les types de dépôt ou de drainage. Par exemple, Meilleur et al. (1997) ont démontré le manque de sites propices au pin rigide (*Pinus rigida* Mill.) à sa limite nordique dans le sud du Québec, ce qui l'empêcherait d'agrandir sa répartition plus au nord. Toutefois, les facteurs édaphiques expliquent rarement complètement la limite de répartition d'une espèce mais font plutôt partie d'une équation de plusieurs facteurs. Messaoud et al. (2007b) ont montré que la répartition des peuplements de sapin baumier était limitée par une diminution de sites potentiels favorables dans la pessière à mousse. Toutefois, le sapin baumier y était incapable de coloniser tous les sites favorables. Ces résultats suggèrent donc que la diminution de l'abondance des sites ne peut expliquer complètement la répartition du sapin. En Alaska, la présence de l'épinette noire est expliquée à la fois par la fréquence des feux et le pH des sols (Lloyd *et al.*, 2007). De plus, Lalonde (1991) a montré que la répartition de l'érable rouge était influencée par le climat mais également par le paysage. À la limite de son aire de répartition, l'érable rouge se trouve à de plus hautes altitudes, où il est confiné au versant sud-est. L'altitude lui procure un avantage thermique et l'orientation sud augmente aussi la quantité de radiations en plus de le protéger des vents de l'ouest et des feux qui sont dirigés par le vent (MacHattie, 1961). Sa limite de répartition coïncide également avec une raréfaction des collines ce qui peut limiter davantage sa distribution.

### **0.4 L'effet des perturbations naturelles sur la répartition d'une espèce**

La forêt boréale de l'Ouest québécois est grandement perturbée par les feux. Les feux y sont très fréquents et peuvent survenir en moyenne tous les 135 ans (Bergeron *et al.*, 2004). Les feux de la forêt boréale sont une perturbation majeure qui influence la composition et

possiblement la répartition des espèces (Rowe, 1973; Suffling, 1995; Bergeron, 2000). Payette et Gagnon (1985) ont constaté que les régimes de feu en combinaison avec le climat contrôlaient la limite des arbres. En effet, certaines espèces requièrent le passage du feu pour se maintenir dans le paysage alors que pour d'autres, la répartition est restreinte par la fréquence et l'intensité des feux. Desponts et Payette (1992) ont montré que le pin gris (*Pinus banksiana* Lamb.) dépend d'un cycle de feu à courts intervalles pour maintenir ses populations à sa limite nordique puisqu'une chaleur intense est essentielle pour ouvrir les cônes et relâcher les graines. Pour sa part, la répartition du pin rouge semble limitée par les feux forestiers puisqu'il semble posséder une dépendance aux feux de moyenne ou faible intensité. De tels feux permettent de supprimer les espèces compétitrices en sous-couvert et de créer des ouvertures dans la canopée pour sa régénération. Toutefois, les feux de grande intensité, que l'on trouve majoritairement au nord de sa répartition, semblent restreindre l'établissement plus au nord de cette espèce (Bergeron et Gagnon, 1987; Flannigan, 1993; Flannigan et Bergeron, 1998). La présence du genévrier commun (*Juniperus communis* L.) semble aussi être entretenue par des feux de moyenne intensité sur les îles du Lac Duparquet, ce qui apparaît comme un facteur important dans sa répartition (Diotte et Bergeron, 1989). D'autres études démontrent également l'influence négative du feu dans l'aire de répartition de certaines espèces. Ils ont montré qu'alors que les feux étaient moins fréquents pendant certaines périodes de l'Holocène, certaines espèces sensibles aux feux en ont profité pour agrandir leur répartition plus au nord (Carcaillet *et al.*, 2001; Messaoud *et al.*, 2007b; Ali *et al.*, 2008).

### **0.5 Les caractéristiques du thuya de l'Est**

Le thuya de l'Est (*Thuja occidentalis* L.) est présent dans tout le sud du Québec et est commun jusqu'au 48° parallèle nord. À partir de cette latitude, l'abondance de peuplements connaît une diminution importante. Au-delà du 49° parallèle, seulement quelques populations isolées survivent, et ce jusqu'au lac Chibougamau et au delta de la rivière Harricana à plus de 200 km de la limite de la répartition continue du thuya. Le thuya occupe une place importante dans les sous-domaines de l'érablière à bouleau jaune et de la sapinière à bouleau jaune. Sa

répartition s'étend sur plusieurs domaines bioclimatiques et conséquemment différentes conditions climatiques et perturbations. Selon Richard (1993), le thuya aurait colonisé les terres de l'Ouest du Québec suite à la déglaciation dans un environnement climatiquement plus favorable, ce qui aurait permis au thuya de s'établir dans des sites plus au nord de sa répartition actuelle. Les quelques peuplements que l'on retrouve présentement à la marge de sa répartition continue seraient des reliques d'anciens peuplements plus importants qui n'auraient pu survivre au refroidissement subséquent (Liu, 1990; Richard, 1993; Carcaillet *et al.*, 2001). En fait, le thuya semble pouvoir tolérer des températures très basses de l'ordre de -80°C, mais il est possiblement susceptible au dessèchement hivernal, ce qui peut grandement affecter la survie des individus à des latitudes nordiques (Sakai, 1973).

Un taux de croissance radiale maximal du thuya est généralement associé à des températures plus basses en été et à un haut taux de précipitations (Archambault et Bergeron, 1992; Kelly *et al.*, 1994; Tardif et Bergeron, 1997; Tardif et Stevenson, 2001). Au Manitoba, à la limite nordique de sa répartition, la croissance est aussi influencée par de plus chaudes températures tardives en automne, suggérant un possible impact du climat sur la répartition de cette espèce (Tardif et Stevenson, 2001). Toutefois, les auteurs signalent également que la croissance du thuya est comparable à une croissance rapportée à d'autres endroits de sa répartition, suggérant ainsi un effet limité du climat.

La régénération du thuya peut être parfois très faible et son abondance semble avoir diminué dans certaines zones de son aire de répartition (Heitzman *et al.*, 1997). Tout d'abord, la germination et l'établissement du thuya requièrent des conditions particulières (Cornett *et al.*, 2000b; Cornett *et al.*, 2001; Simard *et al.*, 2003; Gengarelly et Lee, 2005). L'espèce se trouve en abondance sur un sol minéral ou sur des débris d'arbres au sol. Ces deux endroits sont exempts de la litière des feuillus qui peut inhiber la croissance des semis. Les débris d'arbre assurent également un approvisionnement constant en eau et en nutriments, des conditions importantes pour la survie des semis. Les semis peuvent aussi être grandement affectés par les pratiques forestières inadéquates et l'abondance du cerf de Virginie (Cornett *et al.*, 2000a). D'autre part, dans certaines zones du Maine, dans les zones très humides et très

pauvres en nutriments, près de la moitié des tiges peuvent être de provenance asexuée, soit par marcottage (Curtis, 1946; Johnston, 1990).

Dans la forêt boréale mixte, le thuya se trouve dominant surtout lors des dernières phases de succession (Bergeron, 2000) puisque c'est une espèce de grande longévité (Archambault et Bergeron, 1992) qui tolère très bien l'ombre. Il est souvent associé au sapin baumier avec lequel il se trouve dans les peuplements âgés. Le thuya est peu tolérant au feu puisqu'il possède une écorce mince et un haut taux d'huile inflammable dans ses feuilles (Johnston, 1990). Heinselman (1973) a suggéré qu'il ne pouvait pas se régénérer après des épisodes de feux de forte intensité. D'ailleurs, à la limite de sa répartition continue, il se trouve principalement sur les rives des lacs, ce qui confère une certaine protection contre le feu (Denneler *et al.*, 2008). Il se trouve aussi sur des îles où sa présence est associée à l'absence de feux de forte intensité depuis une longue période (Archambault et Bergeron, 1992).

D'autre part, le thuya est une espèce qui peut tolérer de nombreux types d'habitats, tels que les milieux humides ou mésiques ou des escarpements rocheux et secs (Habeck, 1958; Musselman *et al.*, 1975; Johnston, 1990). Toutefois, il se trouve préférentiellement sur des sols mésiques (Denneler *et al.*, 1999) où le diamètre et la symétrie des thuyas sont généralement plus grands (Tardif et Bergeron, 1997). Il est aussi tolérant à des sols basiques contenant du calcaire (Curtis, 1946).

## **0.6 Objectifs et méthodologie de l'étude**

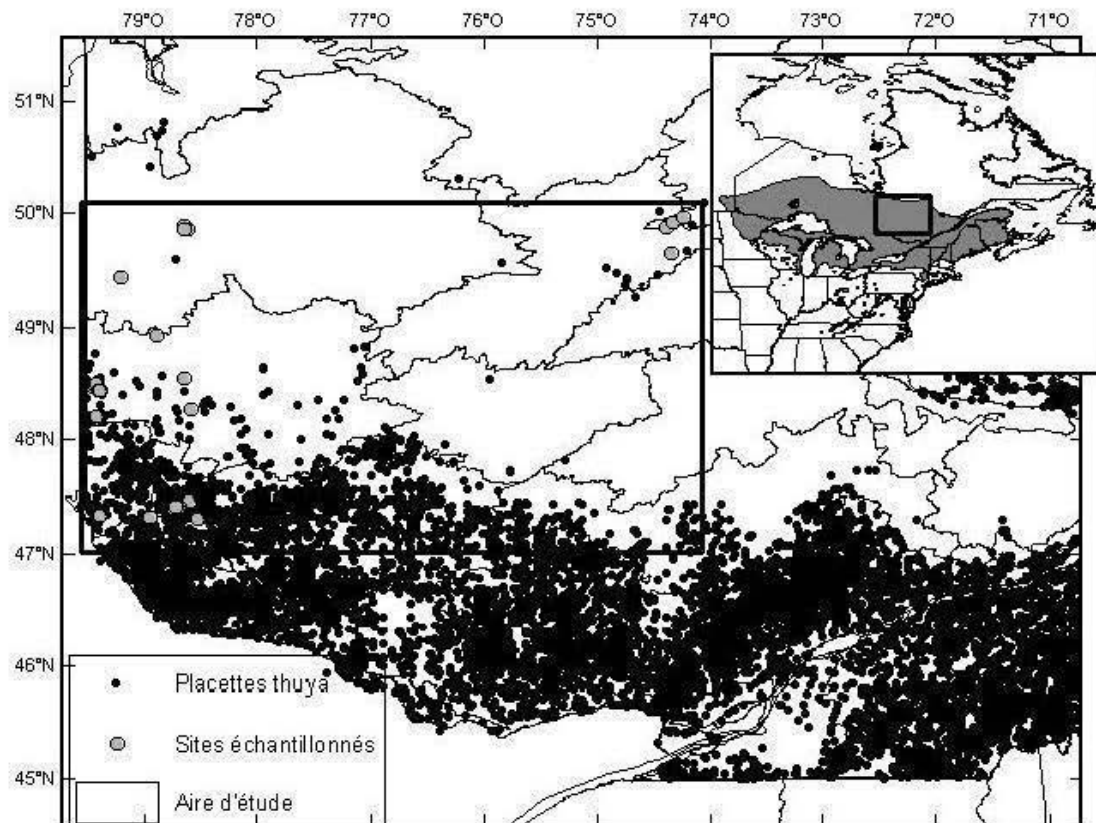
L'objectif du projet était d'étudier l'impact des facteurs climatiques et édaphiques et des feux sur la limite nordique de répartition du thuya de l'Est afin de déterminer les facteurs limitant sa présence. Cet objectif nous a permis d'en connaître davantage sur la croissance, la régénération, la susceptibilité aux feux et l'utilisation de sites particuliers à différentes latitudes. Dans une plus large optique, ces résultats nous ont aussi permis d'évaluer les effets potentiels des changements climatiques sur la répartition du thuya.

La zone d'étude se situait dans la portion ouest du Québec, dans les régions de l'Abitibi-Témiscamingue et du Nord-du-Québec le long d'un gradient latitudinal de 300km. Six à huit peuplements de thuya ont été sélectionnés à trois latitudes différentes pour un total de 22 parcelles. Les peuplements dans la sapinière à bouleau jaune de l'Ouest sont situés dans la portion continue de la répartition et représentent un peuplement non limité, tandis que les peuplements dans la sapinière à bouleau blanc de l'Ouest représentent la limite discontinue de la répartition du thuya. Les peuplements marginaux sont situés en majorité dans la pessière à mousse de l'Ouest (Fig. I.1). Les sites ont été choisis en tenant compte des caractéristiques édaphiques de drainage et de texture du sol similaires afin de pouvoir comparer la croissance et la régénération. De plus, des parcelles échantillonnées par le ministère des Ressources naturelles et de la Faune (MRNF) ont été utilisées.

Le premier chapitre s'intéresse à l'impact du climat sur la croissance radiale, la production de graines et l'établissement de semis et de marcottes du thuya de l'Est à la limite nordique de sa répartition. Les hypothèses de ce chapitre ont pu être testées lors d'un échantillonnage terrain le long d'un gradient latitudinal. Cette section compare la croissance et la régénération entre des peuplements de la répartition continue à des peuplements à la limite de la répartition du thuya afin de mesurer l'impact du climat.

Pour sa part, le chapitre 2 aborde l'effet des perturbations naturelles et des facteurs édaphiques sur la répartition du thuya de l'Est le long d'un gradient latitudinal. Ce chapitre comporte une analyse cartographique afin de tester la limitation par des facteurs édaphiques. L'analyse cartographique a été réalisée à l'aide de parcelles provenant du MRNF. Cette analyse permet de déterminer les caractéristiques importantes à l'établissement du thuya et ainsi de comparer la disponibilité de sites à l'utilisation réelle par le thuya à différentes latitudes. D'autre part, un échantillonnage terrain et une analyse cartographique ont permis de tester l'importance du feu dans la répartition du thuya de l'Est. Le temps approximatif depuis le dernier feu est comparé entre les peuplements de thuya et les peuplements environnants. Ceci permet de déterminer si les peuplements de thuya ont brûlé en même temps que les

peuplements environnants et ainsi de déterminer si le thuya se trouve dans des endroits protégés des feux.



**Figure I.1.** Répartition du thuya de l'Est au Québec (MRNF, 2009) et en Amérique du Nord (USGS, 2009) ainsi que la répartition des sites échantillonnés dans l'aire d'étude



CHAPITRE I

RESPONSE OF EASTERN WHITE-CEDAR (*THUJA  
OCCIDENTALIS* L.) TO CLIMATE AT THE NORTHERN LIMIT OF  
ITS RANGE.

Véronique Paul, Yves Bergeron et Francine Tremblay

## 1.2 Abstract

This study aims to determine if climate can influence eastern white-cedar's (*Thuja occidentalis* L.) northern distribution limit in analysing its effect on radial growth and seed and seedling abundance. Eastern white-cedar stands were selected across a 300 km latitudinal transect following a gradient of abundance of white-cedar stands in north-western Québec, Canada (47°-50° N and 74°- 79° W). In total, 22 sites were selected along the bioclimatic gradient. In the south of the gradient, white-cedar is common while in the north, only outlier stands are found. Radial growth, the number of seeds and the germination rate and the abundance of seedlings were determined for each site along the gradient. Results show that radial growth was the same along the gradient. Also, seed production and germination did not differ along the transect. Abundance of seedlings under 30 cm in height was similar in sites found in the continuous distribution. However, it was found to be less abundant in the northernmost sites compared to the southern stands. Abundance of stems higher than 30 cm, consisting mostly of layers, did not decrease along the gradient. Climate appears to only partially influence white-cedar recruitment in the marginal white-cedar stands. Indeed, radial growth and seed production in the north were found to be equivalent to the south and layers appeared to maintain recruitment all along the gradient. In brief, climate did not completely explain the distribution limit of eastern white-cedar. Other factors, such as fire or site conditions, might in part explain this boundary and further analyses are needed to understand the northern limit of eastern white-cedar. The influence of climate change on species distribution in boreal forest might thus depend more on indirect effects of climate on disturbances regime instead of on the direct effect of climate on species physiology or on demographic properties.

### 1.3 Introduction

Climate is often cited as a main factor controlling species distribution thus climate changes are expected to have major issues on ecosystem's dynamic (Kullman and Kjallgren, 2006, Morin, et al., 2008, Huang, et al., 2010). Studies on past and present ecosystems have already demonstrated shifts in species range in regards to climate change (Richard, 1993, Kullman, 2007). However, different tree species have different sensitivities to climate (Tardif and Bergeron, 1997, Pederson, et al., 2004, Huang, et al., 2010). Moreover, other variables, such as disturbances, edaphic factors, and competition, can limit and modify distributions depending on a given species' characteristics (Meilleur, et al., 1997, Flannigan and Bergeron, 1998, Asselin, et al., 2003, Lafleur, et al., 2010). The relative effect of climate on tree species must be better understood to mitigate potentially negative consequences of climate change on forest ecosystems.

Climate can have a direct influence on tree physiology and affect growth in different ways. Cold temperatures and frost can inflict injuries to buds, branches, and foliage, and even cause death (Sakai, 1973, Hadley and Smith, 1983, Kjallgren and Kullman, 1998, Kullman, 2007). Temperatures and precipitation are also factors known to affect tree's radial growth (Tardif and Bergeron, 1997, Tardif and Stevenson, 2001, Heinrichs, et al., 2007, Vila, et al., 2008). Radial growth is commonly reduced with increasing latitudes (Pärn, 2003, St-Germain and Krause, 2008, Huang, et al., 2010).

According to a process-based model, species distribution is first limited by the effects of climate on tree's phenological aspects (Morin, et al., 2007). Indeed, several studies have showed that climate appears to control species distribution in affecting recruitment through the different phases of reproduction (Pigott and Huntley, 1981, Tremblay, et al., 2002, Kullman, 2007). At a species' northern distribution limit, the low number of growing degree-days (GDD) can be responsible for low seed viability and regeneration failure (Pigott and Huntley, 1981, Sirois, et al., 1999, Sirois, 2000, Asselin, et al., 2003). Tremblay et al. (2002) also showed that seed production for red maple (*Acer rubrum* L.) is likely lowered when

spring frosts occur during flowering. In addition, temperature and precipitation can influence germination success and seedling survival (Flannigan and Woodward, 1993, Messaoud and Houle, 2006, Kullman, 2007, Messaoud, et al., 2007). In affecting recruitment, climate can limit a species abundance and its ability to disperse and expand its distribution. In the absence of sufficient sexual regeneration, some species, like black spruce (*Picea mariana* Mill. (B.S.P.)) or red maple, regenerate mainly by vegetative reproduction at their northern limit (Laberge, et al., 2001, Tremblay, et al., 2002, Lloyd, et al., 2005, Auger and Payette, 2010).

In Western Québec, eastern white-cedar (*Thuja occidentalis* L.) becomes less abundant in the northern part of Abitibi-Témiscamingue (Québec) between the 48<sup>th</sup> and 49<sup>th</sup> parallels. Its distribution becomes increasingly sporadic above the 49<sup>th</sup> parallel with only small, isolated populations and scattered individuals being found at the higher latitudes. It reaches its northernmost limit of distribution at around the 51<sup>th</sup> parallel in the James Bay region. Paleoecological studies suggest that white-cedar was more abundant in northern areas when climate was more favorable (Liu, 1990, Richard, 1993, Carcaillet, et al., 2001), which suggests an influence of climate on its distribution. Isolated populations of white-cedar found 200 km north of the continuous distribution are possibly relicts of old populations established when the climate was more suitable after the last deglaciation. Some studies demonstrated that white-cedar's growth and regeneration are correlated with climate. For example, its radial growth is positively influenced by cool temperature and a high rate of precipitation during the growing season at the margin of its range in Manitoba and Québec (Archambault and Bergeron, 1992, Tardif and Bergeron, 1997, Tardif and Stevenson, 2001). On the other hand, at the margin of its range in Manitoba, Tardif and Stevenson (2001) found that the response of white-cedar's radial growth to climate was only sensible during late fall. Its limited sensitivity to climate can unlikely explain entirely white-cedar's distribution limit in this region. Moisture also constitutes an essential factor for the survival of juvenile white-cedars (Cornett, et al., 2000, Matthes and Larson, 2006). Survival rate during the first years is very low and is attributed to the effects of drought (Matthes and Larson, 2006). In addition, white-cedar often uses branch layering to regenerate, with vegetative propagation accounting

for more than 50% of the standing trees at some sites (Nelson, 1951, Johnston, 1990, de Blois, 1994). Layering generally occurs at poorly drained sites with a thick accumulation of organic matter or mosses, but can also be found at more mesic sites (Johnston, 1990, de Blois, 1994).

The present study investigates the effects of temperature on white-cedar growth and recruitment in stands along a climatic gradient with the goal of determining if the distribution of this species is controlled by climate. We hypothesize both that radial growth is reduced with increasing latitudes and that temperature limits the northern expansion of white-cedar by decreasing seed crop, seed germination, and seedling survival at the northern limit. Regeneration in the northernmost sites would be maintained mainly by branch layering.

## **1.4 Materials and methods**

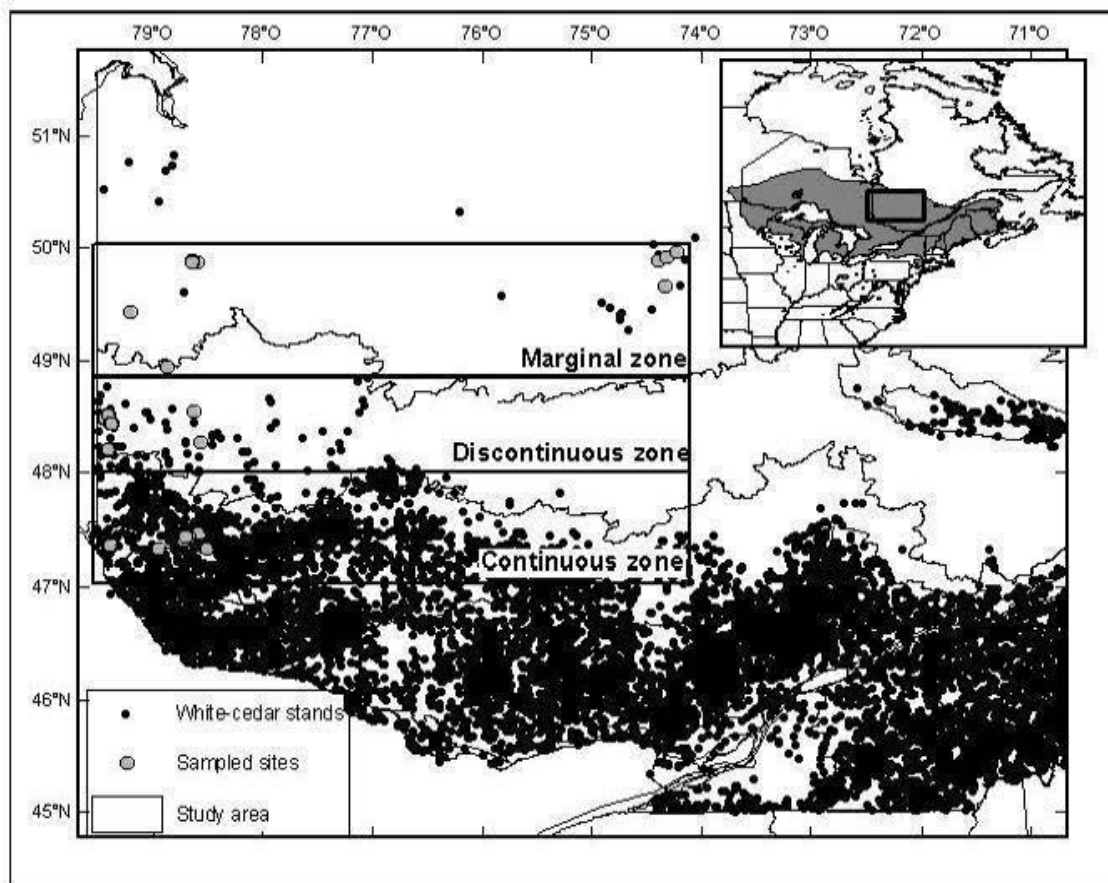
### **1.4.1 Study area**

The study area covers a 300 km long latitudinal gradient in the western part of Québec (47° and 50° N and 74° and 79° W, Fig. 1.1). The climatic gradient was divided in 3 zones based on the abundance of white-cedar stands: continuous, discontinuous, and marginal zones. The zones which appeared to follow the bioclimatic domains for this area, were each ~100 km long along a north-south transect. The continuous zone falls into the balsam fir and yellow birch bioclimatic domain and represents an area where eastern white-cedar is common. The discontinuous zone is in the balsam fir and white birch bioclimatic domain and marks the northern edge of the continuous distribution where white-cedar becomes less common in the forest matrix. The marginal zone is in the black spruce and feather moss bioclimatic domain where only a few isolated stands are found. Mean annual temperatures range from 2.35° C to -0.35° C along the gradient (Table 1.1). Most stands found in the marginal zone were located in poorly drained areas. In order to compare equivalent sites, only poorly drained sites were selected along the gradient. Selected stands were all dominated by white-cedar, at least

constituting 50% of the basal area. Eight stands were selected in the marginal and continuous zone whereas only 6 were sampled in the discontinuous zone.

**Table 1.1** Climatic data for three bioclimatic zones from the last 30 years (Environment Canada, 2011).

<b>Zone</b>	<b>Continuous</b>	<b>Discontinuous</b>	<b>Marginal</b>
Mean temperature (°C)	2.35	0.63	-0.35
Lowest temperature (°C)	-50.5	-48.3	-43.7
Highest temperature (°C)	38.35	35.85	37.2
Number of days with temperature above 0°C	257.65	244.6	184.1
Growing degree-days (above 0°C)	2527.55	2199.8	2074.95
Growing degree-days (above 5°C)	1539.2	1288.6	1202.1
Liquid precipitation (mm)	665.1	665.95	172.25
Snow (mm)	242.7	266.55	933.4
Precipitation during the growing season (mm)	456.9	482.15	638.7



**Figure 1.1** Distribution of eastern white-cedar across North America (insert) (USGS, 2009), Québec (MRNF, 2009). The sampled sites along the 3 abundance zones of the study area are represented.

#### 1.4.2 Data collection

Data were collected in 2007 except for seed counts that were obtained in 2008 and 2009. In every site, quadrats of 400m<sup>2</sup> were delimited. Within the quadrat, every tree larger than 10 cm in DBH was measured. In order to determine the age and growth rates of mature trees, cores were taken from 25 individuals selected randomly at each site, at 1.3 m above ground. Rings were counted to approximate their age. When cores were rotten in part, we used a stencil to complete the core and approximate the age. Cores were however sometimes not even reach and their age were extrapolated using a tree with similar diameter within the same site. The radial growth of the last twenty rings was also measured for each sample to a precision of 0.001 mm using a Velmex measuring system. Radial growth was expressed as an average over the last 20 years. It allows to compare the impact of climate on the overall tree's productivity.

Seed traps were installed at 9 sites, (3 sites in each zone of the gradient) during two consecutive years in 2008 and 2009. Seed traps were 1m X 0.5m in area and 0.3m in depth. At each site, seed traps were installed randomly, four the first summer and four more being added the second year. They were collected during the fall and seeds from each trap were counted. Seeds produced in 2008 were examined using an X-ray scan allowing to determine the number of seeds that were developed. We considered a seed to be developed when it contains more than 50% of seed tissue. Developed seeds were then germinated for a period of 28 days in a controlled greenhouse at 3<sup>o</sup>C in anaerobic condition. Theses two steps were performed at the Centre des semences de Berthier (ministère des Ressources naturelles et de la Faune).

In order to count seedlings, five quadrats were systematically established at each site. Seedlings were divided into 5 age/height classes; 1-one-year seedlings, 2-juveniles: seedlings of 2 to 5 years with juvenile leaves, 3-medium seedlings: 0 to 30 cm in height (other than the previous classes), 4-tall seedlings: 30 to 100 cm in height, and 5-saplings: higher than 1 m but less than 10 cm in DBH. The first two classes were counted in 1 m<sup>2</sup> quadrats. Quadrats



were enlarged to 4m<sup>2</sup> to count medium and tall seedlings. Saplings were counted for the whole site. Seedlings from classes 1 and 2 are always of sexual origin as they bear cotyledons and juvenile leaves, which are easy to recognize in the field. However, individuals included in the 3 other classes are from unknown origin, as it is impossible to determine the origin without digging out the roots.

A transect was established at each site to calculate the layering rate. The first 25 individuals that were touching the transect, excluding age classes 1 and 2, were examined to determine if they were from vegetative or sexual origin. Stems were considered as layers when the root was connected to a parent. Unfortunately, some root connections were difficult to associate to another stem and it was therefore impossible to assess a category for these individuals. A minimum layering rate has been calculated for each site based on the certainty of the layers origin. The estimated layering rate is also presented and includes root systems that were similar to layers, but for which we were not able to determine with certainty if it was connected to a parent stem.

Data for other explanatory variables were also collected during the fieldwork. Percentage cover of decaying wood, mineral soil and understory species, and organic layer depth were measured at every 1m<sup>2</sup> quadrat. Five samples of both mineral soil and organic layer were also collected in every site. When possible, they were collected a few days after precipitations. Soil and organic layer humidity were tested in laboratory. In addition, organic layer and mineral soil samples were sent in a soil laboratory for analyses of C.E.C., phosphorus (P), carbon (C) and nitrogen (N) ratios. Finally, tree density and basal area were also calculated for each site. Climatic data for each site were obtained by interpolation using the software Anusplin which is based on a climatic model (McKenney, et al., 2006). Climatic data were calculated as an average for the last 30 years (Table 1.1).

### 1.4.3 Statistical analysis

Data from radial growth were analyzed with linear mixed models using the average growth from the last 20 years for each sampled tree (Pineiro and Bates, 2000). We determine several candidate models from the available variables which were temperature (zone), diameter at breast height (DBH), tree age, basal area, soil C.E.C., soil C/N ratio, organic layer depth and soil humidity. This analysis did not take into account monthly climatic data but only an average over the last 30 years. Correlated variables were not included in the same models such as temperature and precipitation. Then, the Akaike information criterion (AIC) was performed. This approach allows one to rank the different candidate models and to select the model with the highest goodness of fit (Burnham and Anderson, 2002). From the ranking, we performed multimodel inference when required ( $\Delta AIC < 4$ ). The inference analysis measures the weight of each variable for each candidate models and calculate an estimate to determine its effect on the response variable.

Linear mixed models were performed to analyze the number of seedlings under 100 cm in height. (Annexe 1.2-1.5). Saplings were tested using simple linear regression models as there was only one datum per site (Annexe 1.6). AIC analyses were performed for seedlings and saplings. The candidate models for seedling included temperature (zone), tree age, stand density, humus C.E.C., humus C/N ratio, percentage cover of mineral soil, percentage cover of decaying logs, organic layer depth, humus humidity and drainage. Candidate models for sapling included less variables which were temperature, organic layer depth, soil CEC, soil C/N and percentage cover of understory species.

Seed crop, percentage of filled seeds, and percentage of germinated seeds were all analyzed with a linear mixed model that used the bioclimatic zones along the gradient as the only explicative variable because of the low number of replicates. No statistics were done for layering since the rates are only approximated.

Every time we performed a linear mixed model analysis, site identity was the random factor. Correlated parameters were removed from the analysis or were not included in the same models. Data were log transformed if necessary in order to fulfilled all the assumptions. All analyses were performed using the software R (version 2.10.1, 2010).

## 1.5 Results

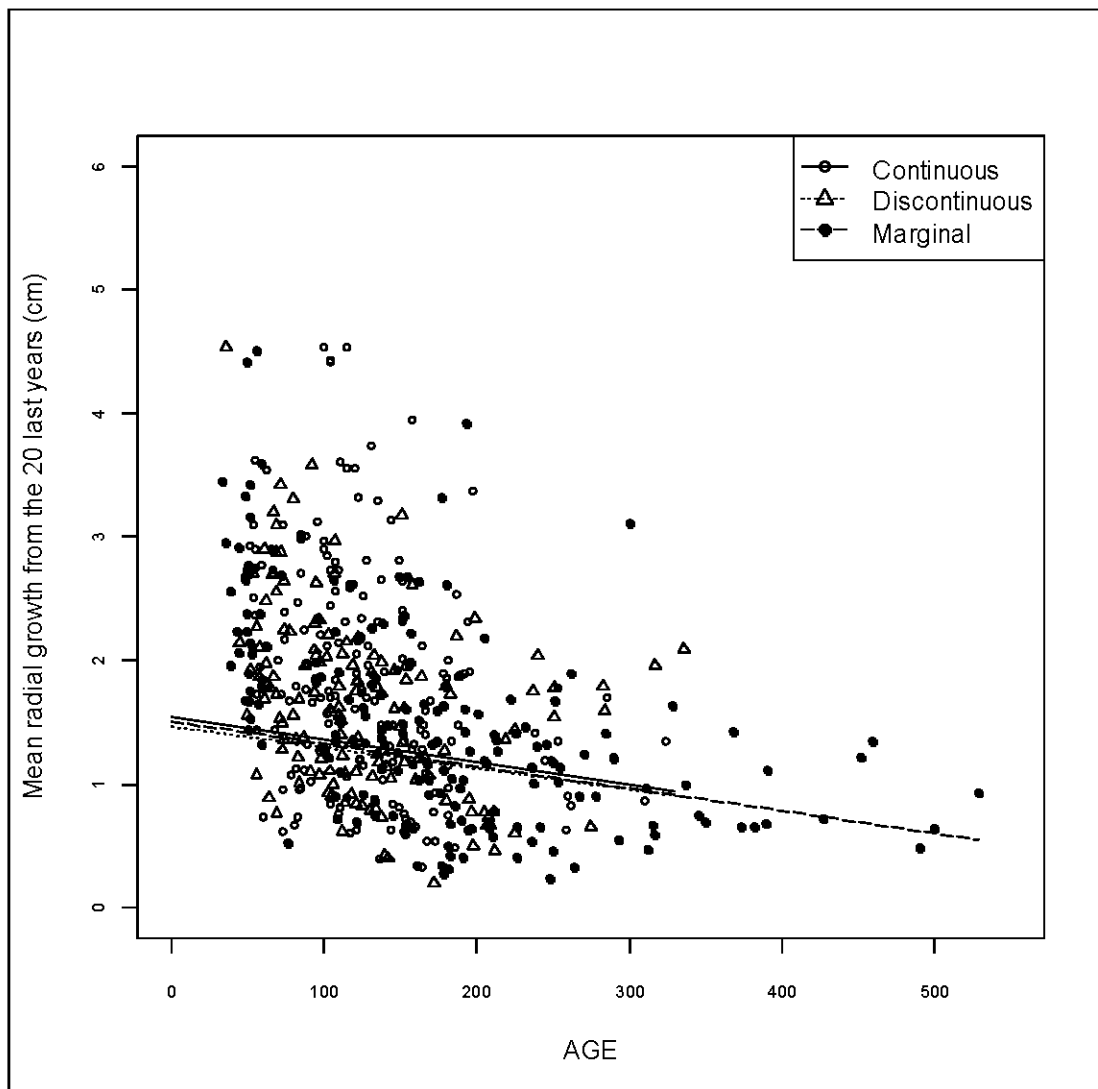
### 1.5.1 Radial growth

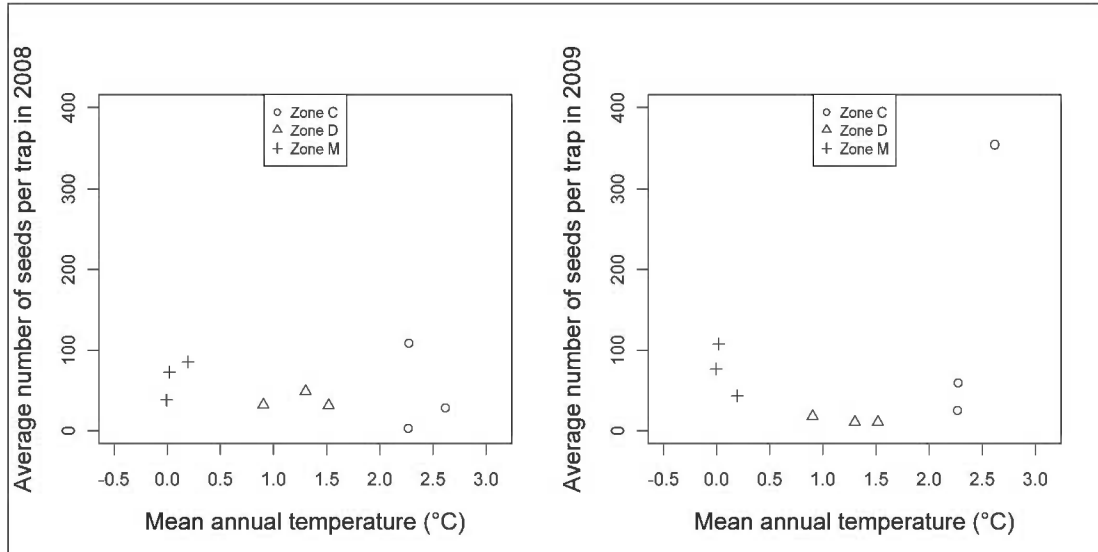
The AIC analysis revealed that more than one model had a  $\Delta$  AICc lower than 4 and therefore multimodel inference was used to evaluate the effect of the different variables the the radial growth (Appendix 1.1). Only DBH and age of tree were found to explain radial growth variation. Tree ring width was found decreasing with increasing tree age (Fig.1.2). However, tree ring width did not appear to be influence by temperature (Table 1.3).

### 1.5.2 Seed production

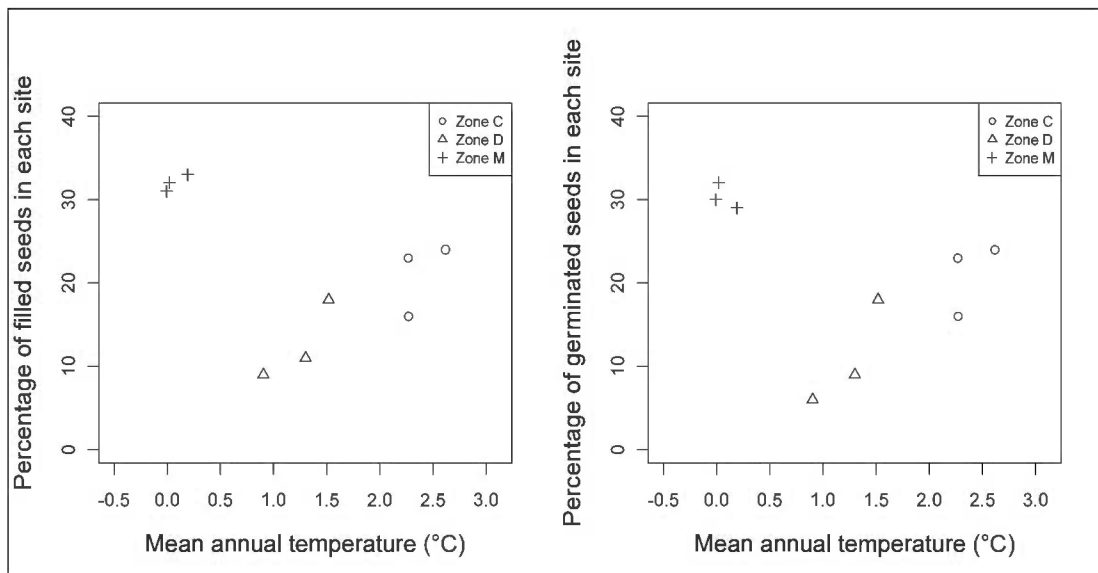
Seed crop was not found to be influenced by temperature during the two consecutive growth seasons studied (Fig. 1.3). Seed crop varied form 37 to 65 seed per trap in 2008. In 2009, more variation in seed crop was found along the gradient, ranging for 13 to 146 seeds per trap. In average, 12% to 28% of the seeds were filled and most of them germinated in the greenhouse. The percentage of both filled and germinated seed was found to be higher in the marginal zone compared to the discontinuous zone. No difference was found with the continuous zone (Fig. 1.4).

Figure 1.2 Relation between radial growth of the last 20 years and tree age at each site. Mean radial growth is illustrated separately for the three climatic zones.





**Figure 1.3** Average number of seeds per trap collected in each bioclimatic zone for 2008 and 2009. Temperatures are an average over 30 years for each site.



**Figure 1.4** Percentage of filled seeds and germinated seeds for each bioclimatic zone in 2008. Temperatures are an average over 30 years for each site.

### 1.5.3 Seedlings

Many models relating to one-year seedlings were found to have a  $\Delta$  AICc lower than 4 and therefore multimodel inference was used to evaluate the effect of the different variables (Appendix 1.2). One-year seedlings were found to be significantly less abundant in the northern sites than in the continuous and discontinuous zones (Table 1.2). Their presence was also positively associated to the abundance of mineral soil in the quadrat (Table 1.3). Many models were also found to have  $\Delta$  AICc lower than 4 while testing the abundance of juvenile seedlings. The multimodel inference revealed that juvenile seedlings were only significantly more abundant in the discontinuous zone in comparison to the marginal zone. Abundance of juvenile seedlings in the continuous zone was not found to be significantly different from the marginal zone (Table 1.2). Percentage of decayed woody debris was also found to positively influence the abundance of juvenile seedlings (Table 1.3).

Multimodel inference was also required to analyze the abundance of medium seedlings (Appendix 1.4). Medium seedlings were found to be only affected by latitude (Table 1.3). They were less abundant in the marginal sites than in the more southerly sites along the gradient (Table 1.2). The multimodel inference showed that there was no significant difference among the zones for tall seedlings and that no other variables were found to influence their abundance (Table 1.3). In addition, the multimodel inference, performed on saplings abundance, indicated a difference in the number of saplings between the zones. Indeed, there significantly more sapling in the northernmost sites than in the south (Table 1.3). Their presence was not associated to another variable. In regards to vegetative propagation, most zones had a minimal layering rate higher than 50% for all height classes (Table 1.4). If we consider only the estimated layering rate, this percentage rose as high as 85% for stems higher than 30 cm.

**Table 1.3** Parameter estimates and confidence interval for the multimodel inference on radial growth and seedling abundance. Reference level for the zone is the marginal zone. The values in bold print are statistically significant (the confidence intervals do not include 0).

	Parameters	Estimate	Unconditional standard error	Lower 95% CL*	Upper 95% CL*
Radial growth	Temperature	0.01	0.02	-0.04	0.05
	<b>Age</b>	<b>-0.0031</b>	<b>0.001</b>	<b>-0.0035</b>	<b>-0.0027</b>
	<b>DBH</b>	<b>0.02</b>	<b>0</b>	<b>0.01</b>	<b>0.02</b>
One-year seedlings	<b>Continuous zone</b>	<b>1.64</b>	<b>0.47</b>	<b>0.72</b>	<b>2.56</b>
	<b>Discontinuous zone</b>	<b>1.43</b>	<b>0.52</b>	<b>0.4</b>	<b>2.45</b>
	Organic layer CEC	0	0.01	-0.02	0.02
	Organic layer C/N ratio	-0.04	0.05	-0.14	0.06
	Percentage cover of woody debris	0.02	0.01	0	0.04
	<b>Percentage cover of mineral soil</b>	<b>0.07</b>	<b>0.02</b>	<b>0.02</b>	<b>0.11</b>
	Humus humidity	-0.02	0.02	-0.05	0.02
	Moderate drainage	-0.89	0.55	-1.96	0.18
Juvenile seedlings	Continuous zone	0.67	0.35	-0.02	1.36
	<b>Discontinuous zone</b>	<b>0.84</b>	<b>0.39</b>	<b>0.07</b>	<b>1.61</b>
	Organic layer CEC	-0.01	0.01	-0.02	0
	Organic layer C/N ratio	-0.05	0.04	-0.12	0.02
	<b>Percentage cover of woody debris</b>	<b>0.02</b>	<b>0.01</b>	<b>0.01</b>	<b>0.04</b>
	Percentage cover of mineral soil	0.01	0.02	-0.03	0.05
	Humus humidity	0.02	0.01	0	0.05
	Moderate drainage	-0.2	0.39	-0.98	0.57
Medium seedling	<b>Continuous zone</b>	<b>0.51</b>	<b>0.2</b>	<b>0.12</b>	<b>0.89</b>
	<b>Discontinuous zone</b>	<b>0.61</b>	<b>0.22</b>	<b>0.19</b>	<b>1.03</b>
	Organic layer CEC	0	0	0	0.01
	Organic layer C/N ratio	0.01	0.02	-0.03	0.05
	Percentage cover of woody debris	0.01	0.01	-0.01	0.02
	Percentage cover of mineral soil	0	0.02	-0.04	0.03
	Humus humidity	0	0.01	-0.01	0.01
	Moderate drainage	0.07	0.22	-0.36	0.5
Tall seedlings	Continuous zone	0.02	0.31	-0.58	0.62
	Discontinuous zone	0.19	0.31	-0.47	0.84
	Organic layer CEC	0	0.01	-0.02	0.01
	Organic layer C/N ratio	0.02	0.03	-0.04	0.08
	Percentage cover of woody debris	0	0.01	-0.02	0.01
	Humus humidity	-0.01	0.01	-0.03	0.02
	Moderate drainage	0.04	0.37	-0.68	0.77
	<b>Continuous zone</b>	<b>-0.36</b>	<b>0.17</b>	<b>-0.68</b>	<b>-0.03</b>
Saplings	Discontinuous zone	-0.05	0.18	-0.4	0.29
	Soil CEC	0	0	-0.01	0
	Soil C/N ratio	0	0	-0.01	0
	Cover of understory species	0	0	0	0

\*CL: confidence level

**Table 1.4** Rate of branch layering for stems of three different height classes along the latitudinal gradient.

Layering	Height classes	Continuous	Discontinuous	Marginal
Minimum rate of layering	0-30 cm	64 %	36 %	75 %
	30-100 cm	67 %	67 %	64 %
	> 100 cm	67 %	42 %	55 %
Estimated rate of layering	0-30 cm	80 %	57 %	87 %
	30-100 cm	96 %	96 %	96 %
	> 100 cm	97 %	88 %	95 %

## 1.6 Discussion

### 1.6.1 Radial growth

Contrary to our hypothesis, white-cedar's radial growth was not influenced by annual temperature along the latitudinal gradient. The difference of more than 2°C in annual temperature and more than 300 growing degree days (>5°C) (Table 1.1) between the extremities of the gradient does not seem to significantly influence the radial growth of white-cedar. The absence of effect of latitude on radial growth matches dendrochronological studies made in the same portion of its range. They have showed that white-cedar's growth is negatively correlated to temperature in summer for the same portion of its range. Indeed, warm temperatures and drought during summer can limit radial growth (Archambault and Bergeron, 1992, Tardif and Bergeron, 1997, Tardif and Stevenson, 2001). White-cedar might be able to take advantage of cooler summer temperatures in the north overriding the impact of a shorter growing season. This would explain the absence of difference in growth along the gradient. Tardif and Stevenson (2001) also measured a similar radial growth pattern for white-cedar at the northern range of its distribution in comparison to other parts of its range. Absence of a direct temperature effect could also be associated to the high resistance of white-cedar to cold. This species can survive temperatures as low as -80°C (Sakai, 1970, 1973). Other tree species also have the ability to survive under harsh conditions. A study on



Jack pine (*Pinus banksiana* Lamb.) transplanted 300 km above its northern distribution limit found that axial growth was not restricted by the low number of growing degree-days (Asselin, et al., 2003). Another study, conducted on yellow birch (*Betula alleghaniensis* Britt.) in western Québec, also revealed a weak effect of climate on its radial growth at the edge of its distribution (Guitard, M.-A., unpublished data). White-cedar has been showed to exhibit high plasticity under a wide range of site conditions (Musselman, et al., 1975, Collier and Boyer, 1989). This particular trait could explain why this species can survive and maintain populations in diverse, and sometimes harsh, environments.

### 1.6.2 Recruitment

Seed production was not found to be correlated with climate. Divergent results from our hypothesis could be explained by the cyclical production of seeds. Seeds were only collected for two consecutive years and white-cedar experiences mast years every 2 to 5 years (Johnston, 1990). The previous mast year for white-cedar occurs in 2006. Differences along a climatic gradient might only be perceived during mast years, where only sites in a milder climate would produce an exceptional quantity of seeds. The low number of traps that were collected only during fall could have also biased our results since other seeds could have fallen later in winter. However, our results still confirm that there is sexual regeneration at the northern sites. Contrary to some other studies, flower and seed production at the northern edge of white-cedar's distribution do not seem to be affected by colder spring temperatures during pollination and by a fewer number of growing degree-days (Pigott and Huntley, 1981, Sirois, 2000, Tremblay, et al., 2002, Asselin, et al., 2003). It appears that seeds are correctly developed even at the northern edge of distribution and are able to germinate in ideal conditions.

Seed crop cannot be invoked as a limiting factor in the distribution of white-cedar. Instead, it is possible that the lower abundance of seedlings of sexual origin in the marginal zone could be attributed to failure in the germination process due to the climate or the germination substrate. In this study, decaying woody debris were observed to be essential substrate for

been suggested as one of the main factors limiting white-cedar distribution to its present range (Heinselman, 1973, Ali, et al., 2008). Indeed, eastern white-cedar is poorly resistant to fire. At its northern limit of distribution, in an area where fires are more frequent and severe, white-cedar is limited to shorelines where it is less likely to be burned (Bergeron, et al., 2004, Denneler, et al., 2008). Therefore, we hypothesises that recurrent fires eliminate seed source and prevent white-cedar to colonize new sites (Asselin, et al., 2001). Combined effects of both fire and harsh climate could therefore be responsible for the decreasing number of stands in marginal and discontinuous areas, and thus for the present northern distribution of white-cedar.

### **1.7 Conclusion**

The intergovernmental panel on climate change predicts modification in the distribution of many species in response to global warming (IPCC 2007). Many scenarios are possible for white-cedar distribution. Some climatic models demonstrate that white-cedar range will have a northward expansion, but they differ in degree of reaction (Environment Canada 2011). Results of our study and paleoecological studies allow us to predict some possible changes in white-cedar's natural range. Seedling abundance and survival could be improved with a more favorable climate at the marginal sites. This could allow the isolated populations to disperse and colonize the surrounding habitats. On the other hand, the effects of climate could be dissipated by the survival rate of seedlings, which was found to be very low along the gradient. White-cedar seeds also seems to be limited in their capacity to disperse, which was evaluated at a maximum of 20m (Cornett, et al., 1997, Asselin, et al., 2001). The low reproductive success could increase the reaction time in response to climate change. Other limiting variables, such as effects of fire and habitat availability (Bergeron and Gagnon, 1987, Diotte and Bergeron, 1989, Richardson and Bond, 1991, Meilleur, et al., 1997, Flannigan and Bergeron, 1998, Bergeron, et al., 2010, Lafleur, et al., 2010), should be analyzed before predicting a possible effect of climate change on white-cedar distribution or on other boreal species. In particular, the influence of climate on the fire regime should be looked at more closely to better model the effect of climate change on the distribution of

boreal species (Suffling, 1995, Asselin, et al., 2003). The impact of climate change on migration pattern might not be as linear as climate-based model supposed.

## **1.8 Acknowledgements**

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## 1.9 Appendix

**Appendix 1.1** AICc candidate models for radial growth. Many models were found to explain the relation ( $\Delta \text{AICc} < 4$ ) and therefore a multimodel inference was performed.

Candidate models	K <sup>1</sup>	AICc <sup>2</sup>	$\Delta \text{AICc}^3$	AICc Wt <sup>4</sup>	Cum Wt
Radial growth ~ DBH + Age	5	-13.02	0	0.76	0.76
Radial growth ~ Temperature + DBH + Age	6	-9.24	3.77	0.11	0.87
Radial growth ~ DBH + Age + Basal area	6	-9.22	3.79	0.11	0.99
Radial growth ~ Temperature + DBH + Age + Basal area	7	-4.89	8.13	0.01	1
Radial growth ~ Temperature + DBH + Age + Basal area + Soil C/N + Soil CEC + Organic layer thickness + Drainage	12	26.94	39.96	0	1
Radial growth ~ Temperature	4	154.02	167.04	0	1
Radial growth ~ Soil C/N + Soil CEC + Organic layer thickness + Drainage	8	167.53	180.54	0	1
Radial growth ~ Temperature + Soil C/N + Soil CEC + Organic layer thickness + Drainage	9	170.62	183.64	0	1

<sup>1</sup> : Number of parameters, <sup>2</sup> : AIC coefficient, <sup>3</sup> : AIC relative to the best model

<sup>4</sup> : AIC model weight [for more details see (Burnham and Anderson, 2002)]

**Appendix 1.2** AICc candidate models for one-year seedlings. Many models were found to explain the relation ( $\Delta$  AICc < 4) and therefore a multimodel inference was performed.

Candidate models	K	AICc	$\Delta$ AICc	AICcWt	Cum Wt
One-year seedlings~ Temperature + Mineral soil + Woody debris	7	364.63	0.00	0.48	0.48
One-year seedlings ~ Temperature + Mineral soil	6	365.01	0.37	0.40	0.88
One-year seedlings~ Mineral soil + Woody debris	5	367.23	2.60	0.12	0.89
One-year seedlings ~ Temperature	5	367.35	2.71	0.11	1.00
One-year seedlings ~ Temperature + Humus C/N + Humus CEC + Organic matter + Humus humidity + Drainage	10	388.76	24.12	0.00	1.00
One-year seedlings ~ Mineral soil + Woody debris+ Humus C/N + Humus CEC + Organic matter + Humus humidity + Drainage	11	389.72	25.08	0.00	1.00
One-year seedlings ~ Temperature + Mineral soil + Woody debris+ Humus C/N + Humus CEC + Organic matter + Humus humidity + Drainage	13	389.12	33.49	0.00	1.00

<sup>1</sup> : Number of parameters, <sup>2</sup> : AIC coefficient, <sup>3</sup> : AIC relative to the best model

<sup>4</sup> : AIC model weight [for more details (Burnham and Anderson, 2002)]

**Appendix 1.3** AICc candidate models for juvenile seedlings. Many models were found to explain the relation ( $\Delta \text{AICc} < 4$ ) and therefore a multimodel inference was performed.

Candidate models	K	AICc	$\Delta \text{AICc}$	AICcWt	Cum Wt
Juvenile seedlings ~ Mineral soil + Woody debris	5	322.41	0.00	0.50	0.50
Juvenile seedlings ~ Temperature	5	323.15	0.74	0.35	0.85
Juvenile seedlings ~ Temperature + Mineral soil + Woody debris	7	325.68	3.27	0.10	0.95
Juvenile seedlings ~ Temperature + Mineral soil	6	327.00	4.59	0.05	1.00
Juvenile seedlings ~ Temperature + Humus C/N + Humus CEC + Organic matter + Humus humidity	9	340.13	17.72	0.00	1.00
Juvenile seedlings ~ Mineral soil + Woody debris + Humus C/N + Humus CEC + Organic matter + Humus humidity + Drainage	10	342.43	20.02	0.00	1.00
Juvenile seedlings ~ Temperature + Mineral soil + Woody debris + Humus C/N + Humus CEC + Organic matter + Humus humidity + Drainage	12	357.98	35.57	0.00	1.00

<sup>1</sup>: Number of parameters, <sup>2</sup>: AIC coefficient, <sup>3</sup>: AIC relative to the best model

<sup>4</sup>: AIC model weight [for more details see (Burnham and Anderson, 2002)]

**Appendix 1.4** AICc candidate models for medium seedlings. Many models were found to explain the relation ( $\Delta \text{AICc} < 4$ ) and therefore a multimodel inference was performed.

Candidate models	K	AICc	$\Delta \text{AICc}$	AICcWt	Cum Wt
Medium seedlings ~ Temperature	5	272.59	0.00	0.83	0.83
Medium seedlings ~ Temperature + Mineral soil	6	276.31	3.72	0.13	0.96
Medium seedlings ~ Mineral soil + Woody debris	5	279.62	7.03	0.02	0.98
Medium seedlings ~ Temperature + Mineral soil + Woody debris	7	280.42	7.83	0.02	1.00
Medium seedlings ~ Temperature + Humus C/N + Humus CEC + Organic matter + Humus humidity	9	286.31	13.72	0.00	1.00
Medium seedlings ~ Mineral soil + Woody debris + Humus C/N + Humus CEC + Organic matter + Humus Humidity + Drainage	10	300.87	28.28	0.00	1.00
Medium seedlings ~ Temperature + Mineral soil + Woody debris + Humus C/N + Humus CEC + Organic matter + Humus humidity + Drainage	12	310.59	38.00	0.00	1.00

<sup>1</sup> : Number of parameters, <sup>2</sup> : AIC coefficient, <sup>3</sup> : AIC relative to the best model

<sup>4</sup> : AIC model weight [for more details see (Burnham and Anderson, 2002) ]

**Appendix 1.5** AICc candidate models for tall seedlings. Many models were found to explain the relation ( $\Delta \text{AICc} < 4$ ) and therefore a multimodel inference was performed.

Candidate models	K	AICc	$\Delta \text{AICc}$	AICcWt	Cum Wt
Tall seedlings ~ Organic matter	4	276.75	0.00	0.80	0.80
Tall seedlings ~ Temperature	5	280.09	3.34	0.15	0.95
Tall seedlings ~ Temperature + Organic matter	6	283.54	6.79	0.03	0.98
Tall seedlings ~ Temperature + Woody debris	6	283.91	7.15	0.02	1.00
Tall seedlings ~ Temperature + Humus C/N + Humus CEC + Organic matter + Humus humidity	9	296.78	20.03	0.00	1.00
Tall seedlings ~ Woody debris + Humus C/N + Humus CEC + Organic matter + Humus humidity + Drainage	9	298.75	22.00	0.00	1.00
Tall seedlings ~ Temperature + Woody debris + Humus C/N + Humus CEC + Organic matter + Humus humidity + Drainage	11	312.12	35.37	0.00	1.00

<sup>1</sup>: Number of parameters, <sup>2</sup>: AIC coefficient, <sup>3</sup>: AIC relative to the best model

<sup>4</sup>: AIC model weight [for more details see (Burnham and Anderson, 2002)]



**Appendix 1.6** AICc candidate models for saplings. Many models were found to explain the relation ( $\Delta \text{AICc} < 4$ ) and therefore a multimodel inference was performed.

Candidate models	K	AICc	$\Delta \text{AICc}$	AICcWt	Cum Wt
Saplings ~ Temperature	4	20.05	0	0.68	0.68
Sapling ~ Temperature + Organic layer	5	23.16	3.11	0.14	0.82
Temperature + Cover of understory species	5	23.45	3.4	0.12	0.95
Temperature + Soil CEC +Soil C/N	6	26.05	6	0.03	0.98
Temperature + Soil CEC +Soil C/N + Cover of understory species	7	28.16	8.11	0.01	0.99
Soil CEC +Soil C/N + Cover of understory species	6	29.77	9.72	0.01	1
Temperature + Soil CEC +Soil C/N + Cover of understory species + Organic layer	8	33.00	12.95	0	1

<sup>1</sup> : Number of parameters, <sup>2</sup> : AIC coefficient, <sup>3</sup> : AIC relative to the best model

<sup>4</sup> : AIC model weight [for more details see (Burnham and Anderson, 2002) ]

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## CHAPITRE II

### INFLUENCE OF FIRE AND SITE CONDITIONS ON THE NORTHERN RANGE OF EASTERN WHITE-CEDAR (*THUJA OCCIDENTALIS* L.)

**Véronique Paul, Yves Bergeron et Francine Tremblay**

## 2.1 Résumé

Le feu et les conditions édaphiques peuvent constituer des facteurs limitant importants dans la limite nordique de répartition d'une espèce. Le thuya de l'Est (*Thuja occidentalis* L.) n'est que partiellement limité par le climat à la limite de son aire de répartition supposant l'effet d'autres facteurs. La présente étude analyse l'effet des conditions édaphiques et du feu sur la présence du thuya de l'Est le long d'un gradient latitudinal de 300 km établi selon l'abondance de thuya dans le nord-ouest du Québec, Canada (46-50° N and 74°- 79° W). Des placettes d'échantillonnage provenant du ministère des Ressources naturelles et de la Faune ont été utilisées afin de déterminer l'utilisation de sites par le thuya. Une régression logistique basée sur l'absence et la présence de thuya a permis de distinguer les facteurs influençant l'établissement du thuya et de déterminer le taux d'occupation des sites adéquats à différentes latitudes. D'autre part, des peuplements de thuya ont été échantillonnés le long du gradient afin de tester l'effet des feux. Une comparaison du temps approximatif depuis le dernier feu entre des peuplements de thuya et des peuplements adjacents a permis de déterminer si les peuplements situés au nord se trouvent dans des endroits protégés des feux, suggérant une influence de cette perturbation. Les résultats démontrent que le thuya de l'Est ne semble pas limité par les conditions de sites trouvées au nord de sa répartition. En effet, le thuya ne peut occuper la plupart des sites adéquats au nord de sa répartition suggérant qu'un autre facteur empêche le thuya d'utiliser tous les sites disponibles. D'autre part, l'âge maximal des peuplements de thuya est significativement plus élevé que celui des peuplements adjacents. La différence est aussi plus marquée avec la latitude. Ce résultat suggère que les peuplements plus nordiques de thuya sont possiblement situés dans des endroits protégés des feux. Ainsi, le feu, en association avec le climat, semble limiter l'expansion de l'aire de répartition du thuya de l'Est. Le climat diminue la régénération sexuée tandis que le feu élimine les arbres semenciers ainsi que les peuplements nouvellement établis dans des sites à haut risque de feu, résultant à la répartition sporadique actuelle du thuya.

## 2.2 Abstract

Fire and edaphic conditions might be important factors explaining a species distribution. White-cedar (*Thuja occidentalis* L.) has been found to be only partially limited by climate and other factors seemed to interact in the northern distribution limit. Therefore, this study aims to determine the influence of fire and site conditions on the presence of eastern white-cedar along a 300 km latitudinal transect following a gradient of white-cedar stands abundance in north-western Québec, Canada (46-50° N and 74°- 79° W). Sample plots from the ministère des Ressources naturelles et de la Faune were used in order to determine conditions for thuya's establishment. A logistic regression based on absence/presence of cedar allowed to distinguish factors influencing its establishment and to determine the occupation rate of suitable sites at different latitudes. Moreover, eastern white-cedar stands were sampled across the gradient in order to analyze the impact of fire. A comparison between age of white-cedar stands and their surrounding stands, considered as the minimum time since last fire, allowed to determine if white-cedar northern stands are located in fire breaks areas, suggesting an influence of this disturbance. The results suggest that white-cedar doesn't appear to be limited by site conditions at its northern distribution. Indeed, white-cedar was found unable to occupy most suitable sites, suggesting that other factors prevent white-cedar to colonize more stands northward. On the other hand, white-cedar has been found older than surrounding stands all along the gradient but the difference was more pronounced in the northern stands. This suggests that the remaining white-cedar stands in the north might be found in areas protected from fires. Therefore, fires, in association with climate, seem to limit the expansion of white-cedar's northern range. Climate diminishes sexual regeneration while fire eliminates seed sources and newly dispersed stands established in high fire risk's zone, leading to its scarce present distribution.



### 2.3 Introduction

Tree species distribution can be limited by different factors such as climate, fire or site conditions depending on species traits (Woodward, 1987, Richardson and Bond, 1991, Prentice, et al., 1992). In western Québec, eastern white-cedar (*Thuja occidentalis* L.) reaches its northernmost limit of distribution around the 51<sup>th</sup> parallel where only few isolated populations are found. South of this limit, a drastic abundance's decrease of white-cedar populations is encountered around the 48<sup>th</sup> parallel. Chapter 1 demonstrated that white-cedar's distribution is not in equilibrium with climate at its limit of distribution. The radial growth was found to be similar along a 300 km latitudinal gradient. Furthermore, recruitment of white-cedar was found to be lower in outlier populations but was still sufficient to maintain locally the populations. In addition, no difference in recruitment and growth was observed between the continuous and the discontinuous distributions, where the abundance of white-cedar stands is remarkably decreasing. White-cedar distribution can't be explained by climatic factors only and therefore other factors seem to be involved in the process to explain the limitation of its distribution.

In north-western Québec, fire is the main disturbance of the balsam fir (*Abies balsamea* L.)-white birch (*Betula papyrifera* Marsh.) and black spruce (*Picea mariana* (Mills. (BSP)))-feathermoss forests. Fires increase in frequency, severity and size from southern bioclimatic domains (46<sup>th</sup> parallel) to northern domains (50<sup>th</sup> parallel) (Payette, et al., 1989, Bergeron, et al., 2004, Bergeron, et al., 2006). Some studies demonstrated the effect of fire on distribution limits (Flannigan, 1993, Asselin, et al., 2003). In order to establish in fire-susceptible areas, species must be either dependant on fire or adapted to or on the other hand, restricted to areas where fire events are of low severity or less frequent. Indeed, some species, like jack pine (*Pinus banksiana* Lamb.), require fire for their regeneration and their distribution follows corridors where fire is more frequent (Asselin, et al., 2003, Parisien and Sirois, 2003). On the other hand, species that are ill-adapted to fire might be restricted in their distribution without having attained their bioclimatic limit (Flannigan, 1993). Without this disturbance, they would probably have established populations in northern locations. Red pine (*Pinus resinosa*

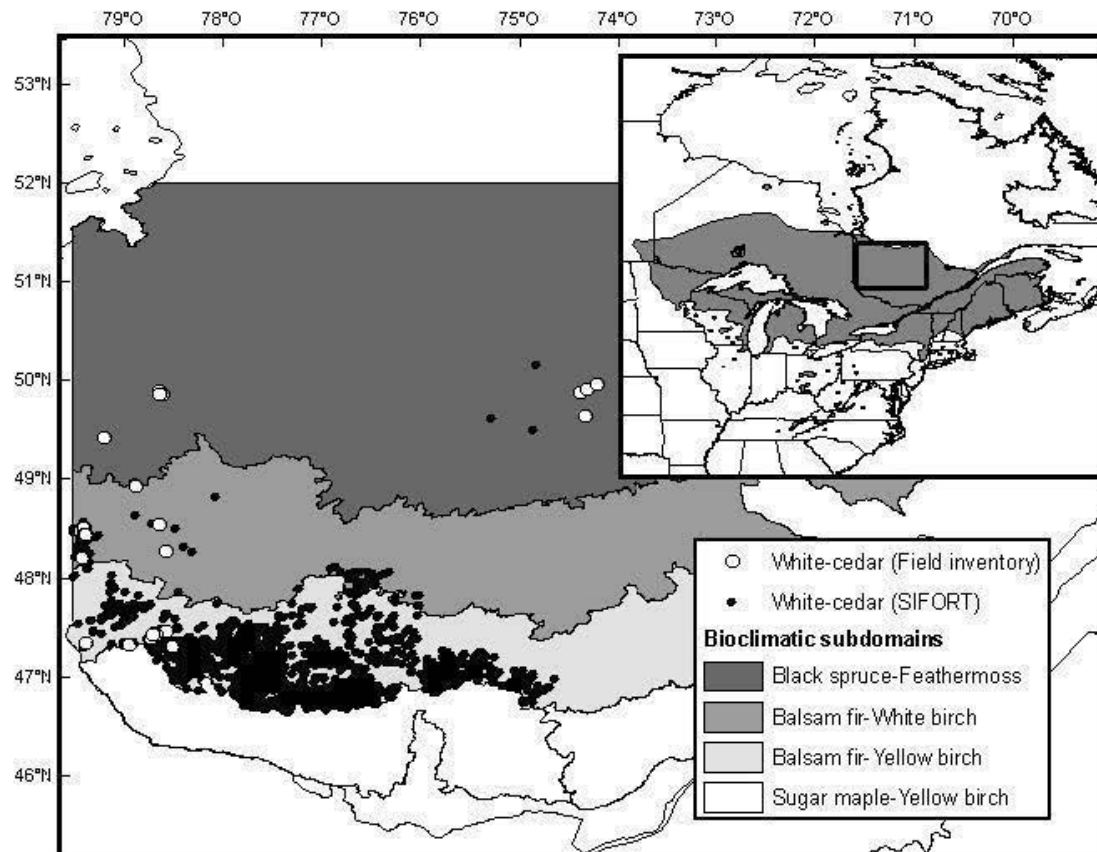
(Lalonde, 1991, Lloyd, et al., 2007, Messaoud, et al., 2007). At the limit of the continuous distribution of white-cedar (ca. 48° parallel), a large clay deposit is encountered and hills become less abundant. Clay deposit is replaced northward by organic soil with low decomposition rate and paludificated soil (Simard, et al., 2007).

This study proposes to analyse the effect of edaphic conditions and fire on eastern white-cedar distribution. In the first place, the availability of suitable habitats along a latitudinal gradient was tested as well as the capacity of white-cedar to saturate the available sites. Secondly, the effect of fire frequency was analysed to determine if this could restrict white-cedar to its present limit. It was hypothesized that white-cedar stands found at the limit of its distribution would be located in areas protected from fires.

## 2.4 Materials and Methods

### 2.4.1 Study area

This study took place in the north-western part of Québec between 46° and 50° N and 74° and 79° W (Fig. 2.1). It encompassed 4 forest subdomains, from abundant white-cedar stands in the south to outlier stands in the north. The southern part of the gradient is located in the western sugar maple (*Acer saccharum* Marsh.) - yellow birch (*Betula alleghaniensis* Britt.) (Sm-Yb) bioclimatic subdomain and this is the subdomain where white-cedar is the most common. The gradient goes across the western balsam fir-yellow birch (Bf-Yb) subdomain where white-cedar is still common. Within the western balsam fir-white birch (Bf-Wb) subdomain, white-cedar becomes rarer. Then, in the western black spruce-feathermoss (Bs-Fm) subdomain, white-cedar is scarce and uncommon. Some stands are also found above the 51th parallel but were difficult to reach and were not sampled. In addition, the historical burn rate increases with latitude along the gradient (Table 2.1).



**Figure 2.1** Distribution of sampled white-cedar stands from the field inventory and from the database (MRNF, 2009). The smaller figure also presents white-cedar's distribution in eastern North America (USGS, 2009).

**Table 2.1** Fire historical burn rate for each bioclimatic subdomain.

[Adapted from Bergeron *et al.* (2006)]

Bioclimatic subdomains	Historical burn rate (%)
Western Sugar maple-Yellow birch	0.319
Western Balsam fir-Yellow birch	0.4215
Western Balsam fir-White birch	0.6345
Western Black spruce-Feathermoss	0.6545

#### 2.4.2 Sampling design and statistical analysis: effect of site conditions

To test for the effects of edaphic factors, three types of inventory database were pooled in the analysis to have a representative dataset, which were permanent, temporary and ecological sample plots obtained from the ministère des Ressources naturelles et de la Faune du Québec (MRNF). The database totalized more than 56 000 sampled stands for the study area but stands with white-cedar presence accounted less than 10%. In order to perform a logistic regression, the ratio must be higher than 10% (Hosmer and Lemeshow, 2000). Therefore, we subsampled the database to select randomly the same number of stands without white-cedar than with cedar. We reached a total of 5476 sample plots. Moreover, in order to test the predictive capacity of our model, we subdivided the database in 3. We separate the northern plots (Bf-Wb and Bs-Fm) from the south (Sm-Yb and Bf-Yb) and we also divided randomly the southern plots in two distinct datasets. The analysis was first performed on one dataset from the southern areas. The analysis contrasted stands with presence of white-cedars to stands without cedars. Based on a logistic regression, an Akaike information criterion (AIC) was used to first select the model with the highest goodness of fit (Burnham and Anderson, 2002).

The candidate models included texture of B horizon, deposit type, drainage, organic layer thickness, type of organic horizon (humus), slope inclination, position on the slope and aspect (Table 2.4). This allowed determining which site conditions could explain white-cedar occurrence in the south where it is common. All suppositions of logistic regression were fulfilled (Student's residuals, Cook's distance, Hosmer and Lemeshow test (Hosmer and Lemeshow, 2000)). Then, we applied our first model on the two other datasets to test its predictive capacity. The predictive capacity is based on the percentage of accurate predictions from the model.

From the two datasets, we compared the results of site occupation along the gradient. For each of the four bioclimatic subdomains, we compared the proportion of occupation of white-cedar with the expected occupancy for each variable. These data allowed to measure the

saturation rate (Observed/Predicted X 100). This ratio allows to compare the development of white-cedar stands on suitable sites at different latitudes. A value higher than 100% means that white-cedar established on all available suitable sites but also on less suitable sites whereas a small ratio means that white-cedar is unable to establish in all suitable sites.

#### 2.4.3 Sampling design and statistical analysis: effect of fire

To analyze the effect of fire, white-cedar stands were selected in the field along a latitudinal gradient encompassing 3 bioclimatic subdomains from Bf-Yb to Bs-Fm. The study area is approximately 300 km long in latitude (Fig. 2.1). Eight stands were chosen within each subdomain except for the Bf-Yb subdomain where 9 stands were sampled. Stands were about 400m<sup>2</sup> and were always dominated by white-cedar. Within each stand, the 4 biggest trees were cored. We also selected the 4 stands that were the closest stands without white-cedar surrounding the sampled sites. Trees were cored using a Pressler borer and then aged in laboratory. When cores were rotten in part, we used a stencil to complete the core and approximate the age. Cores were however sometimes not even reach and their age were extrapolated using a tree with similar diameter from the same site. These data allowed us to compare the approximate time since last fire for the white-cedar stands and for the adjacent stands surrounding cedars. Thus, if white-cedars are in fire-skipped areas, maximum age of cedar should be higher than for the adjacent populations. A second analysis was performed using SIFORT database from the MRNF. SIFORT database provides forest inventory data with tessel as a unit. The dimensions of a tessel are 15 seconds longitude and 15 seconds latitude for a mean area of 14 ha. Forest inventory are made by photointerpretation and the maximum age provided is 120 years. Forest inventory is made every 10 years. However, the latest inventory are more accurate but will contain a lot of stands in regeneration because of clearcuts. Therefore, we used the latest forest inventory to select all the white-cedar stands. We used the older version of the forest inventory to select all the closest adjacent stands (maximum 500m). This allowed to eliminate as much as possible stands in regeneration because of clearcuts. Also, remaining clearcut stands were removed from the databases. Stands were selected from western Sm-Yb through western Bf-Wb subdomains. An ANOVA

was performed, on both datasets separately (SIFORT and field inventory), in order to test age difference between adjacent and white-cedar stands. A Tukey test was also used to compare the difference between white-cedar stands along the gradient.

## 2.5 Results

### 2.5.1 Presence of white-cedar according to site conditions

The best model selected from the AIC analysis was the global model (Table 2.2). This model included all of the variables but four of them, position on the slope, slope inclination, aspect and drainage, were found to explain white-cedar presence (Table 2.3). According to the analysis, white-cedar was significantly associated to bottom of slope, steep inclination ( $\geq 30\%$ ), western aspect and poor drainage.

The differences between estimates of significant classes and of the other classes appeared sufficient to consider the effect of these factors as being biologically significant (Fig. 2.2). In addition, the predictive capacity based on accurate predictions of the model was verified for the two other datasets. Dataset from the southern areas had a predictive capacity of 63% whereas the northern dataset had a low predictive capacity of 23%.

### 2.5.2 Availability and saturation of suitable sites

Site conditions that explained white-cedar establishment had different availability along the gradient. Western side of slopes became slightly less available in the landscape in the north. In addition, excessive slopes ( $\geq 16\%$ ) was less abundant with latitude. On the other hand, poorly drained sites and bottom of slope were more abundant in the northern areas (Fig. 2.3). However, as latitude increased, white-cedar was less able to saturate every suitable site in the two northernmost areas. Low saturation rates were calculated for all classes of variables in the northern sites, meaning that white-cedar was found unable to occupy most suitable sites.

Overall, the model predicted 78% and 81% of suitable sites in the south (Sm-Yb and Bf-Yb subdomains respectively) and 78% and 81% of suitable sites in the north (Bf-Wb and Bs-Fm subdomains respectively). Although there was a high proportion of suitable sites in the north, white-cedar was clearly unable to occupy most of the available sites in the northern areas (Fig. 2.5). The low saturation rates clearly illustrated the inability of white-cedar to establish in suitable sites in the northernmost subdomains (Table 2.5)

### 2.5.3 Effects of fire

From the field data inventory, the ANOVA revealed a difference in age between adjacent and white-cedar stands all along the gradient. White-cedar stands were older than stands that were surrounding them, revealing a mean age difference of 185 years ( $p < 0.0001$ ). Moreover, the ANOVA showed a contrast in the age difference between white-cedar and surrounding stands along the three bioclimatic subdomains ( $p = 0.003$ ). The Tukey test also confirmed that the difference for white-cedar stands in Bs-Fm subdomain was more important than in white-cedar stands of the two other subdomains, a difference exceeding 130 years (Fig. 2.6a). The difference in age was about the same for white-cedar stands in balsam fir-yellow birch and balsam fir-white birch subdomains. In addition, the other test made with the database SIFORT also indicated a significant difference in age (19 years in average) between adjacent and white-cedar stands ( $p < 0.0001$ ). However, this difference was the same along the climatic gradient (Fig. 2.6b).

**Table 2.2** AIC candidate models and results for the analysis on white-cedar presence/absence on different types of site conditions.  
The best selected model is in bold.

Candidate models	K <sup>1</sup>	AIC <sup>2</sup>	$\Delta$ AIC <sup>3</sup>	AIC Wt <sup>4</sup>
<b>White-cedar ~ Organic layer thickness + Type of organic horizon + Drainage + Aspect + Position on the slope + Slope inclination + Texture of B horizon + Deposit type</b>	<b>25</b>	<b>3006.94</b>	<b>0</b>	<b>1</b>
White-cedar ~ Deposit type	5	3116.03	109.09	0
White-cedar ~ Texture of B horizon	4	3117.35	110.41	0
White-cedar ~ Organic layer thickness	4	3117.90	110.97	0
White-cedar ~ Aspect	5	3124.24	117.3	0
White-cedar ~ Drainage + Position the slope + Slope inclination + Aspect	13	3020.56	13.62	0
White-cedar ~ Organic layer thickness + Type of organic horizon + Drainage	8	3044.53	37.60	0
White-cedar ~ Drainage + Texture of B horizon + Deposit type	10	3053.46	46.53	0
White-cedar ~ Drainage	3	3061.42	54.48	0
White-cedar ~ Organic layer thickness + Drainage	6	3062.89	55.95	0
White-cedar ~ Organic layer thickness + Drainage + Texture of B horizon	9	3064.30	57.37	0
White-cedar ~ Aspect + Position on the slope + Slope inclination	11	3069.76	62.82	0
White-cedar ~ Type of organic horizon	3	3083.29	76.35	0
White-cedar ~ Position on the slope	3	3104.94	98.00	0

<sup>1</sup>: Number of parameters, <sup>2</sup>: AIC coefficient, <sup>3</sup>: AIC relative to the best model

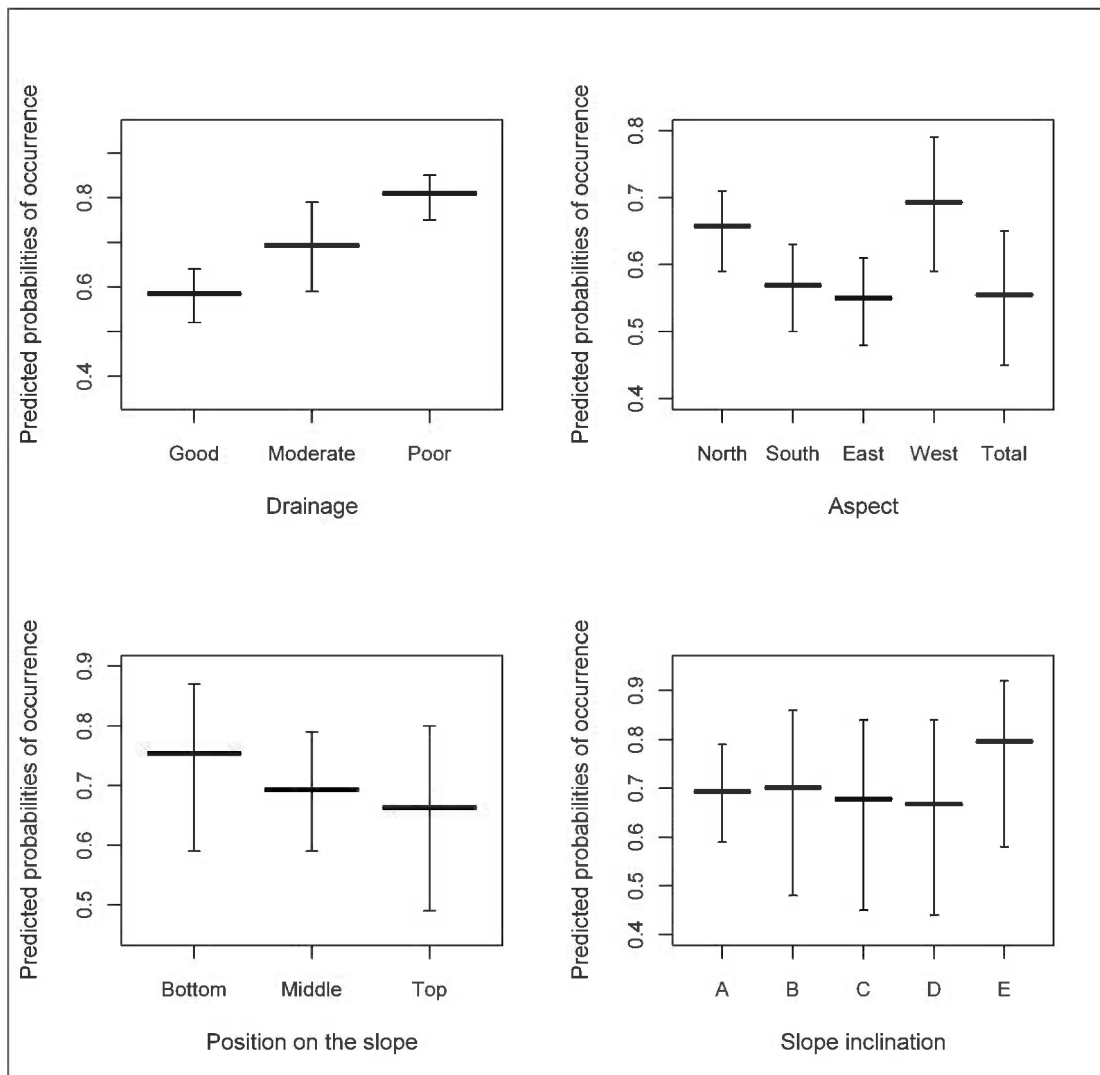
<sup>4</sup>: AIC model weight [for more details see (Burnham and Anderson, 2002)]



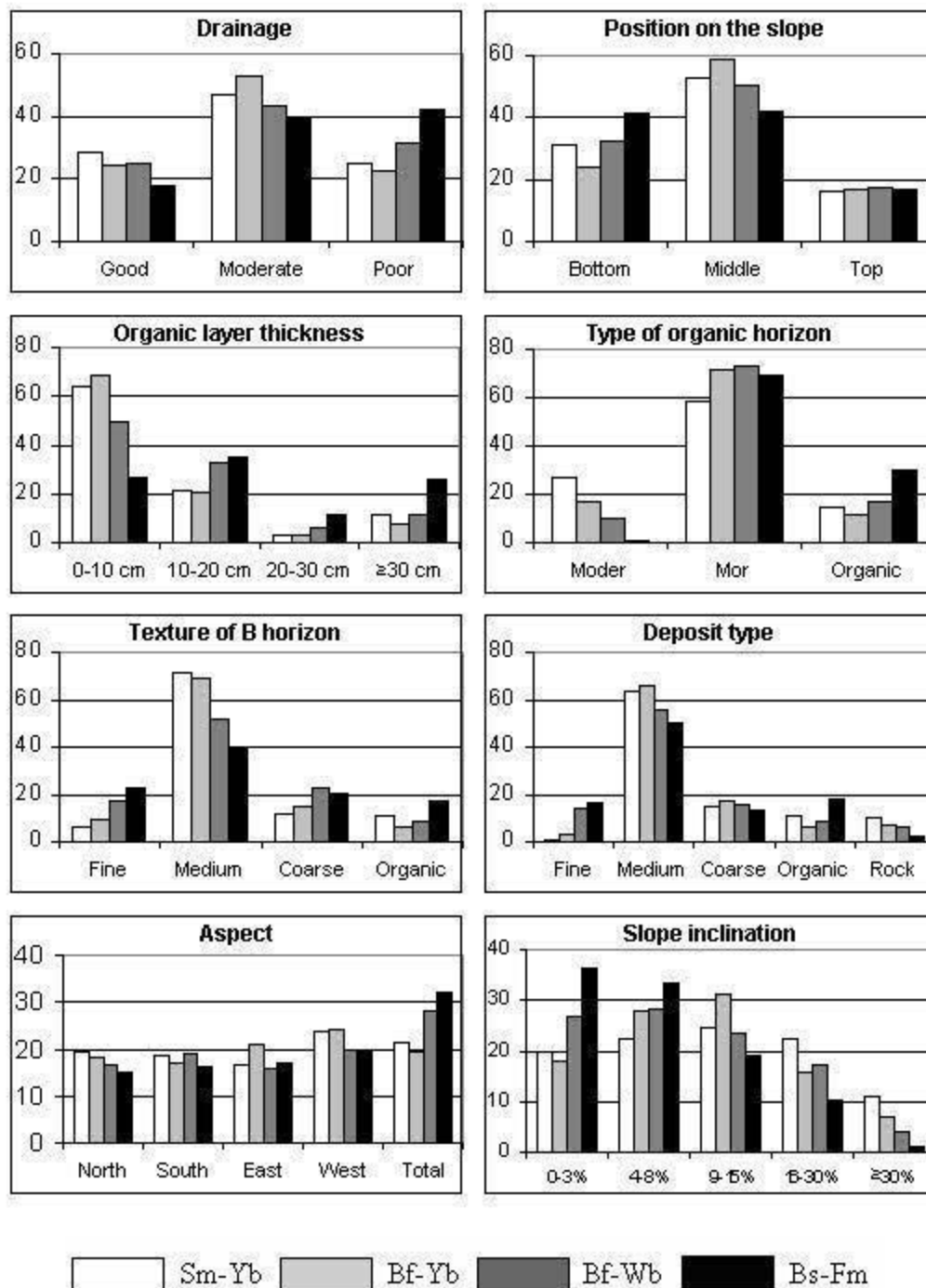
**Table 2.3.** Parameter estimates and confidence intervals for the analysis on white-cedar presence/absence on different types of site conditions. Reference levels are showed in parentheses. The values in bold print are statistically significant relative to the reference level (the confidence intervals do not include 0).

Parameter	Class	Estimate	Unconditionnal standard error	Lower 95% CL*	Upper 95% CL*
Organic layer thickness (0-10cm)	10-20 cm	-0.17	0.12	-0.4	0.05
	20-30 cm	-0.02	0.36	-0.73	0.69
	> 30 cm	-0.57	0.44	-1.44	0.3
Type of organic horizon (Organic soil)	Moder	-0.49	0.32	-1.13	0.14
	Mor	-0.09	0.31	-0.7	0.52
Drainage (Poor)	Good	-1.1	<b>0.19</b>	-1.47	<b>-0.73</b>
	Moderate	<b>-0.63</b>	<b>0.16</b>	<b>-0.95</b>	<b>-0.31</b>
Aspect (West)	North	-0.16	0.14	-0.43	0.11
	South	<b>-0.54</b>	<b>0.13</b>	<b>-0.8</b>	<b>-0.27</b>
	East	<b>-0.61</b>	<b>0.14</b>	<b>-0.08</b>	<b>-0.35</b>
	Total	<b>-0.59</b>	<b>0.22</b>	<b>-1.02</b>	<b>-0.17</b>
Position on the slope (Bottom)	Middle	<b>-0.3</b>	<b>0.14</b>	<b>-0.57</b>	<b>-0.04</b>
	Top	<b>-0.44</b>	<b>0.17</b>	<b>-0.77</b>	<b>-0.12</b>
Slope inclination ( $\geq 30\%$ )	0-3%	-0.55	0.28	-1.1	0.01
	4-8%	<b>-0.51</b>	<b>0.2</b>	<b>-0.9</b>	<b>-0.12</b>
	9-15%	<b>-0.62</b>	<b>0.19</b>	<b>-0.99</b>	<b>-0.24</b>
	16-30%	<b>-0.66</b>	<b>0.19</b>	<b>-1.03</b>	<b>-0.3</b>
Texture of B horizon (Organic)	Fine	0.05	0.81	-1.53	1.63
	Medium	0.03	0.8	-1.54	1.6
	Coarse	-0.09	0.81	-1.68	1.5
Deposit type (Organic)	Fine	-1.32	0.89	-3.05	0.42
	Medium	-0.98	0.82	-2.6	0.63
	Coarse	-1.01	0.83	-2.63	0.62
	Rock	-0.46	0.82	-2.07	1.15

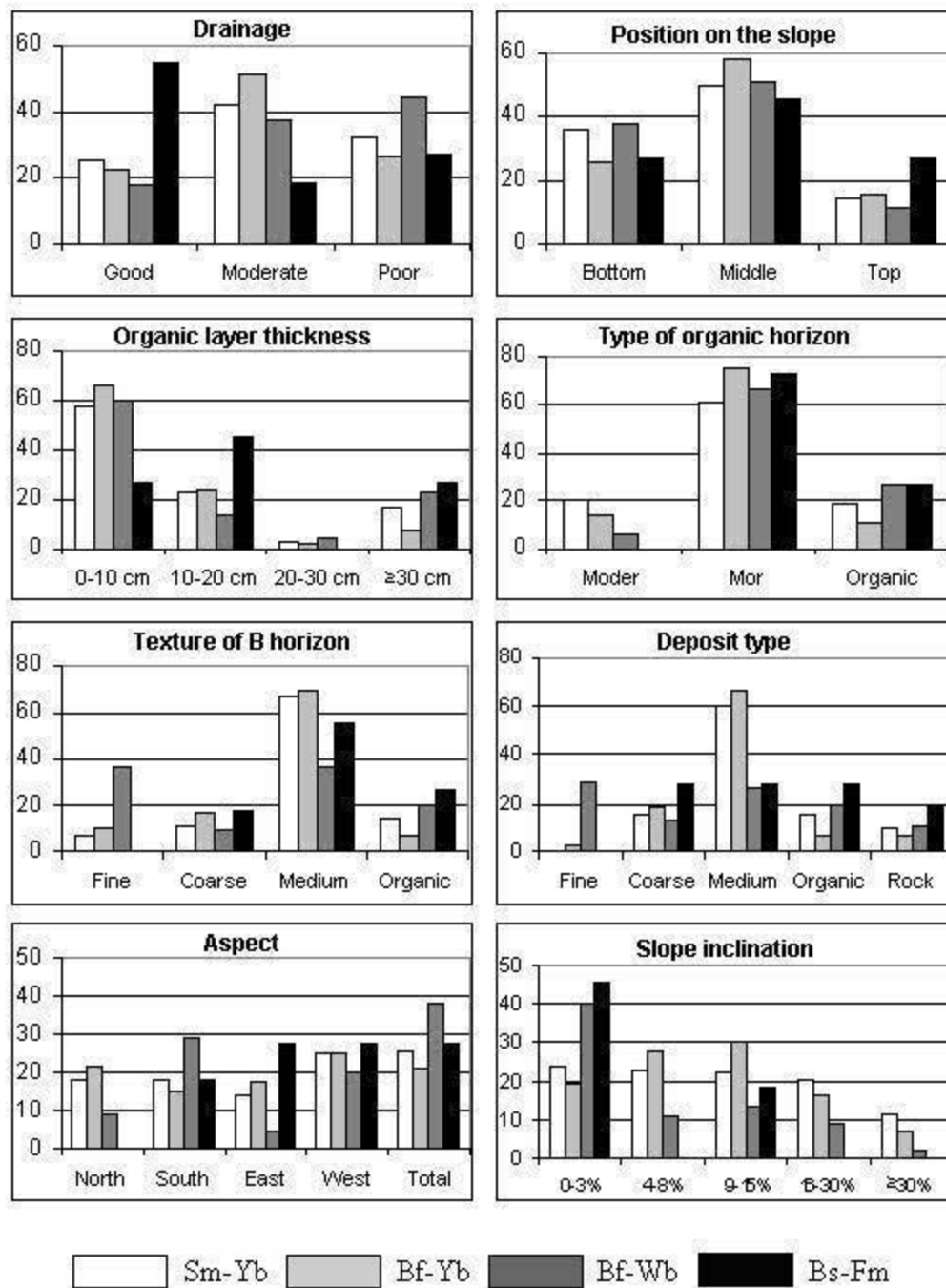
\*CL: confidence level



**Figure 2.2.** Effect of drainage, aspect, position on the slope and slope inclination on probabilities of white-cedar occurrence. Errors bars are 95% confidence intervals.



**Figure 2.3** Observed distribution (%) of each class of factors for each bioclimatic subdomain.

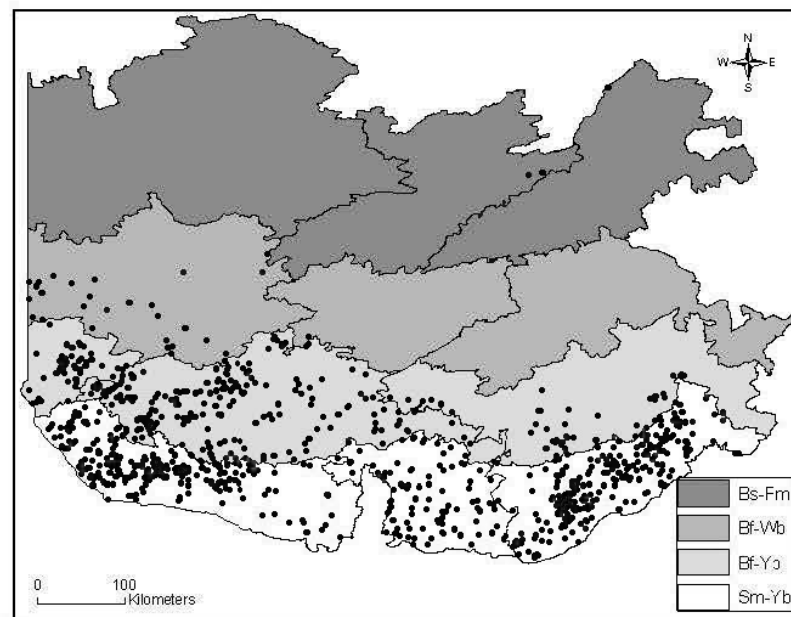


**Figure 2.4** Proportion of utilisation by white-cedar of the different classes of factors for each bioclimatic subdomain.

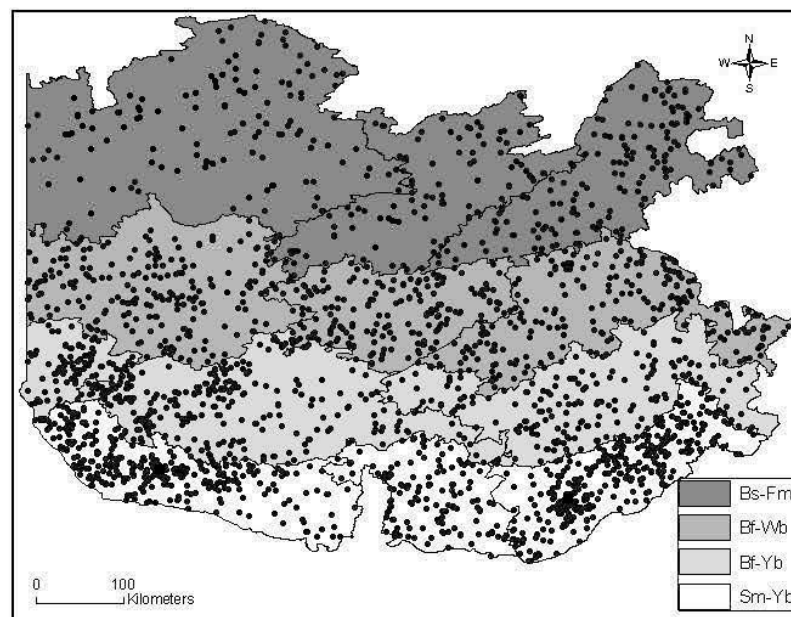
**Table 2.4** Saturation rate of the suitable sites (Observed / Predicted X 100) for each class of factors. (Classes in bold were found significant ( $\alpha=0.05$  level).)

Factors	Classes	Bioclimatic subdomains			
		Sugar maple- Yellow birch	Balsam fir- Yellow birch	Balsam fir- White-birch	Black spruce- Feathermoss
Drainage	Good (00-19)	118%	90%	11%	26%
	Moderate (20-39)	73%	64%	8%	1%
	<b>Poor (<math>\geq 40</math>)</b>	86%	65%	10%	2%
Organic layer thickness	0-10 cm	81%	67%	11%	3%
	10-20 cm	96%	82%	4%	5%
	20-30 cm	69%	55%	6%	0%
	$\geq 30$ cm	93%	58%	14%	3%
Type of organic horizon	Moder	77%	61%	18%	0%
	Mor	106%	80%	4%	4%
	Organic soil	82%	68%	6%	5%
Soil texture of the B horizon	Fine	92%	60%	17%	4%
	Coarse	107%	95%	12%	0%
	Medium	79%	67%	8%	4%
	Organic	89%	60%	11%	2%
Deposit type	Fine	81%	62%	9%	2%
	Coarse	83%	68%	9%	4%
	Medium	114%	87%	9%	8%
	Organic	88%	64%	11%	3%
	Rock	79%	66%	3%	0%
Position on the slope	<b>Bottom</b>	86%	71%	6%	4%
	Middle	96%	81%	6%	0%
	Top	76%	61%	4%	0%
Slope inclination	0-3%	73%	70%	9%	0%
	4-8%	99%	72%	14%	3%
	9-15%	96%	86%	3%	7%
	16-30%	76%	58%	6%	2%
	<b><math>\geq 30\%</math></b>	93%	69%	14%	4%
Aspect	North	86%	52%	17%	0%
	South	90%	82%	9%	9%
	East	85%	68%	4%	2%
	<b>West</b>	92%	60%	17%	4%
	Total	73%	63%	14%	29%

a)



b)



Western subdomains: **Bs-Fm**: Black spruce Feathermoss, **Bf-Wb**: Balsam fir-White birch, **Bf-Yb**: Balsam fir-Yellow birch, **Sm-Yb**: Sugar maple-Yellow birch

**Figure 2.5** Distribution of stands with a) presence of white cedar and b) suitable sites for white-cedar through the bioclimatic subdomains.

**Table 2.5** Predicted percentage of available sites  
and the observed occupation rate of the available sites

	<b>Sugar maple- Yellow birch</b>	<b>Balsam fir- Yellow birch</b>	<b>Balsam fir- White-birch</b>	<b>Black spruce- Feathermoss</b>
Predicted percentage of available sites	78%	81%	78%	81%
Observed saturation rate of the available sites	85%	55%	9%	3%

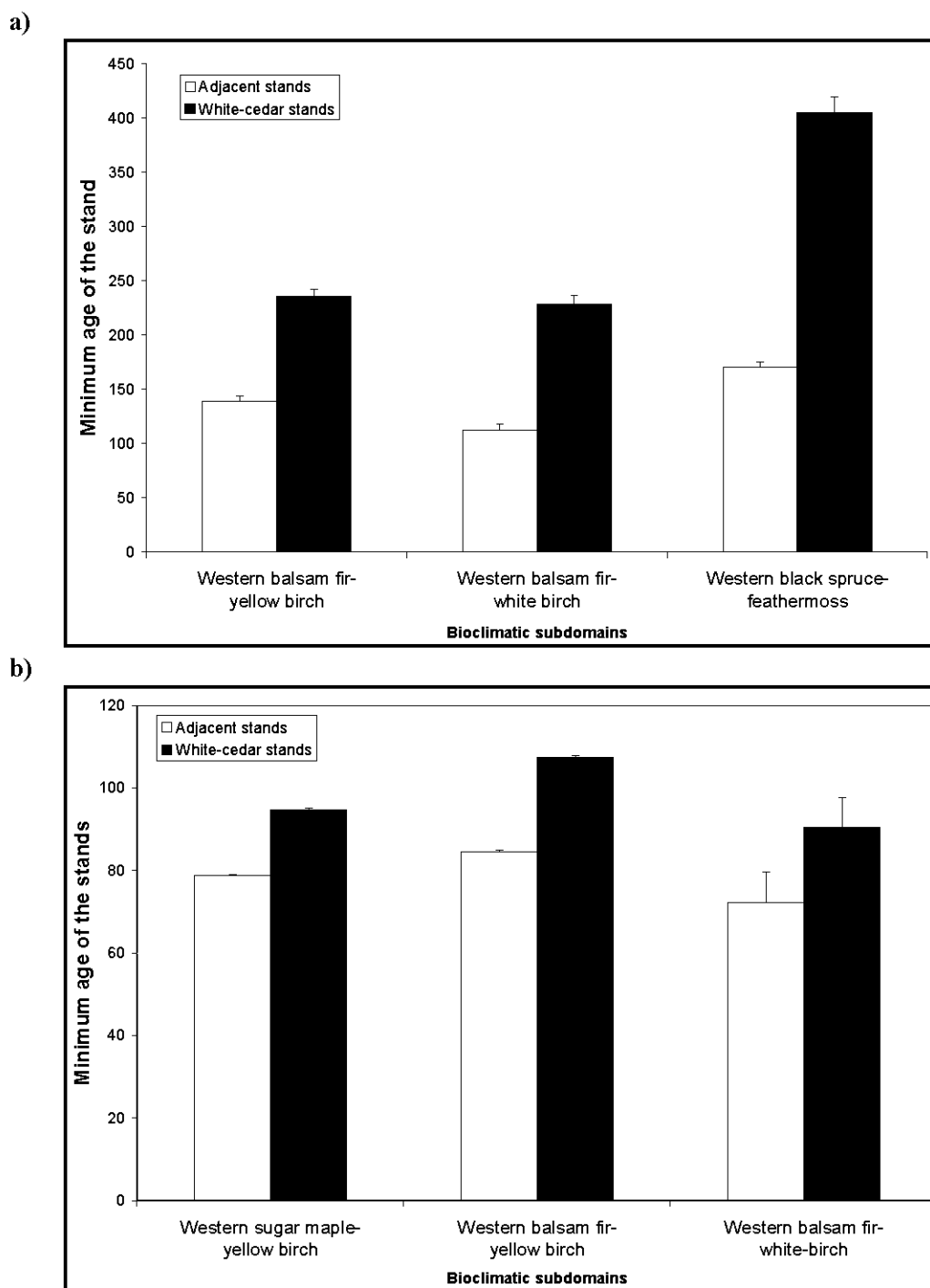


Figure 2.6 Comparison between stand's minimum age of white-cedar and their surrounding stands. a) from the field inventory, b) from the database SIFORT.



## 2.6 Discussion

The results showed that presence of white-cedar increase according to four factors, which are aspect (west), drainage (poor), slope inclination ( $\geq 30\%$ ) and position on the slope (bottom). These conditions represent the extreme of the moisture gradient suggesting that white-cedar is better adapted than its competitors in more stressed sites. However, the association with west facing slopes has never been reported. West aspect do not offer particular conditions such as increased solar radiation for south facing slopes and it is therefore difficult to explain this association. Despite these associations, white-cedar appeared to use a large array of sites in the south of the gradient where white-cedar stands are common (Fig. 2.4). Indeed, white-cedar can support different type of conditions, occurring on a gradient of sites from upland to wet lowland sites (Habeck, 1958, Musselman, et al., 1975, Johnston, 1990) and can acclimate of different conditions (Collier and Boyer, 1989).

Some important classes of factor increased in abundance northward, such as poor drainage and bottom of slope but on the other hand, a decrease in availability of slopes was encountered northward. However, according to the model, the northern subdomains appeared to offer the same percentage of suitable sites than in the south but the observed occupation rates of the suitable sites were very low for all sites in the north accounting for the incapacity of white-cedar to saturate them. In the north, organic soil with low decomposition rate and paludificated soil replaced well decomposed organic soil found in the south (Simard, et al., 2007). Therefore, there might be less suitable sites found in the north than the model's prediction.

Nevertheless, white-cedar was found unable to establish in most suitable sites. It clearly showed that the variation in site conditions along the latitudinal gradient can't explain the limitation since white-cedar is unable to saturate neither the significant classes of variables in the northern sites, nor other classes where it could have been found. In the south, the predictive capacity is high, suggesting that white-cedar has the capacity to establish in suitable sites. However, the low predictive capacity for the dataset of the northern area

suggests that other factors, possibly landscape or historical factors, probably play an important role in explaining presence of white-cedar (McCune and Allen, 1985, Messaoud, et al., 2007).

Response to fire analysis confirmed our second hypothesis, suggesting that fire plays an important role in limiting white-cedar's northern range in the north-west of the province of Québec. Indeed, outlier white-cedar stands were found to be very old and older than their adjacent stands. Considering that the maximum age of a stand is the minimal time since the last fire event, it is possible that fire occurred more recently in adjacent stands without entering or burning all of the white-cedar stands as it has been demonstrated in the field analysis. Results from the database were less significant possibly because the maximum age of this database is 120 years and that stand age could be underestimated. Also, the age estimation can't completely reflect the time since last fire since they are based on photointerpretation. However, at least, this indicates a difference in age between white-cedar and their adjacent stands. In addition, the field survey revealed that all stands found in the northernmost latitudes were located at proximity to water bodies or in poorly drained areas (Appendix 2.1). It has been showed that about 10% of forest areas do not burn and most of these areas are found at proximity of water or in wetlands (Roman-Cuesta, et al., 2009, Madoui, et al., 2010). Most stands were also found in areas protected from dominant winds and therefore from fire main direction. Dominant winds mainly occur from west side (Archambault, 1989) and a lot of stands found in the northernmost area where located on the eastern side of a waterbody or on the bottom of a slope were they could also be protected from fires (Appendix 2.1). Archambault (1989) also found that a large proportion of cedar where on east side of a lakes which can offer a protection from fires coming from the western side. The association with western aspect in the south is difficult to interpret but might also reveal a certain impact of fire at these more southerly latitudes. As wind is generally coming from the west, patch of forests facing west may be skipped when fire is carried by strong wind. Age and location of stands indicate that most sampled sites might have been avoided by fire since a long time and this might explain why white-cedar has a scarce distribution in the northern latitudes.

During the mid Holocene period, fires were found to be less frequent (Carcaillet, et al., 2001, Cyr, et al., 2009). Late-successional species like balsam fir (*Abies balsamea* L.) and white-cedar could have taken advantage of this low fire frequency to disperse in northern areas (Ali, et al., 2008). During the late Holocene period, climate evolved to cooler and drier summers which contributed to increase severity and frequency of fire events (Carcaillet and Richard, 2000, Asselin and Payette, 2005). This period corresponds to a decrease in balsam fir abundance (Ali, et al., 2008). The high fire frequency since this time could also have triggered the decrease in abundance of white-cedar at its northern limit. The historical burn rates estimated by Bergeron *et al.* (2006) clearly show that the rates are higher in Bf-Wb and Bs-Fm subdomains compared to the southern subdomains (Table 2.1). Bf-Wf and Bs-Fm have similar burn rates but fires cover larger areas in Bs-Fm (Bergeron, et al., 2004). Today's outlier stands of white-cedar might be relict of stands that established when climate was warmer and more humid and fire frequency lower. Relict would now be only found in areas that are avoided or partially affected by fire, for example near watercourse (Denneker, et al., 2008), explaining why white-cedar is unable to saturate suitable sites. The few remaining stands in the north would not be able to disperse because of low recruitment and high fire frequency and large fire size. Furthermore, fire size in the Bf-Wb subdomain would allow white-cedar to maintain more stands than in the Bs-Fm but would explain the drastic decrease compared to the southern areas.

Chapter 1 already demonstrated the partial influence of climate on white-cedar's northern distribution limit. Indeed, only recruitment of seedling was found to be lower in outlier stands but climate could not explain the drastic decrease in abundance occurring in northern areas. Therefore, white-cedar seems to be limited by both climate and fire events. Climate might limit the recruitment and dispersal of white-cedar at the northern distribution limit. Frequent fire, on the other hand, may eliminate seed source from the landscape, thus limiting the dispersal of the species by preventing new stands to establish. Thus, white-cedar is not in equilibrium with its bioclimatic limit because of frequent fire events that prevented white-cedar to disperse and establish northwards.

## **2.7 Conclusion**

The results demonstrate the complexity of species distribution dynamic and highlight limitations of models that predict future species distribution. While trying to understand migration pattern in changing climate, other inputs along with climate must be considered in the equation. Fire has an important effect in forest ecosystem dynamics and its role in species distribution limitation and its relation with climate must be better understood in order to better predict northward migration. In western Québec, global warming might trigger an increase in fire frequency, thus impacting many species distribution (Bergeron, et al., 2006, Bergeron, et al., 2010). An increase in fire frequency could give a disadvantage to species ill-adapted to fire (Bergeron, 2000, Messaoud, et al., 2007). White-cedar or other boreal species distribution could be negatively affected by such an increase and be reduced to lower latitudes even if climate might favour a better regeneration potential.

## **2.8 Acknowledgments**

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## 2.9 Appendix

**Appendix 2.1** Site characteristics for the sampled sites within the black spruce-feathermoss forest domain

Sites	Slope	Aspect	Drainage	Proximity to water	Estimated maximum stand age	Minimum stand age
M1	Bottom of slope	West	Poor	Shoreline (East side)	300	101
M2	No slope	Total	Poor	No	264	174
M3	Middle and bottom of slope	North-East	Moderate	Shoreline (South side)	529	227
M4	Bottom of slope	South	Poor	Shoreline (North-East side)	262	151
M5	No slope	Total	Good	Shoreline (East side)	458	177
M6	No slope	Total	Poor	No	500	197
M7	Middle and bottom of slope	West	Poor	Shoreline (East side)	490	237
M8	Bottom of slope	North-East	Poor	No	350	162
M9	No slope	Total	Moderate	No	390	143

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## CONCLUSION GÉNÉRALE

### 3.1 Principaux résultats

L'objectif de cette étude était d'évaluer l'effet de différents facteurs, soit le climat, les conditions de sites, et le feu, sur la limite nordique de répartition du thuya de l'Est. Ces facteurs ont été évalués le long d'un gradient latitudinal déterminé selon l'abondance des peuplements de thuya. Au sud, le thuya est abondant et son abondance diminue graduellement alors qu'au nord, les peuplements sont rares et dispersés.

Pour évaluer l'effet du climat, des peuplements de thuya ont été sélectionnés le long du gradient latitudinal afin de mesurer et de comparer la croissance radiale, la production de graines viables et la survie des semis. Il en ressort que le climat n'influence que partiellement la limite de répartition du thuya. En effet, seulement les populations marginales connaissent une diminution d'abondance de semis d'origine sexuée comparativement aux peuplements situés au sud de l'aire d'étude. La régénération n'est pas apparue différentes entre les peuplements les plus au sud de l'aire d'étude et ceux qui se retrouvent au centre. La croissance radiale et la production de graines viables se sont toutefois révélées similaires dans tous les peuplements le long du gradient. De plus, les peuplements marginaux, à l'extérieur de la répartition continue, étaient tous capables de produire des graines viables pouvant germer en condition contrôlée, suggérant que le climat a possiblement un impact modéré sur la germination ou la survie des semis. Le climat ne peut donc être à lui seul responsable de la limite de répartition puisque la limite bioclimatique ne semble pas atteinte.

D'autre part, la disponibilité et la saturation de sites potentiels pour le thuya le long d'un gradient ont été évaluées à l'aide de placettes d'échantillonnage. La disponibilité de sites adéquats était similaire tout au long du gradient. Toutefois, un autre facteur semble empêcher

le thuya de saturer tous les sites adéquats dans le nord de l'aire d'étude puisqu'une très faible proportion des sites adéquats était occupée.

L'effet du feu a été évalué à l'aide d'un échantillonnage terrain et également de données provenant des inventaires forestiers. Les résultats montrent que le feu semble limiter le thuya à sa répartition actuelle puisqu'il se trouve dans des endroits protégés des feux. En effet, les peuplements du nord ont été trouvés beaucoup plus vieux que les autres peuplements les entourant suggérant que ceux-ci ont été protégés des feux. Les peuplements marginaux seraient ainsi les derniers survivants de peuplements plus grands alors que les feux étaient moins fréquents et sévères. Les feux à la marge de la répartition continue sont aussi fréquents qu'au nord mais couvrent de plus petites superficies, permettant aux peuplements qui possèdent un meilleur potentiel de régénération de se disperser plus aisément. Le feu explique donc que le thuya connaisse une diminution d'abondance à cette latitude mais également pourquoi il se trouve en plus grande abondance qu'au nord.

Les résultats suggèrent que le thuya de l'Est est restreint à sa répartition actuelle par une combinaison d'au moins deux facteurs, le climat et le régime de feux. Le climat diminue la régénération et le potentiel de dispersion du thuya à sa limite nordique tandis que le feu élimine les arbres semenciers du paysage, limitant ainsi la dispersion et l'abondance des peuplements. Il semble donc que le thuya pourrait s'établir plus au nord sans l'influence du régime de perturbations actuelles.

### **3.2 Réactions des espèces face aux changements climatiques**

En raison de l'accumulation importante de gaz à effet de serre dans l'atmosphère, la température à la surface de la terre a augmenté de 0,74°C entre 1906 et 2005 (GIEC, 2007). Il est attendu une augmentation encore plus marquée pour les 100 prochaines années entre 1,1 et 6,4°C. La modification des températures et du régime de précipitations pourrait grandement affecter la dynamique des écosystèmes (McKenney *et al.*, 2007). En effet, le

climat a un effet important sur la biologie des espèces et une modification pourrait entraîner d'importantes conséquences.

Toutefois, les résultats de cette étude permettent de faire ressortir que le climat n'influence que partiellement la limite de répartition du thuya. Le chapitre 1 démontre que la répartition du thuya ne semble pas en équilibre avec les conditions climatiques, c'est-à-dire qu'il pourrait potentiellement atteindre de plus hautes latitudes si aucun autre facteur ne l'en empêchait. L'équilibre climatique semble avoir été affecté notamment par l'historique de feux dans le secteur étudié. Les résultats de cette étude mettent en lumière les principales limitations des modèles prédictifs actuels. En effet, les modèles de migration d'espèces basés uniquement sur le climat pourraient dans certains cas être incapables de prédire la réaction d'une espèce. La plupart des modèles partent de la prémisse que les espèces sont en équilibre avec le climat. Il semble donc primordial d'améliorer les modèles de prédiction, basés uniquement sur la répartition, en tenant compte de la phénologie de l'espèce en question. Toutefois, ces modèles ne tiennent pas compte d'autres effet. L'impact des perturbations naturelles, tels que les feux, ne doit pas être négligé puisque le feu semble avoir un impact des plus importants dans les limites de répartition nordique de certaines espèces boréales. Dans une optique de changement climatique, la migration de plusieurs espèces vivant en forêt boréale pourrait dépendre davantage de l'effet du climat sur les cycles de feu que de ses effets directs sur la biologie de l'espèce.

Certains modèles climatique prédisent une migration importante vers le nord pour le thuya (Ressources naturelles Canada 2011). Toutefois, si le réchauffement climatique induit une augmentation de la fréquence et de la superficie des feux, il se pourrait que le cèdre soit incapable de migrer vers le nord et devienne encore plus rare là où les feux sont très fréquents. Il semble donc important de pousser plus loin les recherches à cet égard afin de mieux comprendre les interactions entre ces divers facteurs et leurs impacts sur la répartition des espèces.

### 3.3 Perspectives de recherches

Suite aux conclusions de cette étude, de nombreuses questions demeurent. Certaines études en lien avec ce sujet sont présentement en cours et permettront de renforcer les présents résultats. Par exemple, des analyses génétiques permettront de mettre en lumière les modes de reproduction utilisés à différentes latitudes, et de comparer l'effet du climat à long terme sur les populations. Nos analyses permettent de montrer que la survie des semis sexués est plus compromise au nord. Il est donc probable que la majorité des tiges matures soient d'origine asexuée. Dans le sud, malgré une forte reproduction sexuée, le taux de survie des semis demeure toutefois très bas. Notre étude portant sur le marcottage n'a pas pu permettre de déterminer le réel taux de marcottage présent dans les peuplements et ainsi avoir une meilleure idée du taux de survie des semis.

D'autre part, des analyses dendroclimatiques plus approfondies permettront de mieux comprendre la relation entre le climat et la croissance du thuya. Les précédents résultats n'ont révélé aucune différence de croissance radiale le long d'un gradient latitudinal. Toutefois, cette analyse ne ciblait que les 20 dernières années et n'a pas tenu compte des variables climatiques mensuelles. De plus, les thuyas se trouvaient déjà dans des conditions contraignantes, ce qui a pu empêcher la détection d'une influence du climat. Ces études plus poussées permettront de comprendre d'avantage le comportement du thuya à différentes latitudes.

Par ailleurs, une autre étude basée sur les charbons de bois trouvés dans les peuplements marginaux ou en zone discontinue permettrait de mettre en lumière le réel impact des derniers feux et ainsi de valider avec une meilleure exactitude le patron d'établissement du thuya de l'Est. Des sites de thuya ont été répertoriés par photo-interprétation jusqu'à l'embouchure du delta de la rivière Harricana, aux environs du 51° parallèle. L'existence de thuya à ces latitudes n'a cependant pu être démontrée hors de tout doute, mais met tout de même en lumière la possibilité que des individus aient survécu à ces endroits très en marge

de la répartition actuelle du thuya. L'étude de ces peuplements marginaux serait des plus intéressants afin de bien comprendre le patron d'établissement des peuplements de thuya.

Finalement, les résultats de cette étude amènent une autre perspective concernant l'influence du climat dans la dynamique de répartition d'une espèce. Les résultats nous amènent à penser que d'autres espèces sont possiblement davantage influencées par les feux que le climat en forêt boréale à leur limite de répartition. Il serait ainsi nécessaire d'approfondir cette question pour différentes espèces. Il semble aussi essentiel d'augmenter nos connaissances concernant l'impact des feux dans la dynamique d'un écosystème forestier. Cela permettra de mieux prévoir les conséquences des changements climatiques sur les régimes de feux et ainsi l'impact sur la répartition des espèces peu adaptées à des épisodes de feu fréquents.

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