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INFLUENCE DU CLIMAT ET
DE L'ÉPAISSEUR DE LA COUCHE ORGANIQUE
SUR LA CROISSANCE ET LA DISTRIBUTION
DU PEUPLIER FAUX-TREMBLE ET DE L'ÉPINETTE NOIRE
DANS LE NORD-OUEST DU QUÉBEC

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PAR
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AVANT-PROPOS

Le corps du texte de ce mémoire présente deux chapitres et est rédigé en anglais et sous forme d'articles scientifiques intitulés : « Impacts of soil organic layer thickness on sensitivity to climate of black spruce and aspen in western Quebec, Canada » et « Species-specific growth responses of black spruce and aspen enhance resilience of boreal forest to climate change ». Les articles seront soumis pour publication au cours de l'année 2011.

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RÉSUMÉ

Les changements climatiques affectent la distribution et la croissance d'espèces arborescentes telles que le peuplier faux-tremble et l'épinette noire, deux espèces dominantes de la pessière à mousses de l'ouest du Québec, et peuvent ainsi mener à d'importantes modifications de la composition et de la productivité future des forêts. Sur la ceinture d'argile du Québec, l'accumulation de matière organique au sol peut mener à des conditions d'humidité très variables. L'épaisseur de la couche organique est directement liée à un gradient de conditions édaphiques et affecte la croissance et la distribution des arbres à l'échelle du paysage. Afin de mieux comprendre comment les changements climatiques affecteront la croissance de la forêt boréale, l'importance des conditions de site, les relations croissance-climat et les réponses aux extrêmes climatiques du peuplier faux-tremble et de l'épinette noire ont été évaluées. Des régressions ont permis de mettre en évidence l'effet limitant de l'épaisseur de la couche organique sur la distribution et la croissance du peuplier faux-tremble, alors que l'épinette noire n'était pas affectée. Les relations croissance-climat des deux espèces ont été déterminées avec des analyses dendrochronologiques, qui ont montré que le climat affectait différemment la croissance radiale des deux espèces. La croissance de l'épinette noire était favorisée par des printemps doux et des étés frais. Le peuplier faux-tremble était principalement influencé par les conditions climatiques de l'année précédente la croissance et la température au mois de juin. Les extrêmes climatiques n'affectaient qu'une des deux espèces à la fois ou généraient des réponses de croissance opposées entre les deux espèces. L'épaisseur de la couche organique n'avait que peu d'effet sur les relations croissance-climat de l'épinette noire, mais modifiait la réponse du peuplier faux-tremble à certaines variables climatiques. L'épinette noire aura probablement une réponse relativement uniforme aux changements climatiques dans la région, alors que la réponse du peuplier faux-tremble pourrait varier localement selon l'épaisseur de la couche organique. Les réponses spécifiques à chacune des deux espèces au climat annuel et aux anomalies climatiques pourraient induire une séparation temporelle des niches écologiques et permettre une accumulation de biomasse plus constante lors d'extrêmes climatiques dans les peuplements mixtes, comparées aux peuplements purs. Que les changements climatiques aient des effets bénéfiques sur ces deux espèces ou non dépendra principalement de la balance entre la hausse des températures et l'augmentation des précipitations. Les changements climatiques auront des impacts spécifiques sur chaque espèce, qui varieront aussi selon les conditions édaphiques, ultimement menant à des taux de croissance différents entre les espèces et les sites. En augmentant la résilience de la forêt boréale, conserver des peuplements mixtes pourrait permettre de réduire les risques d'observer des effets néfastes des changements climatiques sur la productivité des forêts.

Mots clés : *Picea mariana*, *Populus tremuloides*, changements climatiques, couche organique, croissance radiale.

INTRODUCTION GÉNÉRALE

Problématique

Selon le quatrième rapport du Groupe intergouvernemental d'experts sur l'évolution du climat, la température moyenne globale a augmenté de 0,74°C de 1906 à 2005 (IPCC 2007). Cette augmentation doit se poursuivre au cours du 21^{ème} siècle et sera la plus marquée dans les régions nordiques. En effet, selon les données du Modèle Régional Climatique Canadien (MRCC) générées et fournies par Ouranos (2010), on prévoit une hausse des températures de 1,5°C à 5,2°C d'ici le milieu du 21^{ème} siècle pour l'ouest du Québec. La hausse des températures sera également accompagnée d'une augmentation des précipitations de 10% à 25%, sauf en été où on prévoit une variation de -2% à maximum +15% des précipitations. Le réchauffement et l'augmentation des précipitations seront les plus marqués durant la saison hivernale, alors que la saison estivale pourrait devenir nettement plus sèche si l'augmentation des précipitations ne surcompense pas la hausse des températures. Aussi, une augmentation de la fréquence des événements climatiques extrêmes est prévue pour les décennies à venir (Bonsal *et al.* 2001; IPCC 2007; Mailhot *et al.* 2010).

Le climat est le principal facteur influençant la dispersion, la productivité et la croissance des arbres d'une population. Les changements climatiques peuvent ainsi avoir une répercussion directe sur la croissance et la distribution des arbres, et ultimement sur le taux de migration d'espèces arborescentes et la composition des forêts (Hansen *et al.* 2001; Mohan *et al.* 2009). Afin de prévoir la migration et la distribution des espèces sous le climat futur, des modèles statistiques, qui se basent sur les relations existantes entre les arbres et les conditions environnementales, dont principalement le climat, sont utilisés (Lafleur *et al.* 2010). Mais bien que les conditions climatiques soient le principal facteur affectant la distribution des espèces arborescentes à l'échelle continentale et subcontinentale, des facteurs locaux, tels que les conditions de site, jouent un rôle important dans la distribution des arbres à l'échelle du paysage et du peuplement (Hansen *et al.* 2001; Pearson & Dawson 2003). Toutefois, les facteurs édaphiques sont trop peu souvent pris en compte dans les modèles statistiques, probablement dû à un manque de connaissances quant aux effets des conditions de site sur la distribution et les relations croissance-climat des espèces arborescentes.

Le peuplier faux-tremble (*Populus tremuloides* Michx.) et l'épinette noire (*Picea mariana* [Mill.] B.S.P.) sont des espèces importantes de la forêt boréale de l'ouest du Québec, autant d'un point de vue environnemental qu'économique, l'épinette noire étant la plus exploitée (Gagnon *et al.* 1998). Des études récentes ont déterminés les relations croissance-climat de ces deux espèces et démontrent la spécificité de ces relations (Hofgaard *et al.* 1999; Tardif *et al.* 2001; Hoffer & Tardif 2009; Drobyshev *et al.* 2010; Huang *et al.* 2010). Plusieurs autres études ont aussi montré que le climat peut avoir des impacts différents sur la croissance des arbres en fonction des caractéristiques du site (Webb *et al.* 1993; Hogg *et al.* 2008; Leonelli *et al.* 2008; Wilmking et Myers-Smith 2008), et dans l'ouest du Québec, Drobyshev *et al.* (2010) ont révélé que la réponse de l'épinette noire au climat varie le long d'un gradient d'épaisseur de la couche organique au sol. En effet, la région de la ceinture d'argile dans l'ouest du Québec se caractérise par une importante variation des conditions édaphiques due à la variabilité de l'épaisseur de la couche organique. Une meilleure compréhension des effets des conditions de site sur la distribution à l'échelle du paysage et la croissance du peuplier faux-tremble et l'épinette noire est donc inhérente à des prédictions plus précises sur les impacts des changements climatiques sur ces deux espèces.

Dans le contexte des changements climatiques, il apparaît aussi important de mieux comprendre les interactions des espèces dans les peuplements mixtes. Dans certaines conditions, des peuplements mixtes ont le potentiel d'être plus productifs et plus résilients que des peuplements purs, pour autant que les essences composant le peuplement mixte aient des caractéristiques fonctionnelles ou des niches écologiques complémentaires (Man & Lieffers 1999; Chen *et al.* 2003; Bauhus *et al.* 2004; Green 2004; Pretzsch *et al.* 2010; Brassard *et al.* 2011). L'épinette noire et le peuplier faux-tremble se distinguent par leur tolérance à l'ombre et une utilisation différente de l'espace dans le sol, menant à une certaine complémentarité des niches (Burns & Honkala 1990a, 1990b; Brassard *et al.* 2011). Des relations croissance-climat spécifiques à chacune des deux espèces contribueraient à cette complémentarité des niches, en permettant une meilleure utilisation des ressources édaphiques à l'échelle temporelle et ainsi une accumulation de biomasse plus constante dans les peuplements mixtes de peuplier faux-tremble et d'épinette noire, comparé aux peuplements purs (Green 2004).

État des connaissances

Relations croissance-climat du peuplier faux-tremble et de l'épinette noire

La croissance radiale de l'épinette noire est surtout influencée par la température et peut répondre différemment au climat selon les conditions d'humidité. Au Québec l'épinette noire est favorisée par des étés frais et humides durant l'année de croissance et celle avant, lorsqu'elle pousse sur des sites xériques et mésiques (Hofgaard *et al.* 1999; Tardif *et al.* 2001; Drobyshev *et al.* 2010). Mais elle pourrait également être favorisée par des températures estivales plus chaudes dans le nord (vers le 54°N) (Huang *et al.* 2010). Aussi, un printemps chaud et donc un début de la saison de croissance précoce, contribue fortement à la croissance radiale de l'épinette noire (Hofgaard *et al.* 1999; Tardif *et al.* 2001; Drobyshev *et al.* 2010). Aussi, chez l'épinette noire la relation entre le climat et la croissance peut varier en fonction des caractéristiques du site (Wilmking et Myers-Smith 2008). Ainsi, en Alaska les épinettes noires en milieu forestier ouvert sont généralement plus influencées par le climat et leur croissance présente surtout une corrélation négative avec les températures de fin d'été, alors que la croissance des épinettes noires en tourbière est moins sensible au climat. Dans l'ouest du Québec, une importante couche de matière organique rend l'épinette noire moins sensible aux étés plus chauds et secs, sauf en cas de sécheresse extrême où l'effet est inverse (Drobyshev *et al.* 2010).

La réponse du peuplier faux-tremble aux variables climatiques est différente de celle de l'épinette noire, mais varie aussi selon les conditions de site. Dans l'ouest du Canada, où le climat est nettement plus sec qu'au Québec (Environnement Canada 2010), le manque en eau est le principal facteur causant une diminution de la croissance et de la productivité du peuplier faux-tremble, qui est donc reliée positivement aux précipitations, mais aussi à la présence de limons dans le sol (Hogg *et al.* 2005, 2008). De plus, Leonelli *et al.* (2008) ont constaté que la croissance radiale du peuplier faux-tremble est surtout influencée par le climat de l'année précédente à la croissance et que l'intensité de la réponse au climat dépend fortement des propriétés du site. Les effets du climat sur la croissance des arbres n'augmenteraient pas seulement aux limites de distribution du peuplier faux-tremble, mais aussi dans les sites plus riches et humides, où les nutriments ne constituent pas un facteur

limitant à la croissance. Dans l'est du Canada par contre, la croissance du peuplier faux-tremble est moins affectée par la sécheresse (Cooke et Roland 2007), probablement à cause des conditions climatiques nettement plus humides. Sur un gradient latitudinal du 46° au 54°N dans l'ouest du Québec, les précipitations de l'hiver précédent la saison de croissance deviennent de plus en plus favorables et les températures du début de l'été de l'année précédent la croissance deviennent de plus en plus limitantes du sud au nord (Huang *et al.* 2010). Des automnes frais précédents la saison de croissance, des printemps doux et humides et le rallongement de la saison de croissance sont favorables à la croissance du peuplier faux-tremble.

Accumulation de la matière organique au sol

Dans la ceinture d'argile de l'ouest du Québec, d'importantes accumulations de matière organique au sol mènent à la paludification des forêts. Après feux, les essences, dont le peuplier faux-tremble et l'épinette noire, se régénèrent naturellement sur le sol minéral sur lequel va s'accumuler de la matière organique au cours du temps (Lecomte *et al.* 2006; Simard *et al.* 2007, 2009). Lorsque la couche organique au sol s'épaissit, on observe une augmentation de la capacité de rétention d'eau du sol (Lavoie *et al.* 2007). Ceci cause une montée de la nappe phréatique (Simard *et al.* 2007) et donc un refroidissement du sol, un retardement du dégel et un ralentissement du recyclage des éléments nutritifs (Foster 1985; Oechel et Van Cleve 1986). L'excès d'eau, un sol pauvre et froid diminuent la productivité de l'épinette noire (Oechel et Van Cleve 1986) et plus un site est paludifié, plus la productivité de l'épinette noire diminue (Simard *et al.* 2007, 2009). Dans les sites paludifiés, l'épinette noire présente également plus d'anomalies de croissance caractérisées par des cernes particulièrement étroits (Drobyshev *et al.* 2010). Dans de tels milieux, le peuplier faux-tremble a un effet négatif sur l'accumulation de matière organique (Fenton *et al.* 2005), la qualité de sa litière accélère le recyclage des éléments nutritifs et améliore les propriétés du sol (Légaré *et al.* 2005a; Laganière *et al.* 2010). Cette amélioration des propriétés du sol, l'augmentation du pH et de la disponibilité des éléments nutritifs augmente alors la croissance et la productivité de l'épinette noire (Légaré *et al.* 2004, 2005b). Le peuplier faux-tremble est rarement trouvé dans des milieux organiques, contrairement à l'épinette noire qui

semble éprouver peu de difficultés à croître et à s'établir dans ces milieux. Toutefois, l'effet de la couche organique sur la croissance et la distribution du peuplier faux-tremble à l'échelle du paysage n'est pas bien connu. Bien que le peuplier faux-tremble ait un effet négatif sur l'épaisseur de la couche organique, la possibilité d'un effet limitant de la couche organique sur la croissance et la distribution du peuplier faux-tremble devrait être explorée. En plus d'influencer la croissance et la distribution dans le paysage, l'épaisseur de la couche organique a le potentiel d'avoir un impact sur les relations croissance-climat du peuplier faux-tremble et de l'épinette noire et ainsi sur leur réponse aux changements climatiques (Drobyshev *et al.* 2010).

Peuplements mixtes

Selon Vandermeer (1989), le mélange de différentes espèces peut mener à une plus grande productivité grâce au principe d'exclusion compétitive ou au mécanisme de facilitation. L'exclusion compétitive mène à une meilleure utilisation des ressources du milieu par des espèces qui ont des niches écologiques distinctes. Et lorsqu'une espèce modifie le milieu de façon à affecter positivement une autre espèce on parle de facilitation. Dans la forêt boréale québécoise, l'épinette noire a une grande valeur économique et dans les peuplements mixtes, le peuplier faux-tremble est souvent considéré comme une espèce compétitive et est enlevé des peuplements d'épinettes noires (Gagnon *et al.* 1998). Cependant, l'exclusion compétitive et même la facilitation peuvent avoir lieu dans les peuplements mixtes d'épinette noire et de peuplier faux-tremble. Les racines de l'épinette noire sont peu profondes, alors que celles du peuplier faux-tremble poussent plus profondément dans le sol, ce qui crée une séparation des niches dans le sol, pour ce qui est de l'espace disponible et aussi pour les ressources édaphiques (Burns & Honkala 1990a, 1990b; Brassard *et al.* 2011). Aussi, le cycle de feuillaison mène à une séparation temporelle des niches. Lorsque le peuplier faux-tremble ne porte pas de feuilles, l'épinette noire peut bénéficier d'une plus grande luminosité et aussi d'une plus grande disponibilité des ressources édaphiques, principalement au début de la saison de croissance, qui commence bien plus tôt pour l'épinette noire (Man & Lieffers 1997, 1999; Green 2004). Le peuplier faux-tremble a un effet bénéfique sur les propriétés du sol et peut avoir un impact positif sur l'épinette noire, selon les conditions de site et la proportion

de peuplier faux-tremble dans le peuplement (Légaré *et al.* 2004, 2005a, 2005b; Laganière *et al.* 2010). Des réponses distinctes des deux espèces au climat peuvent ajouter à cette complémentarité des niches et il y aurait une certaine assurance quant à l'accumulation de biomasse dans les peuplements mixtes dans le contexte des changements climatiques.

Objectifs et hypothèses de travail

Les objectifs de cette étude sont donc (1) de déterminer l'effet des conditions de site sur la distribution à l'échelle du paysage et la croissance radiale de l'épinette noire et du peuplier faux-tremble; (2) d'évaluer la spécificité de la réponse au climat des arbres en fonction de l'espèce et des conditions de site et (3) d'inférer les conséquences possibles des changements climatiques sur la croissance de l'épinette noire et du peuplier faux-tremble. Les hypothèses de travail furent que (1) l'épaisseur de la couche organique limite la distribution du peuplier faux-tremble à l'échelle du paysage; (2) la croissance radiale diminue avec une couche organique plus épaisse; (3) le peuplier faux-tremble répond différemment au climat que l'épinette noire; (4) dans les sites avec une couche organique épaisse, les arbres bénéficient plus d'étés chauds et secs et sont peu sensibles aux variations de précipitations, comparés aux arbres des sites mésiques et xériques; (5) les extrêmes climatiques n'affectent pas les deux espèces de la même façon. La question de l'épaisseur de la couche organique et de ses effets sur la distribution, la croissance et la réponse au climat des arbres sera abordée dans le chapitre I. Le chapitre II portera sur la spécificité des réponses de croissance au climat des deux espèces dans les conditions climatiques normales et en cas d'extrêmes climatiques.

CHAPITRE I

**IMPACTS OF SOIL ORGANIC LAYER THICKNESS ON SENSITIVITY TO
CLIMATE OF BLACK SPRUCE AND ASPEN IN WESTERN QUEBEC, CANADA**

Sylvie Gewehr, Yves Bergeron, Igor Drobyshev and Frank Berninger

1.1 Abstract

In the Quebec Clay Belt, the accumulation of soil organic layer (SOL) leads to highly variable site conditions. SOL thickness integrates complex gradients in soil conditions, affecting tree growth and distribution within landscape. Results of regression analyses showed that an organic layer thicker than ~20-30 cm was limiting for distribution of aspen at the landscape scale, but not for black spruce. Over the SOL gradient covered by this study (from ~1 to 25 cm), SOL thickness showed negative impact on mean annual increment of aspen, while no effect was observed in black spruce. Dendroclimatic analyses showed that radial growth of black spruce was favoured by higher temperatures in early winter and in spring, and by low temperatures in summer. The cooler soil temperatures and the high soil moisture both induced by SOL thickness appeared therefore of little importance for black spruce growth, at least not over the gradient covered by this study. SOL thickness also had very little effect on the climate-growth relationships in black spruce. In aspen, weather conditions of the previous year and current June temperature were the most important factors affecting growth. Cool and moist conditions induced by the SOL could be limiting radial growth in aspen, especially in moist sites. Increases in winter, spring and fall temperatures that are predicted by current Canadian Regional Climate Models, might benefit black spruce growth, whereas the warmer summer temperatures might induce drought stress in this species. As opposed to black spruce, aspen growth could benefit from an increase in summer temperatures, but higher fall temperatures and amounts of snowfall could have a negative effect on aspen growth. For both species, whether climate change will benefit their growth or not, will highly depend on the balance between changes in temperatures and precipitation regimes. The response of black spruce to climate change should be rather uniform across the study region, while the growth response of aspen to climate change is likely to be mediated by site conditions. Aspen growing on thick SOL would likely benefit from warmer and drier summers. Modifications of site conditions induced by altered climate conditions and fire cycle are likely to play a key role in future distribution of aspen within landscape in the Clay Belt.

Keywords: *Picea mariana*, *Populus tremuloides*, climate change, soil organic layer, radial growth, distribution.

Résumé

Sur la ceinture d'argile du Québec, l'accumulation de matière organique au sol peut mener à des conditions d'humidité très variables. L'épaisseur de la couche organique est directement liée à un gradient de conditions édaphiques et affecte la croissance et la distribution des arbres à l'échelle du paysage. Les résultats obtenus à partir d'analyses de régression indiquent que la distribution du peuplier faux-tremble dans le paysage était limitée par une épaisseur de la couche organique de plus de 20-30 cm, alors que celle de l'épinette noire ne l'était pas. L'accroissement moyen annuel du peuplier faux-tremble diminuait avec une couche organique plus épaisse, qui par contre, n'affectait pas l'accroissement moyen annuel de l'épinette noire. Des analyses dendroclimatiques ont montré que la croissance radiale de l'épinette noire était favorisée par des printemps doux et des étés frais. Les basses températures et l'humidité du sol causées par une couche organique plus épaisse, ne seraient donc pas défavorables à l'épinette noire. Aussi, l'épaisseur de la couche organique n'avait que peu d'effet sur les relations croissance-climat de l'épinette noire. Dans l'ensemble, les conditions climatiques de l'année précédent la croissance et la température du mois de juin affectaient le plus la croissance du peuplier faux-tremble. Les corrélations avec le climat indiquent que les conditions fraîches et humides induites par une couche organique plus épaisse seraient défavorables au peuplier faux-tremble. La profondeur de la couche organique influençait surtout les corrélations croissance-climat pour les variables climatiques qui peuvent causer une amélioration ou détérioration des conditions de site pour le peuplier faux-tremble. La croissance de l'épinette noire pourrait bénéficier de la hausse des températures en hiver, au printemps et en automne prévue par les Modèles Régionaux Canadiens du Climat actuels, alors que les étés plus chauds pourront lui être défavorables en causant un stress hydrique. À l'opposé, la croissance du peuplier faux-tremble pourrait être favorisé par une hausse des températures en été, mais des automnes plus chauds et d'avantage de neige en hiver pourraient lui être nuisibles. Les changements climatiques pourront être favorables ou défavorables à la croissance des deux espèces, tout dépendant de la balance entre la hausse des températures et l'augmentation des précipitations. L'épinette noire aura probablement une réponse relativement uniforme aux changements climatiques dans la région, alors que la réponse du peuplier faux-tremble pourrait varier localement selon l'épaisseur de la couche organique. Dans les sites humides, le peuplier faux-tremble bénéficiera le plus d'étés plus chauds et secs et connaîtra une amélioration de sa croissance radiale. La modification des conditions de site causées par l'altération des conditions climatiques et du cycle de feu jouera un rôle primordial pour la distribution future du peuplier faux-tremble dans le paysage forestier de l'ouest du Québec.

Mots clés : *Picea mariana*, *Populus tremuloides*, changements climatiques, couche organique, croissance radiale, distribution.

1.2 Introduction

According to the most recent report of the Intergovernmental Panel on Climate Change, worldwide surface temperatures have increased by 0.74°C between 1906 and 2005 (IPCC 2007). Temperatures are expected to increase the most at mid to high northern latitudes (IPCC 2007), and are projected to rise by 1.5 to 5.2°C by the middle of the 21st century over western Quebec (Ouranos 2010). The higher temperatures are expected to be accompanied by increased precipitation by 10-25%, except during the summer months for which precipitation is projected to know a slight decrease (2%) or to increase by no more than 15% (Ouranos 2010). Climate change directly affects tree growth and distribution and consequently, influences the migration potential of tree species and the composition of forests (Hansen *et al.* 2001; Mohan *et al.* 2009). Simulation models, most of which only integrated climate variables, have been used extensively to forecast migration rates of tree species and future forest composition (Hansen *et al.* 2001; Lafleur *et al.* 2010). Although climate is the major determinant factor for tree distribution at the continental and subcontinental scales, other more local factors, such as soil conditions, are important for tree distribution when considered at the landscape and stand scales (Hansen *et al.* 2001; Pearson & Dawson 2003). However, soil conditions are often omitted from the simulation models used to forecast tree migration rates (Lafleur *et al.* 2010), which can be partly due to a lack of studies determining the relationships between tree growth, distribution and response to climate and local soil conditions.

Growth responses to climate of aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* [Mill.] B.S.P.), the dominant species of the eastern Canadian boreal forest, have been assessed in recent dendroclimatological studies. In eastern Canada, aspen growth has been shown to be mostly influenced by climatic conditions of the previous year, while black spruce is influenced by temperatures at the start of and during the growing season (Hofgaard *et al.* 1999; Tardif *et al.* 2001; Drobyshev *et al.* 2010; Huang *et al.* 2010). These climate-growth relationships, as well as growth and distribution at the landscape scale of the two species in general have however proven to be affected by variations in soil conditions. Hogg *et al.* (2005, 2008) pointed out the role of proportions of silt present in the mineral soil on aspen productivity in western Canada and Leonelli *et al.* (2008) found that aspen climate

sensitivity varied between stands with different soil moisture conditions and nutrient availability. In western Quebec, black spruce climate sensitivity was reported to vary across a soil organic layer (SOL) depth gradient characterized by highly variable soil conditions (Drobyshev *et al.* 2010).

In the Clay Belt of northern Ontario and western Quebec, important accumulation of organic matter on the forest floor leads to high SOL depths and to paludification of the forests, i.e. the successional development towards forest peatlands (Fenton *et al.* 2005; Lecomte *et al.* 2006). Natural stands are typically initiated by stand-replacing fires leaving an exposed mineral soil on which SOL will accumulate over time (Fenton *et al.* 2005; Lecomte *et al.* 2006; Simard *et al.* 2007, 2009). Consequently, age of the trees and SOL thickness will vary together, both being function of the age of a stand, which is directly related to the time since last fire (Simard *et al.* 2009). SOL accumulation improves the water-holding capacity (Lavoie *et al.* 2007), leading to excess moisture, and ultimately to the rise of the water table, inducing a decrease of soil temperature and nutrient cycling (Foster 1985; Oechel & Van Cleve 1986; Simard *et al.* 2007). SOL accumulation causes important decreases in stand productivity (Oechel & Van Cleve 1986; Simard *et al.* 2007) and accounts for more frequent negative growth anomalies (i.e. particularly narrow growth rings) in black spruce (Drobyshev *et al.* 2010).

Both aspen and black spruce are very frequent in the boreal forest, both regenerate naturally after fire (Lecomte & Bergeron 2005), and both are harvested and have high economical value (Gagnon *et al.* 1998). The considerable modifications of the forest landscape (i.e. changes in composition and structure) that could result from major climate changes could thus have substantial impacts on economics. In the Clay Belt the influence of SOL thickness on black spruce and aspen growth and distribution within landscape may therefore be important. The high variability of SOL depths, and of soil conditions it induces, is likely to be a major local factor in mediating different growth responses of the two species to climate change. The aim of this study was to assess the effects of SOL depth on the distribution at the landscape scale, growth and climate-growth relationships of black spruce and aspen. The following hypotheses were tested: (1) tree growth diminishes with a thicker organic layer, (2) aspen has different growth-responses to climate than black spruce, and (3)

trees growing on a thick organic layer have a strong positive response to warmer temperatures and are less sensitive to precipitation, whereas trees growing on mesic to xeric sites are disadvantaged by warm and dry growing seasons. By integrating the role of soil conditions in tree growth and distribution within landscape, this study should lead to a better understanding of the complexity of tree responses to climate change and of the importance to include various determinant factors, depending on the scale considered, when trying to predict migration rates and future forest composition.

1.3 Methods

1.3.1 Study area

The study area (49°03' – 49°29'N; 78°46' – 79°09'W) is located in the black spruce-feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) bioclimatic domain of western Quebec and the Northern Clay Belt of Quebec and Ontario (Fig. 1.1; Simard *et al.* 2008). The Clay Belt consists of thick clay deposits covering the Precambrian Shield left by proglacial Lake Barlow-Ojibway and forms a vast clay plain (Veillette *et al.* 2004). The topography of the study area is rather flat, with a mean altitude of 250 m to 300 m above sea level, and a few bedrock hills breaking the monotony of the clay plain. Half of the glaciolacustrine deposits are covered by thick layers of SOL, reaching depths of 60 cm or even more and causing paludification of the forests in some areas. In absence of paludification, the soils found in the Clay Belt are mostly luvisols and gleysols (Groupe de travail sur la classification des sols, 2003).

The climate of the area is continental and characterized by cold and dry winters and by warm summers. During the winter very cold continental arctic air masses coming from the north dominate, whereas the climate of summer months is influenced by moist Atlantic maritime tropical air masses from the south and by dry maritime arctic air masses from the north (Pigott & Hume 2009). According to the climate normals calculated from the data recorded at the La Sarre and Joutel meteorological stations (located 30 km south and about 40 km northeast of the study area respectively) from 1971 to 2000, the mean annual temperature of the area varies between 0.1°C and 0.7°C. Total annual precipitation is around 890mm,

with 35% received during growing season and 30% falling as snow (Environment Canada, 2010). Ground frosts are common during the growing season, but the study area is not subject to permafrost (Brown & Gangloff, 1980).

The area is dominated by black spruce stands with variable height and density (Simard *et al.* 2008). Jack pine (*Pinus banksiana* Lamb.) and aspen are common in the region as well and can be found in pure stands or mixed stands with black spruce. Fire is the main natural disturbance in the black spruce-feathermoss domain (Simard *et al.* 2008). The fire cycle in the region has increased from around 100 years before 1850, to 360 years since 1920 (Bergeron *et al.* 2004). In the study area, the spruce budworm (*Chorisonneura fumiferana* Clem.) remains of low impact on black spruce population dynamics, compared to what is observed in most of its range (Gray *et al.* 2000; Lussier *et al.* 2002; Gray, 2008). The forest tent caterpillar (*Malacosoma disstria* Hubner.) is an important defoliator of aspen, but outbreaks in the study area are of short duration, relatively low amplitude and occur less often than south of the 49°N (Cooke & Lorenzetti, 2006; Huang *et al.* 2008).

1.3.2 Data collection

Sampling took place in 2008 and 2009 in three sub-areas with mixed black spruce and aspen stands with different SOL depths. A humidity gradient ranging from xeric stands to paludified stands was covered with ten sampling sites distributed within the three sub-areas of Villebois (VIL), Selbaie (SEL), and Wawagosic (WAW) (Fig. 1.1). The 10 sampling sites covered a mean SOL depth gradient ranging from 2.41 cm to 15.55 cm (Table 1.1), but the sampled trees were found on SOL depths from 1cm up to 23cm. The soil in sites SEL3 and VIL3 was clay loam and the soil in VIL4, which was located on a rocky outcrop, was sandy loam. In all the other sites, the mineral soil was mostly clay. The 10 sites were located within mixed black spruce-aspen stands. Stands on a thick SOL were dominated by black spruce and aspen never exceeded 30% of the stand. The number of aspen increased on mesic and xeric sites, where jack pine, balsam fir (*Abies balsamea* (L.) Mill.), paper birch (*Betula papyrifera* Marsh.), and some balsam poplar (*Populus balsamifera* L.) were present too. Understorey vegetation of moist sites was mostly composed of feathermosses (*Pleurozium schreberi* (Brid.) Mitt., *Ptilium crista-castrensis* (Hedw.) De Not. and other species), and ericaceous

shrubs (*Vaccinium* spp. L., *Rhododendron groenlandicum* (Oeder) K.A. Kron & W.S. Judd, *Kalmia angustifolia* L., *Chiogenes hispidula* (L.) Torr. & Gray). Herbaceous species were more frequent in the mesic and xeric sites, and shrubs like speckled alder (*Alnus incana* (L.) Moench ssp. *rugosa* (Du Roi) R.T. Clausen), squashberry (*Viburnum edule* (Michx.) Raf.) and northern bush honeysuckle (*Diervilla lonicera* Mill.) were dominant in the xeric sites' understory.

In each of the 10 sites, 10 to 19 circular 0.063 ha plots were established, depending on the availability of aspen and black spruce in the site ($n_{\text{total}} = 145$; Table 1.1). The plots were positioned around a living and healthy looking aspen and were encompassing at least one of the bigger black spruces of the stand. Thus one aspen and one black spruce were sampled per plot. For each of the selected aspen and black spruce, two cores were extracted on two opposite sides of the trunk, at a height of about 30 cm above the ground. However, in one site (SEL1), cross-sections had to be taken from five of the ten sampled aspens as no readable core could be extracted from their rotten trunks. Two of those five aspens had died recently (in the years 2000), but were selected anyway as there were not enough living aspens on the site.

To characterize soil properties, three pits were dug at approximately 20 cm around each of the sampled trees. SOL thickness was measured, samples of mineral soil and organic layer were taken and the mineral soil texture was determined in the field by the feel method (Thien 1979; Béland *et al.* 1990). In the summer of 2009, SOL relative humidity was measured at 10 plots within each site (100 plots in total) with a soil moisture sensor (ThetaProbe Soil Moisture Sensor Type ML2x, Delta-T Devices, Cambridge, England). Five measures were taken in every plot and the two most extreme values were later excluded to calculate a mean value of the SOL moisture. The measures were taken within two days and after two sunny days in August, on August 16th and 17th 2009. Thirty data loggers (iButton DS1921G, Maxim Electronics, Dallas, Texas, USA) recorded the soil temperatures every 255 minutes for 12 months (August 2009 to August 2010). The data loggers were buried between the SOL and the mineral soil in 30 plots of different sites distributed along the SOL thickness gradient.

1.3.3 Soil analyses

To determine the texture of the mineral soil sampled for each of the 290 sampled trees, particle size analysis was conducted. The three soil samples taken around each tree were mixed together, air dried and sieved through a 2 mm grid. The hydrometer method was then used to determine the soil texture and soil water content was determined by oven drying with the gravimetric method (Audesse 1982; Sheldrick & Wang 1993; Topp 1993).

The three SOL samples for each tree were mixed as well, sieved at an aperture of 4 mm and oven-dried at 40°C during 60 hours. Total carbon (C, %), total nitrogen (N, %), total sulphur (S, %), total phosphorus (P, %) and Ph in CaCl₂ were determined as in Laganière *et al.* 2010 (Appendix 1.1; D. Paré, Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Québec, Québec).

1.3.4 Tree-ring data

The cores and cross-sections taken from black spruce and aspen were prepared and measured following standard methods in dendrochronology (Stokes & Smiley 1968; Speer 2010). The samples were first mounted, sanded and visually cross-dated using the skeleton plot method. The ring widths were then measured using a Velmex micrometer (Velmex Incorporated, Bloomfield, New York, USA) and TSAP-Win Professional, version 0.55 (Rinntech, Heidelberg, Allemagne) at a precision of 0.01 mm. Measurements were visually verified with TSAP-Win Professional, before the dating of tree-ring series were validated using the program COFECHA (Grissino-Mayer 2001; Speer 2010). Two radii measured for each tree (on the two cores or on two radii on cross-sections) were then averaged.

Raw ring-width series represent growth variability at multiple frequencies. In this study the focus of the analyses was on high frequency variability and the treatment of time series was therefore designed to remove lower frequencies in tree-ring series. To obtain high frequency annual growth chronologies, the cross-dated tree ring series were detrended in the ARSTAN program using a 32 year cubic smoothing spline with a 50% frequency response

(Cook 1987; Fritts 1991; Speer 2010). By dividing the original chronology values by the predicted values, ring-width measures were transformed into index values. To remove temporal autocorrelation, the series were prewhitened by autoregressive modelling (Cook 1987). Residual single-tree chronologies were computed (by using the “core series save” option) to analyse climate-growth relationships on single trees for the two species (black spruce $n = 145$ and aspen $n = 143$).

In western Quebec severe defoliation of aspen can occur during insect outbreaks caused by the forest tent caterpillar. Years of severe defoliation, manifested by very narrow and/or white rings (Sutton & Tardif 2005), were observed in some of the sampled trees in 1980 and 1999-2001. These years were previously identified as years of severe outbreaks (Huang *et al.* 2008). Years of growth suppression in the chronologies can be identified and the impact of defoliation on growth could be potentially removed by using a chronology of a non-host species (Swetnam *et al.* 1985; Speer 2010). However, this procedure requires that the host and non-host species have a similar response to climate. This was not the case for aspen and black spruce (Huang *et al.* 2010), which precluded use of this method in the current study. Therefore, the aspen residual chronologies were not modified prior to analyses.

1.3.5 Statistical analyses

1.3.5.1 Soil characteristics

Soil data collected for this study (SOL chemical properties and relative humidity, mineral soil texture and water content, and soil temperature) was analysed in order to see the relationships between SOL thickness and other soil variables. A correlation analysis, at a significance level of $\alpha = 0.05$, was conducted on 12 soil variables and relationship between SOL thickness and the age of the trees was explored through linear regressions. The 12 soil variables and the age of the trees were put together in a principal components analysis (PCA) for all of the trees which had the available data ($n = 284$). The 12 soil variables and the age of the trees being expressed in different units, a correlation matrix was used for the PCA. The correlation between the maximum, minimum, mean annual soil temperature and variance of soil temperature recorded with the data loggers and the SOL thickness was analysed as well.

1.3.5.2 Soil organic layer and tree distribution within landscape

Before any analysis were conducted on the dendrochronological data collected for this study, the effect of SOL thickness on the distribution across the landscape of black spruce and aspen was tested with forest inventory data from the Lake Matagami lowland ecoregion (ecoregion 6a) gathered by the Quebec Ministry of Natural Resources (QMNR) in 1996. A total of 1309 circular permanent sampling plots (PSP) of 400 m² were sampled every 250 m along 1.5 km transects in the ecoregion 6a. In each PSP, trees with a diameter > 10 cm were identified to species and tabulated in 2 cm wide diameter classes. Subplots of 40 m² were used to identify and measure trees with a diameter < 10 cm. The basal area (m².ha⁻¹) of each species in the PSPs therefore obtained was plotted against SOL depth measures taken in every PSP. The relationship between SOL thickness and distribution of black spruce was explored using a linear regression of the basal area on SOL depth as the data was fitted well by a normal distribution. The significance was established at $\alpha=0.05$ for estimates of the linear regression coefficient. For aspen the linear regression was inappropriate, but a logistic regression could be used as the data was best fitted by a negative binomial distribution. The basal area of aspen in PSPs was transformed in a variable expressing the presence or absence of aspen in the PSPs.

1.3.5.3 Soil organic layer and mean annual increment

The mean annual increment (MAI) of a tree is an expression of its mean annual radial growth obtained by dividing its age with its diameter and is given in cm.year⁻¹ (Husch *et al.*2003). The age and the diameter of the black spruces and aspens sampled in 2008 and 2009 was determined from the counted and measured cores and were then used to calculate the tree's MAI. In order to establish the only effect of SOL depth on the growth of black spruce and aspen, SOL thickness values were plotted against the MAI of trees that were from 60 to 100 years old, in order to compare trees with similar age, and regression analyses were conducted as well (black spruce: $n = 99$; aspen: $n = 98$).

1.3.5.4 Dendroclimatic analyses

Data used for dendroclimatic analyses were generated using BioSIM (Régnière & Bolstad 1994; Régnière 1996). Monthly climate data for the ten sampling sites and for the period 1900-2009 were obtained by interpolating data from the ten closest weather stations and adjusting for differences in latitude, longitude, and elevation between the data sources and the locations (Girardin 2010). The number of weather stations used as data sources remained the same for the entire period, but as the density of meteorological stations was lower at the first half of the 20th century, the mean distance between the stations and the sampling sites decreased since that time (from 400 km to less than 200 km) and the data reliability increased. Dendroclimatic analyses used the climate data sets generated for the three sub-areas (SEL, VIL and WAW, Fig.1.1) by averaging data from all sites within a particular sub-area. Rationale for uniting sites in a sub-area was distance between sites, which was set to be less than 20 km. The climate variables included monthly mean temperature (°C), monthly total precipitation (mm), monthly total snowfall (mm), and total degree-days (> 5°C), the sum of all individual degree-days, which are the number of degrees by which the mean daily temperature is above 5°C (Allaby 2007). Finally, the Monthly Drought Code (MDC) was calculated from May to October using monthly maximum temperature and monthly total precipitation generated in BioSIM (Girardin & Wotton 2009). The MDC is a monthly version of the Drought Code developed to capture moisture content of deep and compact organic layers of the forest floor (Turner 1972).

The influence of climate on tree growth was investigated using response and correlation functions calculated between *single tree* residual chronologies and climate variables in the software package DENDROCLIM2002 (Biondi & Waikul, 2004). Significance of response and correlation coefficients was tested at the 0.05 level through bootstrapping. Since response function coefficients were obtained through principal component analysis, they represent unique contribution of single climate variables to annual growth. The 288 residual chronologies were compared against (1) the mean monthly temperatures and monthly total precipitation spanning from May prior to the growth year to August of the year of growth, (2) seven composite variables and (3) the total degree-days

above 5°C. Based on patterns in climate-growth relationships determined through prior analysis, seven composite climate variables were developed. Four seasonal drought codes were obtained by averaging MDCs (previous June-August, previous September-October, current April-May, and current June-August) and three composite snow variables (previous Sep-Nov, Dec-Mar, Apr-May) were developed by summing the monthly amount of snowfall.

1.3.5.5 Soil organic layer and climate sensitivity

Organic matter accumulates on the forest soil forming a SOL, being a function of time since the last fire and of the age of the stand (Fenton *et al.* 2005; Simard *et al.* 2007). Up to 40 cm of organic matter can accumulate on the forest floor in the first 100 years after a fire (Simard *et al.* 2009). Therefore it can be assumed that the SOL depth measured during this study has not always been the same and that the trees all started growing on a thinner SOL. To remove the possible effect of SOL accumulation through time on climate-growth response and correlation coefficients established earlier, the response and correlation functions between tree growth and monthly climate variables of annual weather were calculated again but for relatively shorter and fixed intervals of time spanning over the last decades. Also, to ensure the statistical stability of these analyses the number of climate variables had to be reduced as the analysed interval was much shorter than before. Only a subset of selected climate variables which significantly related to the growth of each of the species in the entire chronology correlation coefficients calculated earlier was used. One interval of time spanning from 1982 to 2007, which limited the effect of SOL accumulation and yielded climate-growth correlation and response coefficients close to those obtained for the entire chronologies, was used.

To assess the effect of SOL thickness on climate-growth relationships of black spruce and aspen, linear regressions were fit between climate-growth correlation coefficients and SOL depth, independently for six selected climate variables. In order to compare trees of similar age, only trees that were from 60 to 100 years old were used (black spruce: $n = 99$; aspen: $n = 98$).

1.4 Results

1.4.1 Soil characteristics

The correlation analysis showed that SOL thickness was significantly correlated to all the chemical properties of the SOL (Table 1.2). The C/N ratio had the strongest positive correlation with SOL thickness ($r = 0.70$) and the pH had the strongest negative correlation with SOL thickness ($r = -0.68$). Total C and SOL relative humidity were positively correlated to SOL thickness ($r = 0.45$ and $r = 0.31$ respectively) and total N, total S, and total P were negatively correlated to SOL thickness ($r = -0.42$, $r = -0.29$ and $r = -0.16$ respectively). Mineral soil texture variables didn't show any significant correlation with SOL thickness. Linear regressions showed that the age of the trees and the SOL thickness were related as well (for black spruce: $R^2_{adj} = 0.43$, $p < 0.0001$, $n = 145$; for aspen: $R^2_{adj} = 0.45$, $p < 0.0001$, $n = 143$).

PCA conducted on soil variables showed that the first five principal components (PCs) had an eigenvalue above 1. PCI, PCII, PCIII, PCIV, and PCV represented respectively 29.94%, 16.99%, 15.69%, 11.54% and 7.79% of the total variance for a cumulative total of 81.95% (Fig. 1.2). Only PCI and PCII are presented. For both species, the PCA confirmed the relationships that were observed between SOL thickness, soil variables and age of the trees through correlation and regression analyses.

Correlation analysis from the data provided by the 28 data loggers showed that SOL thickness was strongly and negatively correlated to the mean annual and maximum soil temperatures ($r = -0.80$ and $r = -0.84$ respectively) and to the variance of temperature through the year ($r = -0.86$), but showed no correlation with the minimum temperature (Fig. 1.3).

The linear regression conducted on the age of the trees and SOL thickness revealed a significant relationship between the two variables. In order to compare only trees with the same age, the trees younger than 60 years and older than 100 years were therefore excluded from the dataset for further analyses, reducing the number of black spruce to $n = 99$ and of aspen to $n = 98$. This removed a part of the relationship between age and SOL thickness

(black spruce: $R^2_{adj} = 0.08$, $p = 0.0030$; aspen: $R^2_{adj} = 0.04$, $p = 0.0367$). SOL chemical properties and soil temperatures correlated well with SOL thickness and showed the expected relationships. Mineral soil texture was not related to SOL thickness, neither was it related to tree growth (results not shown). Considering these results and what was already known from the literature, SOL thickness should be considered hereafter as representing not only the impact of the direct effects of thickness of the organic layer but also as an integrator of a complex gradient of associated soil conditions.

1.4.2 Soil organic layer and tree distribution within landscape

The effect of SOL thickness on the distribution across the landscape of black spruce and aspen in the ecoregion 6a was highly significant for aspen but not for black spruce. Plots of the basal area on the PSPs of black spruce and aspen on SOL thickness clearly showed that black spruce can be found on sites with SOL depths up to 100 cm (Fig. 1.4a), whereas the distribution of aspen across the landscape was very limited by SOL depth, with a threshold at 20 cm (Fig. 1.4b). The linear regression indicated that distribution of black spruce was not significantly affected by SOL depth ($p = 0.316$). The logistic regression of distribution of aspen on SOL thickness showed that the probability to find aspen diminished exponentially with increasing SOL thickness (Fig. 1.4c). With a $p < 0.0001$, the effect of SOL thickness on the distribution of aspen was highly significant.

1.4.3 Soil organic layer and mean annual increment

Selecting from the dataset only trees which were 60 to 100 years old effectively eliminated the effect of age on MAI, which allowed for analysis of SOL depth-growth relationship. Prior to selection, the age was related to MAI (black spruce: $R^2_{adj} = 0.44$, $p < 0.0001$, $n = 145$; aspen: $R^2_{adj} = 0.21$, $p < 0.0001$, $n = 143$). For the selected age span, the effect became negligible (black spruce: $R^2_{adj} = 0.01$, $p = 0.1537$, $n = 99$; aspen: $R^2_{adj} = 0.09$, $p = 0.0016$, $n = 98$).

For both of the species, the MAI proved to be influenced by SOL thickness (Fig. 1.5). The linear regression showed that for black spruce the MAI diminished when the SOL depth increased, but this influence was rather low ($R^2_{adj} = 0.03$, $p = 0.0381$, $n = 99$; Fig. 1.5a). MAI of aspen was much more affected by SOL thickness and decreased significantly with increasing SOL depth ($R^2_{adj} = 0.30$, $p < 0.0001$, $n = 98$; Fig. 1.5b), even though the age of the trees accounted for some of the variability ($R^2_{adj} = 0.09$, $p = 0.0016$, $n = 98$).

1.4.4 Growth sensitivity to annual weather

Black spruce and aspen growth displayed different patterns of correlation with most of the climate variables (Fig. 1.6). Only proportions of trees having significant correlation or response function coefficients with the climate variables were, as the highly variable correlation and response coefficients values of the 288 analysed trees could not be expressed by simple mean values such as to be meaningful. Monthly mean temperature and MDC yielded opposite growth responses between the two species. Black spruce growth was negatively correlated to summer temperatures (June to August and July to August of the previous year) and showed positive correlations with early winter (November and December of the previous year) and spring (March to May) temperatures (Fig. 1.6a). For precipitation the highest numbers of positive correlations were found for June of the year before growth and March of the current year and the highest numbers of negative correlations were found for August of the previous year and May of the year of growth. Black spruce growth also related negatively to summer MDC (June and August composite variable) of the year prior to growth and related positively to spring MDC (April-May composite variable). Amount of snowfall in autumn of the previous year (September to November) was mostly negatively correlated with black spruce growth. The total numbers of degree days of the previous and current year were negatively correlated with black spruce growth.

Aspen growth was generally negatively correlated to temperature especially during fall (October-November), in January and in August, and showed a high number of positive correlations to June and July temperature (Fig. 1.6b). Precipitation was found to yield fewer correlations with aspen growth than with black spruce growth. Aspen growth negatively related to June and August precipitation of the previous year, as well as to winter

precipitation (January to March). Autumn MDC (September-October composite variable) of the year prior to growth showed positive correlations and amount of snowfall generally yielded negative correlations, especially in winter (December to March). And as for the degree days the correlations were negative for the previous year and positive for the current year of growth.

1.4.5 Soil organic layer and climate sensitivity

As the age of trees was correlated to MAI, it had to be made sure that age would have no effect on the analysed climate-growth correlations. Once the youngest and the oldest trees were excluded, linear regression showed that for none of the selected climate variables, climate-growth correlation coefficients were influenced by the age of trees (not presented).

The six climate variables that yielded the highest number of significant correlation coefficients in the dendroclimatic analysis and which were used in the linear regressions analyses of climate-growth correlation coefficients on SOL depth for black spruce were the mean temperature of December of the previous year and of April and June of the year of growth, precipitation of previous June and May of the current year and April to May MDC composite variable of the year of growth (Figure 1.7). The linear regressions showed that SOL thickness significantly, but weakly, influenced climate-growth correlation coefficients for only two of the six climate variables. The climate-growth correlation coefficients for previous December mean temperature showed to be the most influenced by SOL depth ($R^2_{adj} = 0.07$, $p = 0.0061$, $n = 99$), whereas previous June precipitation was even less influenced by the SOL depth ($R^2_{adj} = 0.05$, $p = 0.0164$, $n = 99$).

The six climate variables that were selected for aspen were the mean temperature of previous November and current June and August, total precipitation of August prior to the year of growth, previous September to previous October MDC composite variable and the total number of degree-days of the year of growth (Figure 1.8). Only the climate-growth correlation coefficients for previous August precipitation and previous September to previous October MDC were significantly impacted by SOL thickness ($R^2_{adj} = 0.14$, $p = 0.0001$; and

$R^2_{adj} = 0.12$, $p = 0.0003$ respectively with $n = 98$). SOL thickness had no significant effect on the climate-growth correlation coefficients for the other climate variables.

1.5 Discussion and conclusions

1.5.1 Distribution and growth limiting effect of SOL

SOL thickness clearly showed to be limiting aspen distribution within landscape and MAI, whereas it had no effect on distribution and only a weak negative effect on MAI of black spruce. The fact that SOL thickness has not the same effect on the two species could be explained by their differences in root system development. With a bulk usually found in the upper 20 cm of organic horizons, black spruce has a shallow root system that easily grows in SOL and shifts from the mineral soil to the SOL, forming new adventitious roots, as organic matter accumulates around the trunk (Burns & Honkala 1990a; Ruess *et al.* 2003; Krause & Morin 2005). The formation of adventitious roots causes the true root collar to sink below ground level, thus the age of black spruce growing on thick SOL might have been underestimated (Desrochers & Gagnon 1997). A greater effect of SOL depth on MAI of black spruce could have been observed with the true age of all trees. Aspen is characterized by a deeper root system than black spruce, which seems to be very influenced in growth and development by both physical and chemical properties of soil (Burns & Honkala 1990b). Increasing SOL depth modifies considerably physical (e.g. temperature, excess moisture, rise of water table) and chemical (e.g. nutrients, pH) soil properties (see results on soil characteristics; Foster 1985; Oechel & Van Cleve 1986; Lavoie *et al.* 2007; Simard *et al.* 2007, 2009). SOL also lowers the soil temperature (see results on soil characteristics; Oechel & Van Cleve 1986), and the two species seem to have different optimum root growth temperatures, the optimum root growth temperature for black spruce (16°C) being lower than the optimum temperature for aspen (19°C) (Peng & Dang 2003). Landh usser *et al.* (2001) showed that for aspen there was only weak leaf and shoot growth and no root growth at all at low soil temperatures and that assimilation decreased with soil temperature, whereas low soil temperatures only lowered root growth and had no effect on leaf and shoot growth and assimilation for white spruce (*Picea glauca* (Moench) Voss). The distribution of aspen across the landscape was limited by a threshold of 20-30 cm of SOL depth. This threshold may be

explained by a rather drastic change in soil properties as the water table rises above the mineral soil (Simard *et al.* 2007). The deeper root system of aspen would then be drowned in the water table, causing hypoxic conditions and eventually death of the roots (Kozłowski 1997).

The distribution limiting effect of SOL thickness on aspen at the landscape scale observed here could be due to a reverse effect of aspen limiting the accumulation of organic matter. It has been shown that aspen litter improves the decomposition of organic matter in mixed aspen and black spruce stands, due to its higher quality and to its specific conditions and decomposer communities that develop in its forest floor (Fenton *et al.* 2005; Légaré *et al.* 2005; Laganière *et al.* 2010). But our results clearly showed that aspen hardly grows on thick SOL and it seems that regeneration of aspen could also be limited by thick SOL. Aspen seedlings normally develop on mineral soils, and root suckers usually develop from roots that are from 2 to 10 cm beneath soil surface (DeByle & Winokur 1985, cited in Burns & Honkala 1990b; Kemperman 1978, cited in Frey *et al.* 2003). SOL thickness could therefore directly impede aspen regeneration, and indirectly through the cooler conditions and the rise of the water table as low soil temperature and excess soil moisture seem to inhibit sucker production (Crouch 1986; Anderson *et al.* 2001; Frey *et al.* 2003). However, it would be necessary to further investigate the regeneration limiting effect of SOL thickness and to test, whether the observed threshold of 20-30 cm of SOL depth limiting aspen distribution within landscape, is specific to the study region or if it can be observed elsewhere through the entire distribution range of aspen.

In this study MAI of black spruce did not seem to be limited by SOL thickness, but it is to be kept in mind that this study did not cover the entire range of distribution of black spruce along the SOL depth gradient. In other studies, which covered a greater range of SOL depth gradient, higher SOL depths have been found to negatively affect MAI and productivity of black spruce (Oechel & Van Cleve 1986; Simard *et al.* 2007, 2009). Also, in the initial dataset, the age of the trees was significantly correlated to SOL thickness, which can be explained by the fact that organic matter accumulating on the forest soil is a function of time since the last fire (Fenton *et al.* 2005; Simard *et al.* 2007), as well as is the age of the trees when the stand was initiated by a fire, which was the case for the stands sampled in this

study (Bergeron *et al.* 2004). But the exclusion of trees younger than 60 years and older than 100 years from the dataset removed the greatest part of correlation between age and SOL thickness, thus limiting the effect of age on the results.

1.5.2 Climate sensitivity of radial growth

Radial growth of black spruce was mostly influenced by early-winter, spring and growing season temperatures. The positive correlations with early winter temperatures (mostly in December), could be related to the root damage caused by cold temperatures on the shallow root system of black spruce when there is no snow pack (Miller-Rushing & Primack 2008; Bigras 1997). Also, during winter there is less snow with colder temperatures, as low temperatures tend to occur with high pressure systems (Pigott & Hume 2009; Brown 2010). Current March–May temperatures positively influenced radial growth of black spruce, possibly by triggering an early onset of photosynthesis leading to better growth due to a longer growing season (Suni *et al.* 2003; Goodine *et al.* 2008). The negative correlations with current summer temperatures, along with the negative correlations with June-August MDC indicated that black spruce might suffer from drought stress during the summer. Previous summer MDC showed to affect negatively black spruce growth as well, whereas previous June precipitation had a positive influence on radial growth. These results showed that radial growth of black spruce was favoured by higher temperatures in early winter and in spring, allowing an earlier onset of the growing season. Low summer temperatures were not limiting for black spruce growth, but favoured it by reducing temperature-induced water deficit. Overall, these results are supported by other studies conducted in the eastern Canadian boreal forest (Hofgaard *et al.* 1999; Tardif *et al.* 2001; Drobyshev *et al.* 2010; Huang *et al.* 2010).

For aspen, temperature generally had less influence on radial growth variability. Temperatures previous to the growing season (September–November and January especially) negatively affected radial growth. High autumn air temperatures in the previous year may lead to higher consumption of carbohydrates reserved for the current year's growth, by increasing respiration (Fritts 1971). In January, temperature and precipitation are positively correlated as high temperatures tend to occur with low pressure systems bringing precipitation (Pigott & Hume 2009; Brown 2010). The negative correlations with higher

temperatures in January could thus be due to the thicker snow cover, which may delay soil thawing and start of the growing season. The negative correlations with January precipitation and winter snowfall support this hypothesis. June and July temperatures yielded positive correlations with aspen growth. Weather conditions in June and early July have the potential to determine the photosynthetic activity rate and thus the growth and productivity of the trees for the entire growing season, by controlling budburst, root, leaf and shoot growth of aspen in this region (Fahey & Hughes 1994; Wan *et al.* 1999; Burton *et al.* 2000; Landhäusser *et al.* 2001, 2003; Fréchette *et al.* unpublished). Precipitation mostly yielded negative correlations, and summer MDC correlated positively with growth, indicating that aspen did not suffer from drought stress. Overall, the weather conditions of the previous year and current June temperature were the most important factors affecting aspen growth, showing the importance of nutrient storage in the previous year and of good root, shoot and leaf growth at the start of the growing season. Other studies conducted in eastern Canada had similar findings (Cooke & Roland 2007; Lapointe-Garant *et al.* 2009; Huang *et al.* 2010).

The second hypothesis, which stated that the radial growth of aspen would be influenced by other climate variables than that of black spruce, was confirmed by the different climate-growth correlation and response patterns. These differences were expected, as previous studies have shown that boreal coniferous and deciduous tree species were influenced by climate differently (Tardif *et al.* 2001; Huang *et al.* 2010). Temperature and MDC yielded inverse correlations among the two species, while black spruce growth was favoured by warm temperatures in autumn, winter and spring and by cool and wet summers, aspen radial growth was negatively affected by warm temperatures in autumn and winter and reacted positively to hot and dry summers. Black spruce would suffer from moisture stress during the growing season, whereas aspen might be limited by excess moisture. These opposite responses to water stress have been observed before in similar species, *Picea abies* (L.) Karst. and *Populus tremula* L. (Tatarinov *et al.* 2005). This can be explained by the fact that the shallow root system of black spruce is confined to the unsaturated surface layers of SOL (upper 20 cm), which tend to dry out faster than underlying mineral soil during a summer drought (Lieffers & Rothwell 1987; Rothwell *et al.* 1996).

1.5.3 Effects of SOL on growth response to climate

Low summer temperatures and moist conditions during the growing season had a positive effect on black spruce radial growth, the cooler soil temperatures and the high soil moisture induced by SOL thickness would thus not affect negatively black spruce growth, at least not over the gradient covered by this study. This was clearly shown by the little effect SOL depth had on MAI. SOL depth also had very little effect on the climate-growth relationships of black spruce. The only significant effects were observed on the climate-growth correlation coefficients with previous June precipitation and temperature of previous December. The correlations with the temperature of December prior to growth were mostly positive, but grew less positive with a thicker SOL. Black spruces growing on sites with higher SOL depths may suffer less root damage, thanks to better thermal insulation caused by the SOL (Fig. 1.2; Bigras 1997; Gornall *et al.* 2007). Overall, black spruce seemed to become less sensitive to these weather variables with thicker SOL. Wilmking and Myers-Smith (2008) and Webb *et al.* (1993) also found spruce to become less sensitive to climate when it grows on higher SOL depths, but growth sensitivity to climatic extremes appeared to increase with increase in SOL (Drobyshev *et al.* 2010).

SOL thickness mainly influenced the growth responses of aspen to weather variables that enhance or deteriorate soil conditions for aspen growth in moist sites. High SOL depths could thus be impeding radial growth of aspen to respond to climatic variability directly and to benefit from favourable weather as it should. The positive effect of high temperatures and dry conditions during the growing season indicates that the cool and moist conditions induced by the SOL could be limiting radial growth. Indeed, the climate-growth correlations with the precipitation of previous August became more negative with a thicker SOL, due to the increase of excess soil moisture which may lead to hypoxic conditions and death of aspen roots (Kozłowski 1997). The climate-growth correlations with the MDC of previous September and October became more positive with higher SOL depths, indicating that aspen growing on important SOL depths benefit more from warmer and drier weather, as it enhances their site conditions by decreasing soil moisture and increasing organic matter decomposition rates (Anderson 1991; Davidson & Janssens 2006; Domisch *et al.* 2006). SOL

thickness limited aspen growth and distribution within landscape and could be limiting its capacity to completely exploit beneficial weather variations, at least at the scale of this study area. In western Canada, Leonelli *et al.* (2008) found that nutrient limited aspen showed lower climate sensitivity than aspen that were not limited by site conditions, the latter ones being able to completely exploit beneficial weather variations.

The third hypotheses which stated that trees growing on a thick organic layer would have a strong positive response to warmer temperatures and be less sensitive to precipitation, compared to trees growing on mesic to xeric sites, was partly confirmed for aspen. Aspen on thick SOL did benefit more from warmer temperatures, but suffered more from precipitation during the growing season compared to aspen on drier sites. Black spruce generally just grew less sensitive to precipitation as well as to temperatures with higher SOL depths. A significant effect on growth responses to climate could only be detected for two variables in each species. However, it has to be kept in mind that for both species, only the six most important climate variables were analyzed, growth response to less important climate variables could have been more influenced by SOL thickness.

1.5.4 Species- and site-specific response to climate change

Black spruce and aspen growth had different growth responses to climate and thus are likely to show different responses to climate change also. According to the Canadian Regional Climate Models (CRCMs) generated and supplied by Ouranos (de Elia & Coté 2010; Ouranos 2010), the mean temperature as well as the total precipitation will increase by 2046-2065, compared to 1961-1999, in western Quebec. Spring temperature is predicted to increase by 1.5°C to 3.3°C, summer and fall temperatures are predicted to increase by 2.3°C to 3.3°C and winter temperature is expected to show the highest increase with 2.8°C to 5.2°C more. Overall, total precipitation is predicted to increase too, with ~5 to 20% more precipitation in spring and fall, and ~15 to 30% more precipitation in winter. Total summer precipitation is not predicted to increase by more than ~15%, with a possible decrease of ~2%. Total number of growing degree-days above 5°C is expected to increase by 33 to 47%. Predictions for the MDC remain rather imprecise, especially for the summer months, with possible decreases or increases. The important increase in winter, spring and fall

temperatures could benefit black spruce growth, whereas the warmer summer temperatures might induce drought stress for black spruce, especially if summer precipitation is not increasing enough to compensate for the higher summer temperatures, which remains rather uncertain. As opposed to black spruce, aspen growth is likely to benefit from an increase in summer temperatures and even more if summer precipitation does not increase excessively. But higher fall temperatures could impede proper carbohydrates allocation and have negative effect on aspen growth. The important increase in winter precipitation could also have negative effects as the higher amounts of snowfall may delay the start of the growing season, if spring temperatures don't increase enough to promote faster melting of the snowpack. Both species will react individually and whether climate change will benefit their growth or not, will highly depend on the balance between increasing temperatures and precipitation.

According to the results of this study, climate change is likely to differently affect black spruce and aspen, because of the species' different growth responses to climate, but also because of their different relationships to sites conditions. At the landscape and local scale, local factors, such as SOL thickness and the site conditions directly related to it, can play an important role in modifying the tree's responses to climate and need to be considered when trying to assess the potential effects of climate change on tree growth and distribution (Pearson & Dawson 2003). In the Clay Belt and at the scale of the study area, the variability of SOL thickness is rather outstanding and might be one of the most important local factors in mediating different growth responses to climate. Overall, the response of black spruce to climate change should be more or less the same over the study area, as SOL thickness had little effects on the growth response to climate, except maybe of the sites with very high SOL depths (> 30 cm), an effect of SOL depth on black spruce growth response to climate having been observed there (Drobyshev *et al.* 2010). Aspen growth was more influenced by SOL thickness; it can thus be assumed that aspen growth will have different responses to climate change depending on the site conditions. Aspen growing on thick SOL might benefit the most from warmer and drier summers and show an increase in radial growth. Other studies have shown that aspen at the same latitude would suffer from these warmer and drier conditions (Lapointe-Garant *et al.* 2009; Huang *et al.* 2010), but these studies were conducted on drier sites. Aspen growth therefore might suffer or benefit from climate change depending on the moisture conditions of the site.

Climate change may cause a change in site conditions as well. Soil moisture depends on a hydrologic balance between drainage, precipitation and evapotranspiration, the latter ones being climate-driven and likely to be modified under the climate changes to come (Davidson & Janssens 2006). Higher soil temperatures and aeration, due to the reduction in excess soil moisture, promote a higher activity of decomposers, and therefore increase C mineralization and organic matter decomposition rates, eventually leading to a decrease in SOL thickness (Anderson 1991; Davidson & Janssens 2006; Domisch *et al.* 2006). SOL thickness is a limiting factor for aspen in the study area and the effects of climate on tree growth appeared to be species and site specific (see Drobyshev *et al.* 2010 for black spruce). Changing site conditions may cause a change in aspen distribution across the landscape in the study region, a decrease of SOL depth leading to an increased presence of aspen, and a change in climate-growth relationships. How fast organic matter accumulation rates and SOL depths will change can hardly be determined from past records and remains uncertain, as the more subtle climate changes of the last 2000 years did not seem to modify the rather gradual process of paludification (Simard *et al.* 2007). The balance between future precipitation and temperature changes and maybe even more importantly, the change of fire activity will be decisive in the modification of site conditions (Fenton *et al.* 2005; Simard *et al.* 2007, 2009; Bergeron *et al.* 2010).

Climate change can not only have consequences on forest composition, and dynamics by directly affecting tree growth, but also through indirect effects, like the modification of the site conditions or natural disturbances (Lapointe-Garant *et al.* 2010; Lo *et al.* 2010). Rate, type, and intensity of disturbance, (e.g. fire cycle, insect and pathogen outbreaks, weather anomalies like droughts or storms) may become considerably different under a changing climate (Wilf & Labandeira 1999; Bergeron *et al.* 2010; Woods *et al.* 2010). Local factors like topography, soil, aspect, and slope affect tree growth and forest composition at the stand scale (Pearson & Dawson 2003; Lo *et al.* 2010). Interactions between species are another determinant for tree growth and stand composition and might change as well under a changing climate (Davis *et al.* 1998). Depending on the scale considered, many ecological determinants other than climate need to be taken into account when trying to predict the effects of climate change on forests and more holistic studies still need to be conducted to gain a better understanding of the consequences of climate change.

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1.8 Figures

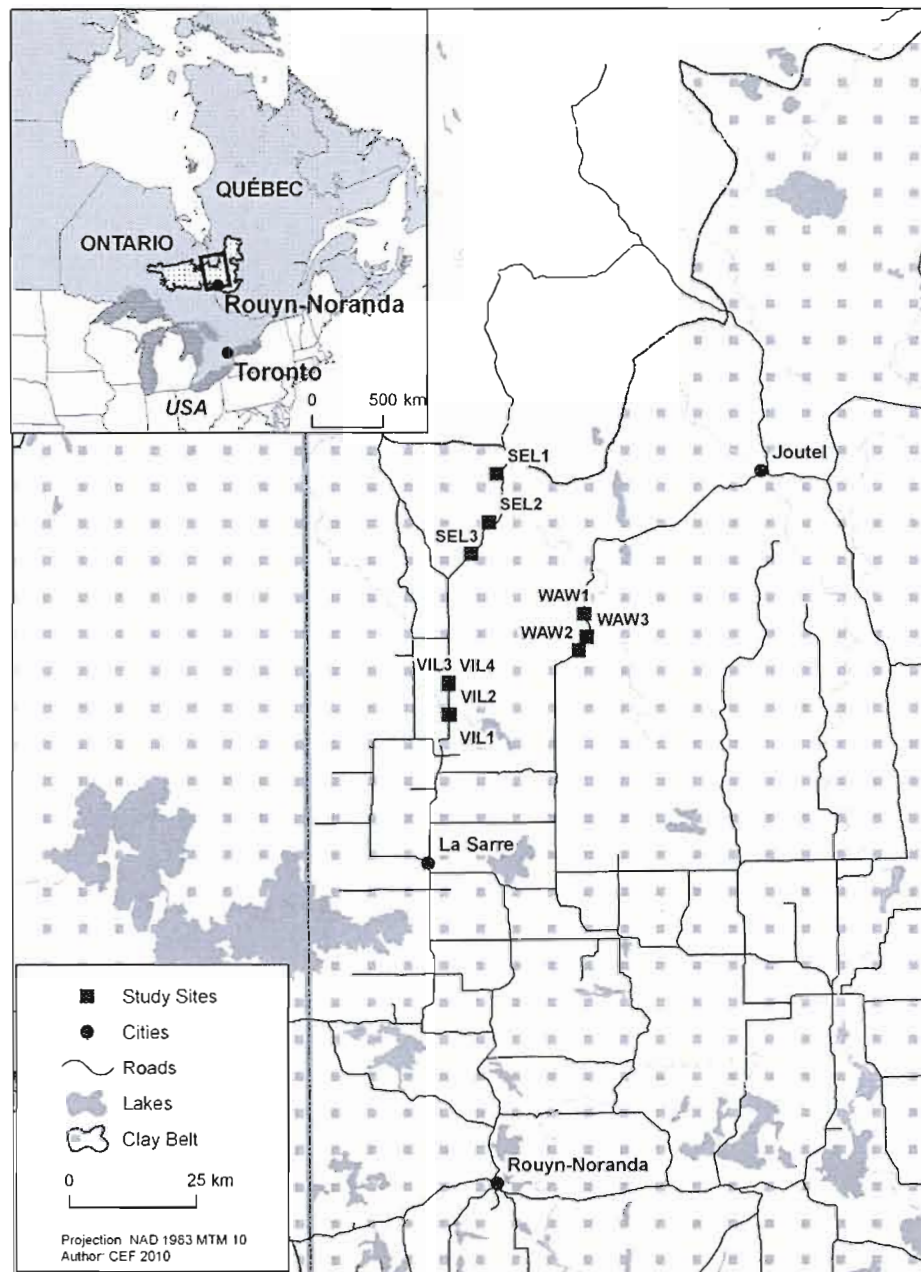


Fig. 1.1 Location map of the study area in western Quebec. The Clay Belt is indicated by the area dotted with grey squares and solid black squares indicate the study sites with their names. VIL1 and VIL2 are indicated by one square only as their locations were very close and so were VIL3 and VIL4 as well.

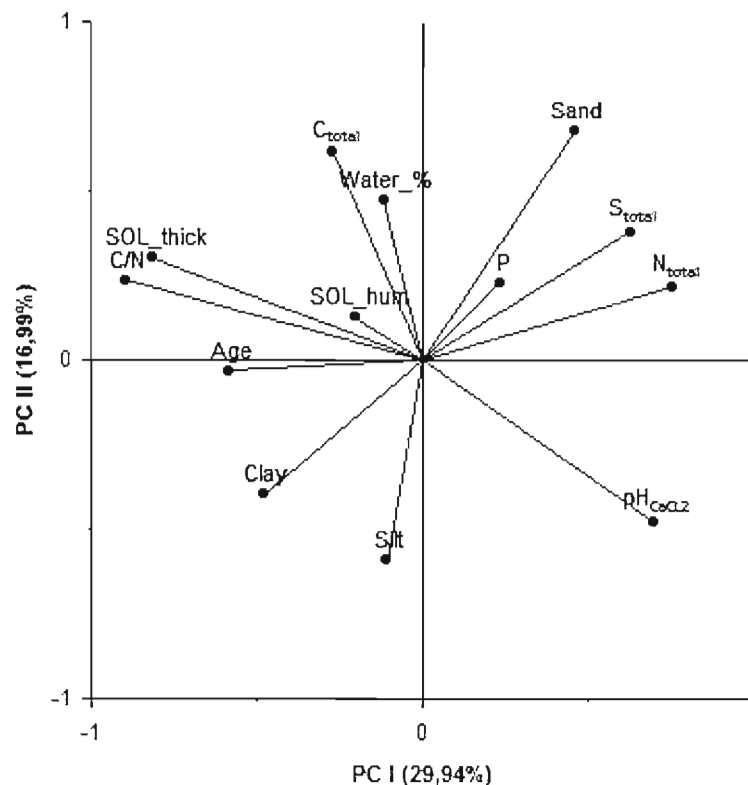


Fig. 1.2 Principal components correlation biplot of the soil variables. The 13 descriptor axes are represented by vectors. Descriptor variables are: age of the trees (Age), SOL thickness (SOL_thick), SOL relative humidity (SOL_hum), total carbon (C_{total}), total nitrogen (N_{total}), carbon/nitrogen ratio (C/N), total sulphur (S_{total}), phosphorus (P), SOL pH in $CaCl_2$ (pH_{CaCl_2}), mineral soil water content (Water_%), and proportion of clay (Clay), silt (Silt) and sand (Sand) in mineral soil. The angle between the vectors represents the correlation between the descriptor variables, with an angle of 0° representing a perfect positive correlation, an angle of 180° representing a perfect negative correlation, and an angle of 90° representing no correlation between variables.

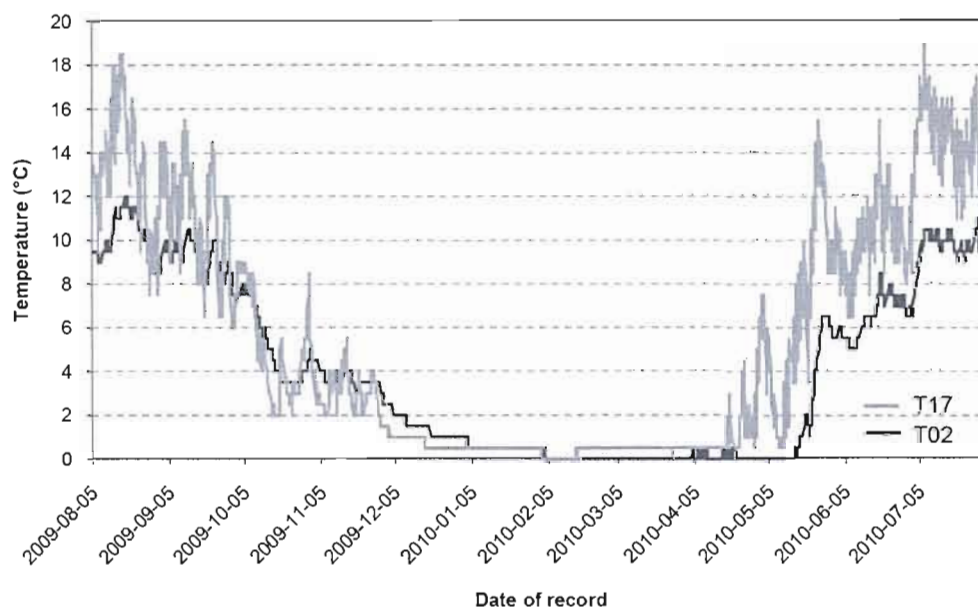


Fig. 1.3 Variation of soil temperature during 12 months. Temperature records from two data loggers: T02 buried under 22 cm of SOL and T17 buried under 2.5 cm of SOL.

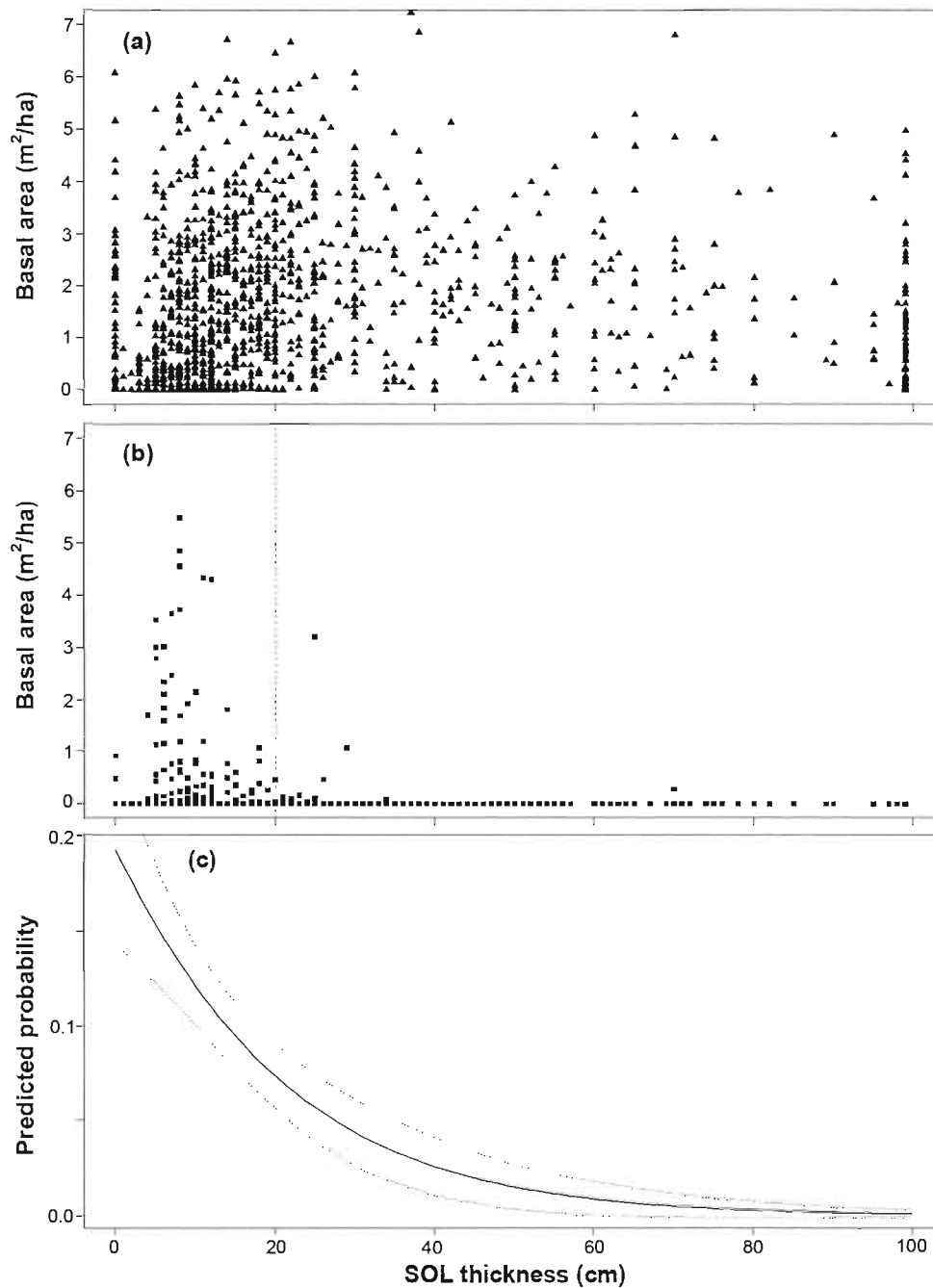


Fig. 1.4 Basal area (m^2/ha) of black spruce (A) and aspen (B) in PSPs plotted against SOL thickness (cm). Distribution of aspen seems to be limited by a threshold (dashed line) of ~20 cm. Predicted probability to find aspen along the SOL thickness gradient in the PSPs (C) with the confidence interval at 95% (dotted lines) determined through logistic regression.

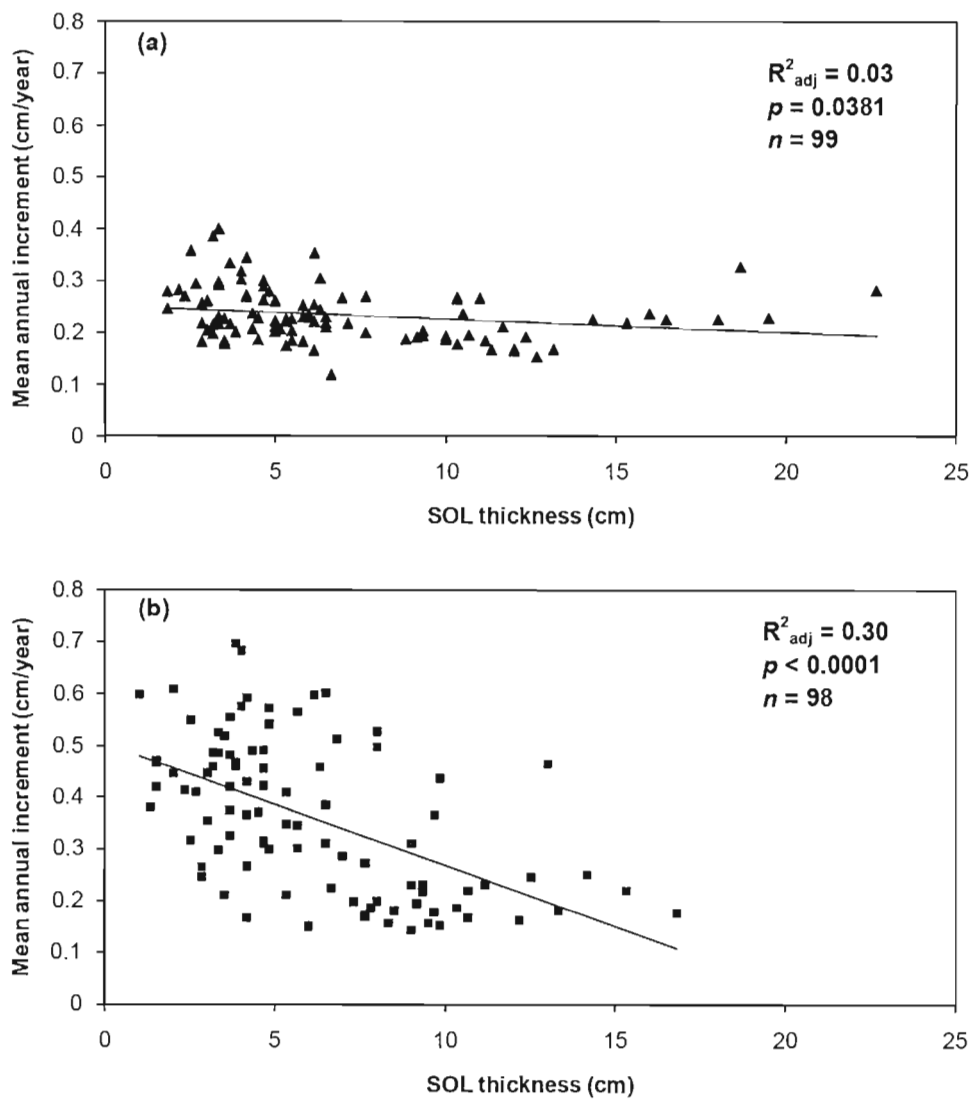


Fig. 1.5 Linear regression of mean annual increment of black spruce (A) and aspen (B) on SOL thickness. Only trees that were between 60 and 100 years old were used. The coefficient of determination, p -value, and sample size are given for each regression.

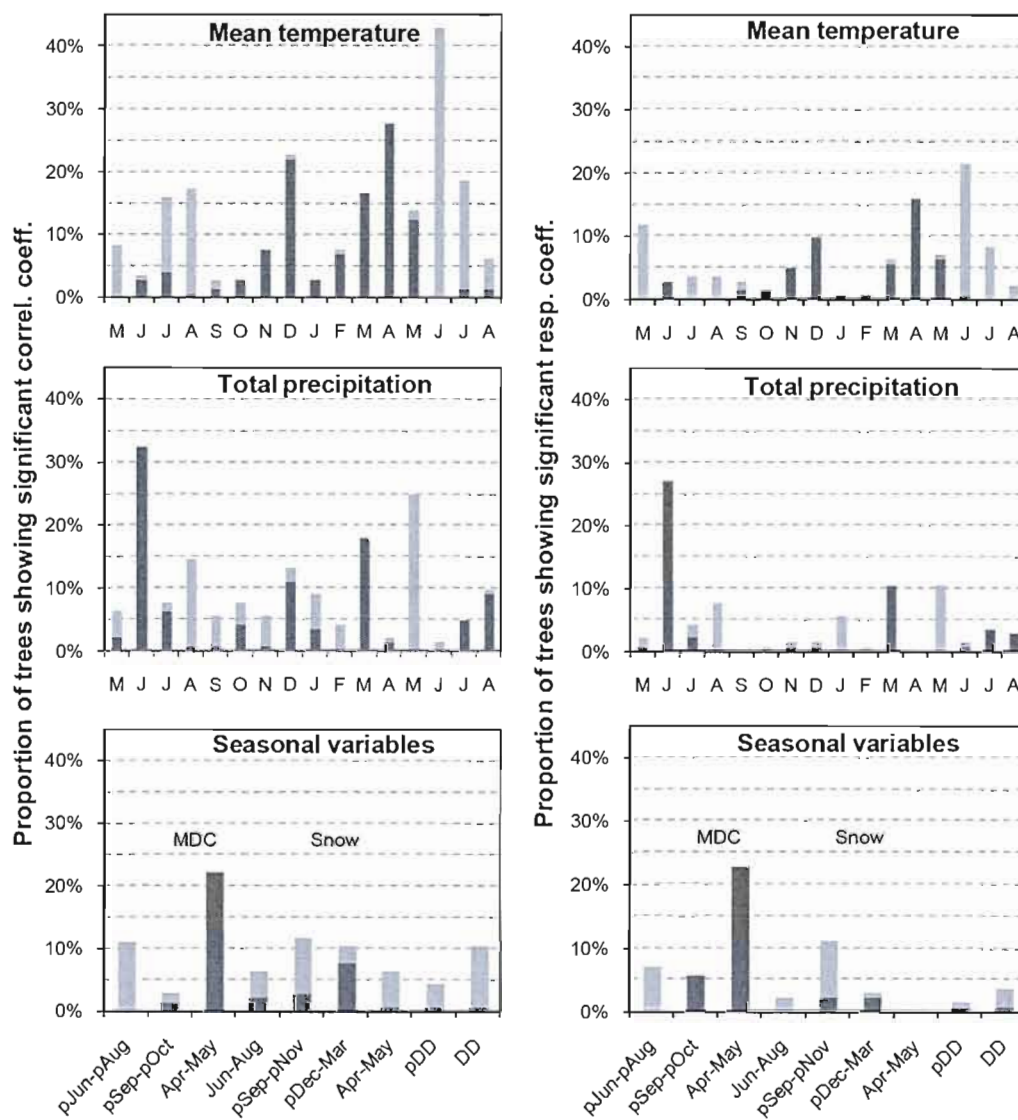


Fig. 1.6a Proportion of black spruce displaying significant positive (dark gray) and negative (light gray) correlation and response function coefficients with climate variables ($n = 145$ trees). Monthly climate variables are mean temperature and total precipitation from previous May to August of the year of growth. Seasonal climate variables are: monthly drought code (MDC) from previous June to previous August, from previous September to previous October, from April to May, and from June to August; amount of snowfall from previous September to previous November, from previous December to March, and from April to May; and total number of degree days (DD) for the previous year and for the current year.

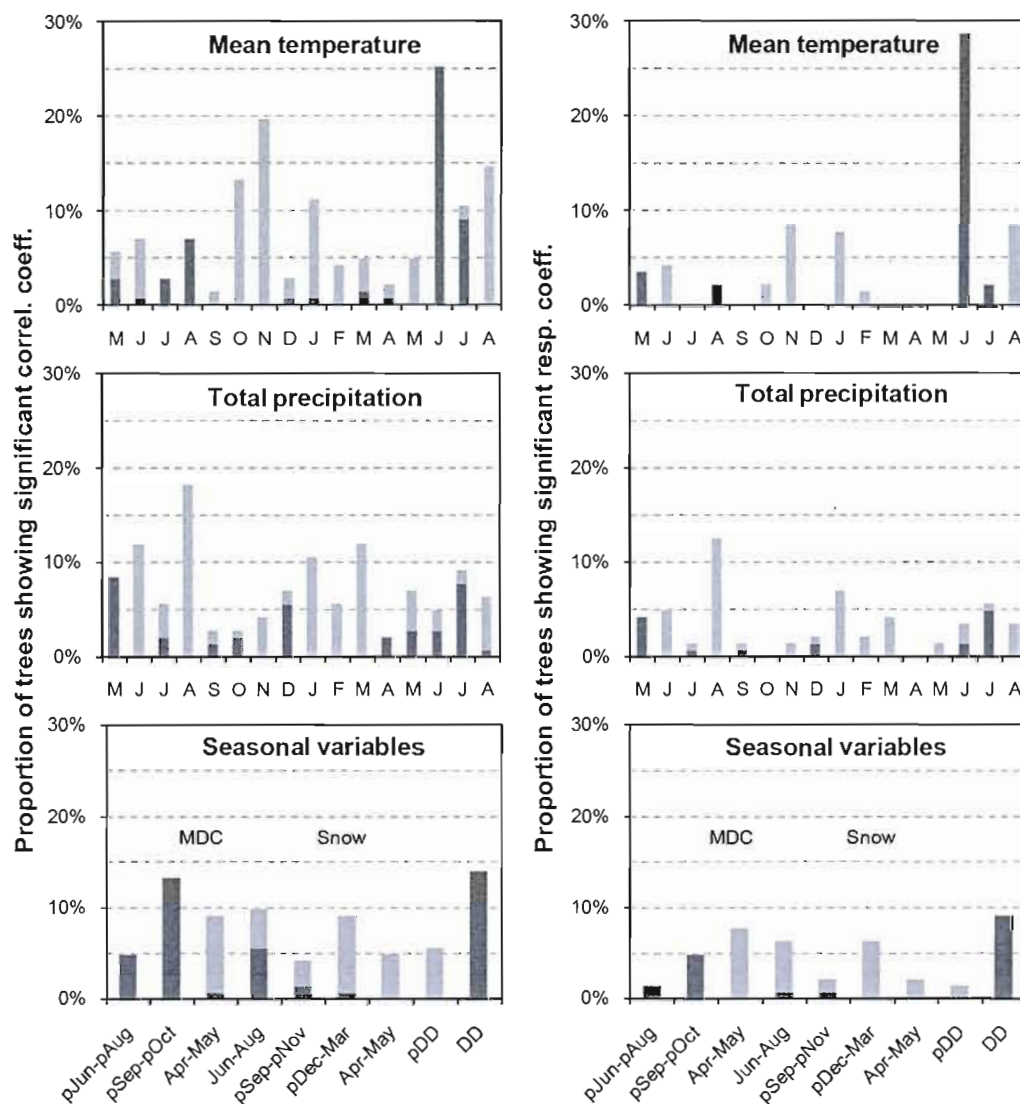


Fig. 1.6b Proportion of aspen displaying significant positive (dark gray) and negative (light gray) correlation and response function coefficients with climate variables ($n = 143$ trees). Monthly climate variables are mean temperature and total precipitation from previous May to August of the year of growth. Seasonal climate variables are: monthly drought code (MDC) from previous June to previous August, from previous September to previous October, from April to May, and from June to August; amount of snowfall from previous September to previous November, from previous December to March, and from April to May; and total number of degree days (DD) for the previous year and for the current year.

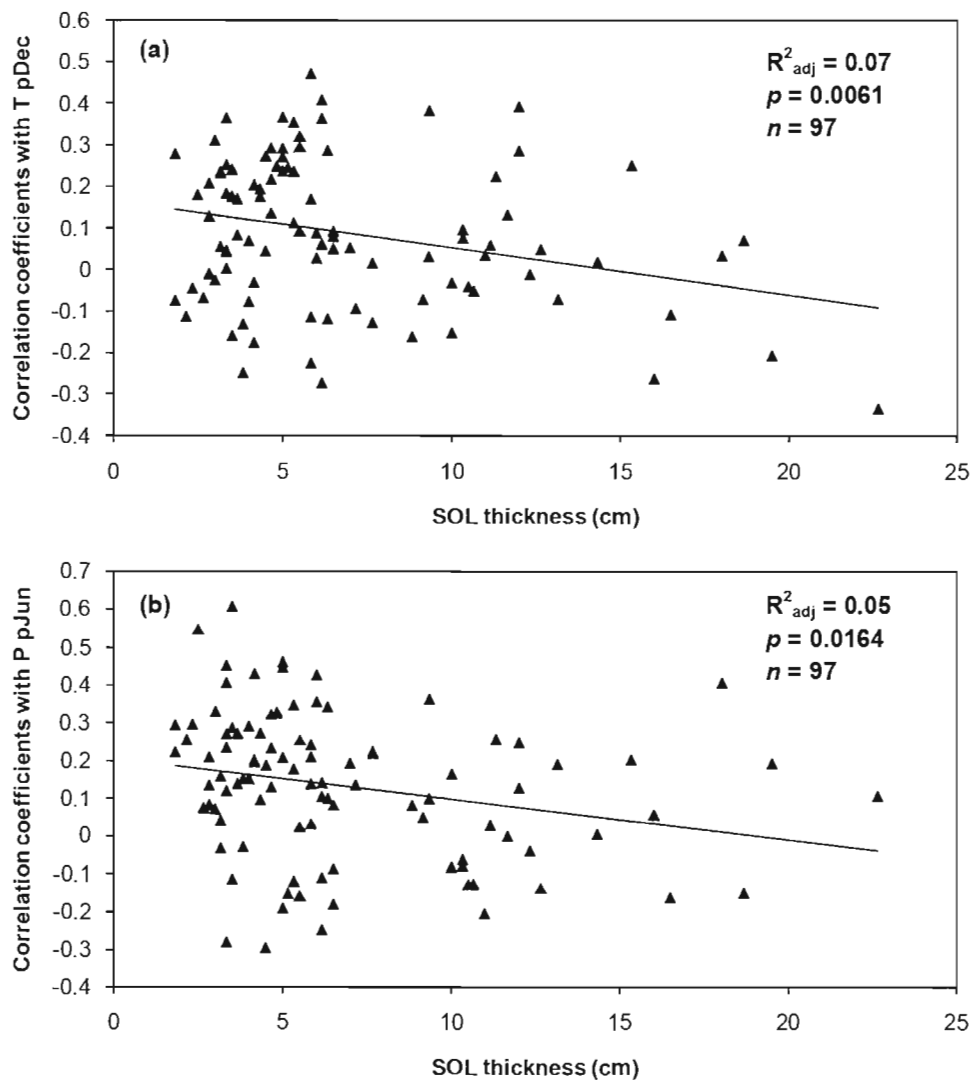


Fig. 1.7 Relationship between climate-growth correlation coefficients and SOL depth for black spruce. Response to only two of the six most important climate variables for black spruce growth was significantly affected by SOL depth: mean temperature of previous December (A); and total precipitation of previous June (B). Only trees that were between 60 and 100 years old were used ($n = 97$) and climate-growth correlation coefficients are for the period 1982-2007. The coefficient of determination (adjusted R^2) and p -value are given for each linear regression. Significance was set at $p < 0.05$.

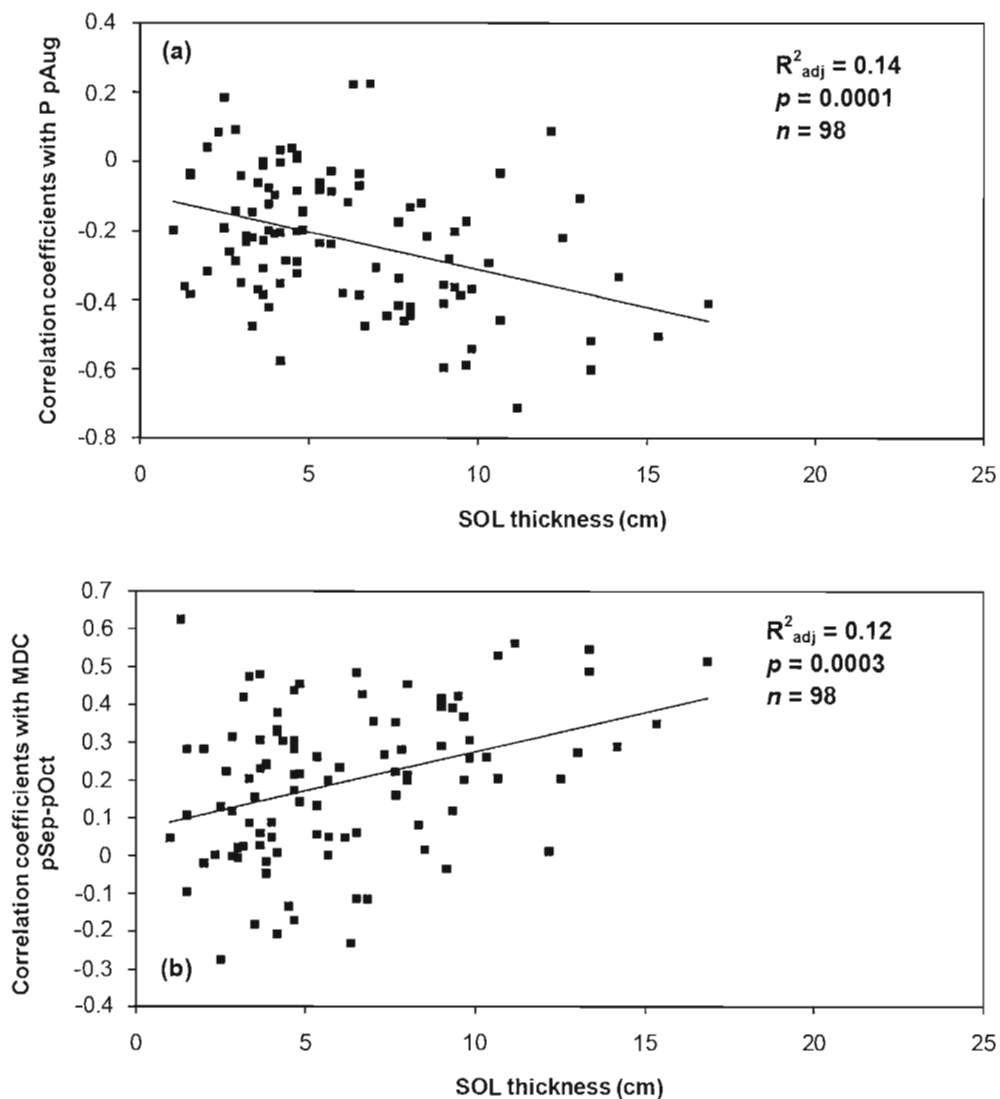


Fig. 1.8 Relationship between climate-growth correlation coefficients and SOL depth for aspen. Response to only two of the six most important climate variables for aspen growth was significantly affected by SOL depth: total precipitation of previous August (A); and previous September to previous October monthly drought code (MDC) (B). Only trees that were between 60 and 100 years old were used ($n = 98$) and climate-growth correlation coefficients are for the period 1982-2007. The coefficient of determination (adjusted R^2) and p -value are given for each linear regression. Significance was set at $p < 0.05$.

1.9 Tables

Table 1.1 Characteristics of the 10 sampling sites distributed within three sub-areas: Selbaie (SEL), Villebois (VIL) and Wawagosic (WAW). Type of mineral soil, mean SOL thickness and standard deviation, and number of plots are given for each site. One aspen and one black spruce were sampled in each plot.

Site	Coordinates	Mineral soil	SOL thickness (cm)	Number of plots
SEL1	N49°28.019'; W79°00.867'	Clay	15.55 (3.84)	10
SEL2	N49°22.969'; W79°02.193'	Clay	4.49 (1.22)	16
SEL3	N49°19.732'; W79°05.062'	Clay loam	2.45 (0.80)	10
VIL1	N49°03.100'; W79°08.800'	Clay	9.05 (2.68)	19
VIL2	N49°03.100'; W79°08.660'	Clay	5.07 (1.28)	19
VIL3	N49°06.383'; W79°08.816'	Clay loam	2.84 (1.30)	18
VIL4	N49°06.275'; W79°08.816'	Sandy loam	2.57 (0.91)	10
WAW1	N49°13.434'; W78°46.883'	Clay	12.25 (3.55)	17
WAW2	N49°09.588'; W78°47.801'	Clay	4.29 (0.97)	15
WAW3	N49°10.984'; W78°46.523'	Clay	2.41 (0.67)	11

Table 1.2 Correlation matrix of soil variables. Variables are: SOL thickness, SOL relative humidity (SOL rel. humidity), total carbon (C), total nitrogen (N), carbon/nitrogen ratio (C/N), total sulphur (S), phosphorus (P), SOL pH in CaCl₂ (pH_{CaCl2}), mineral soil water content (Water content), and proportion of clay (Clay), silt (Silt) and sand (Sand) in mineral soil. Bold values are significant correlations a $p < 0.05$, $n = 288$.

	SOL thickness	SOL rel. humidity	C	N	C/N	S	P	pH _{CaCl₂}	Water content	Clay	Silt	Sand
SOL thickness	1.00	0.31	0.45	-0.42	0.70	-0.29	-0.16	-0.68	0.16	0.08	0.08	-0.13
SOL rel. humidity	0.31	1.00	0.22	0.01	0.14	0.07	-0.18	-0.08	-0.44	-0.06	0.13	-0.05
C	0.45	0.22	1.00	0.27	0.41	0.38	0.09	-0.43	0.18	0.00	0.02	-0.02
N	-0.42	0.01	0.27	1.00	-0.73	0.89	0.12	0.50	-0.08	-0.28	0.05	0.19
C/N	0.70	0.14	0.41	-0.73	1.00	-0.56	-0.08	-0.78	0.22	0.28	-0.05	-0.19
S	-0.29	0.07	0.38	0.89	-0.56	1.00	0.12	0.30	-0.01	-0.26	-0.03	0.23
P	-0.16	-0.18	0.09	0.12	-0.08	0.12	1.00	0.03	0.15	0.05	-0.12	0.04
pH _{CaCl₂}	-0.68	-0.08	-0.43	0.50	-0.78	0.30	0.03	1.00	-0.29	-0.04	0.13	-0.06
Water content	0.16	-0.44	0.18	-0.08	0.22	-0.01	0.15	-0.29	1.00	0.13	-0.55	0.28
Clay	0.08	-0.06	0.00	-0.28	0.28	-0.26	0.05	-0.04	0.13	1.00	-0.10	-0.73
Silt	0.08	0.13	0.02	0.05	-0.05	-0.03	-0.12	0.13	-0.55	-0.10	1.00	-0.61
Sand	-0.13	-0.05	-0.02	0.19	-0.19	0.23	0.04	-0.06	0.28	-0.73	-0.61	1.00

Appendix 1.1

Soil characteristics of the 290 sampled trees. Even tree ID numbers are for black spruce and uneven numbers are for aspen. Mean SOL thickness measured in three holes dug at approximately 20 cm around each tree is given. SOL relative humidity was measured in 10 plots of every site; only mean values for the 10 sites are given. Total carbon (C, %), total nitrogen (N, %), total sulphur (S, %), total phosphorus (P, %) and pH in CaCl₂ were determined as in Laganière *et al.* 2010. Soil texture was determined by the hydrometer method and soil water content was determined by oven drying with the gravimetric method (Audesse 1982; Sheldrick & Wang 1993; Topp 1993). No mineral soil samples could be gathered for trees 36 and 38 as they were growing on rocky outcrops.

SiteID	Tree ID	SOL thickness	SOL rel. humidity	C _{total}	N _{total}	C/N ratio	S _{total}	P _{brayl1}	pH _{CaCl2}	Water content	Clay	Silt	Sand
VIL1	1	9.67	17.90	42.10	1.77	23.75	0.25	0.082	3.17	4.38%	62.95%	12.50%	24.55%
VIL1	2	7.67	17.90	45.11	1.29	34.86	0.20	0.111	2.99	4.91%	52.95%	12.50%	34.55%
VIL1	3	6.67	17.90	40.93	1.32	31.10	0.19	0.116	3.31	3.55%	59.55%	20.90%	19.55%
VIL1	4	6.67	17.90	44.56	1.22	36.61	0.18	0.126	3.22	3.51%	57.05%	23.40%	19.55%
VIL1	5	7.67	17.90	45.60	0.97	46.94	0.16	0.051	2.87	3.03%	59.55%	25.90%	14.55%
VIL1	6	7.67	17.90	41.38	1.07	38.82	0.16	0.065	2.84	3.06%	62.05%	28.40%	9.55%
VIL1	7	10.33	17.90	43.40	0.93	46.60	0.16	0.054	2.81	5.05%	57.05%	18.40%	24.55%
VIL1	8	10	17.90	39.99	1.09	36.65	0.16	0.055	2.98	6.06%	49.55%	25.90%	24.55%
VIL1	9	8.33	17.90	47.16	1.18	39.86	0.19	0.083	2.95	6.58%	52.05%	10.90%	37.05%
VIL1	10	11.67	17.90	47.20	1.03	45.65	0.18	0.088	2.80	4.34%	59.55%	23.40%	17.05%
VIL2	11	5.67	14.90	42.04	1.52	27.71	0.22	0.133	3.54	4.02%	61.15%	12.50%	26.35%
VIL2	12	6.33	14.90	43.12	1.35	31.94	0.21	0.071	3.64	3.98%	51.15%	25.00%	23.85%
VIL2	13	7	14.90	38.58	1.19	32.39	0.19	0.118	3.52	3.07%	53.65%	32.50%	13.85%
VIL2	14	5.33	14.90	42.78	1.48	29.00	0.19	0.124	3.59	3.69%	58.65%	30.00%	11.35%
VIL2	15	3.67	14.90	42.00	1.44	29.11	0.21	0.166	4.23	3.41%	58.65%	25.00%	16.35%
VIL2	16	3.5	14.90	40.50	1.43	28.26	0.21	0.127	4.02	3.30%	48.65%	30.00%	21.35%

VIL2	17	4.17	14.90	41.76	1.47	28.35	0.22	0.147	3.81	2.58%	61.15%	30.00%	8.85%
VIL2	18	6	14.90	45.34	1.54	29.46	0.25	0.091	3.36	2.78%	56.15%	35.00%	8.85%
VIL2	19	3.5	14.90	42.50	1.47	28.93	0.22	0.107	4.14	2.91%	51.15%	35.00%	13.85%
VIL2	20	5	14.90	45.34	1.51	30.07	0.24	0.087	3.92	2.72%	51.15%	35.00%	13.85%
VIL3	21	3.67	20.50	32.61	1.52	21.44	0.19	0.114	4.08	2.13%	40.45%	32.50%	27.05%
VIL3	22	2.67	20.50	27.28	1.28	21.28	0.16	0.085	4.00	2.70%	17.50%	61.60%	20.90%
VIL3	23	1	20.50	28.91	1.60	18.10	0.20	0.108	4.31	17.10%	50.45%	20.00%	29.55%
VIL3	24	1.83	20.50	38.57	1.64	23.52	0.22	0.196	4.43	33.51%	57.95%	10.00%	32.05%
VIL3	25	2.33	20.50	29.25	1.20	24.46	0.17	0.167	4.00	2.46%	32.50%	25.70%	41.80%
VIL3	26	2.33	20.50	29.42	1.22	24.17	0.17	0.153	4.18	7.07%	32.95%	25.00%	42.05%
VIL3	27	2	20.50	27.65	1.05	26.46	0.14	0.140	3.93	3.25%	30.45%	17.50%	52.05%
VIL3	28	1.67	20.50	36.45	1.46	24.90	0.20	0.190	3.98	4.93%	35.00%	18.65%	46.35%
VIL3	29	1.67	20.50	32.94	1.38	23.84	0.20	0.133	3.64	3.00%	40.45%	30.00%	29.55%
VIL3	30	2	20.50	39.06	1.54	25.41	0.22	0.195	3.84	5.33%	27.50%	26.15%	46.35%
VIL4	31	1	24.10	25.56	0.91	27.94	0.13	0.087	3.68	2.55%	15.45%	15.00%	69.55%
VIL4	32	2	24.10	36.89	1.60	23.01	0.25	0.113	3.78	7.22%	17.95%	30.00%	52.05%
VIL4	33	3	24.10	36.96	1.43	25.79	0.22	0.204	3.30	1.18%	10.00%	15.00%	75.00%
VIL4	34	3.17	24.10	41.68	1.64	25.35	0.23	0.241	3.62	1.14%	15.00%	16.60%	68.40%
VIL4	35	2.83	24.10	47.48	1.86	25.60	0.27	0.251	3.50	4.96%	7.95%	17.50%	74.55%
VIL4	36	1.67	24.10	46.76	1.77	26.39	0.24	0.226	4.04	NA	NA	NA	NA
VIL4	37	1.5	24.10	47.75	1.77	26.96	0.26	0.208	3.30	5.66%	7.95%	22.50%	69.55%
VIL4	38	1.5	24.10	48.19	1.97	24.52	0.27	0.183	3.71	NA	NA	NA	NA
VIL4	39	2	24.10	47.36	2.02	23.43	0.29	0.190	3.55	0.80%	5.45%	10.00%	84.55%
VIL4	40	1.83	24.10	44.65	1.84	24.28	0.26	0.167	3.80	3.18%	8.40%	11.15%	80.45%
VIL4	41	1.67	24.10	47.14	1.75	27.00	0.26	0.208	3.44	0.45%	5.45%	19.10%	75.45%
VIL4	42	2	24.10	44.19	1.67	26.54	0.24	0.058	3.69	2.16%	12.95%	21.15%	65.90%
VIL3	43	2.17	20.50	37.16	1.57	23.65	0.22	0.142	4.19	2.47%	42.05%	30.25%	27.70%

VIL3	44	2.67	20.50	41.92	1.66	25.30	0.22	0.174	4.46	2.78%	50.00%	25.70%	24.30%
VIL2	45	2.83	14.90	38.53	1.29	29.85	0.20	0.145	4.03	3.45%	51.15%	27.50%	21.35%
VIL2	46	3.5	14.90	41.18	1.37	30.15	0.21	0.130	3.58	3.76%	56.15%	20.00%	23.85%
VIL1	47	5.33	17.90	47.50	1.15	41.48	0.19	0.036	2.88	2.99%	57.05%	30.90%	12.05%
VIL1	48	6.5	17.90	45.69	1.10	41.54	0.19	0.079	2.83	3.72%	57.05%	18.40%	24.55%
VIL3	101	2.83	20.50	25.21	1.37	18.37	0.11	0.141	4.23	3.67%	37.95%	24.55%	37.50%
VIL3	102	3.33	20.50	40.05	1.55	25.92	0.21	0.117	3.30	6.65%	42.95%	27.05%	30.00%
VIL3	103	1	20.50	18.92	0.91	20.81	0.12	0.096	4.51	4.37%	32.95%	14.55%	52.50%
VIL3	104	3.16	20.50	28.08	1.14	24.57	0.16	0.168	3.87	4.92%	35.45%	24.55%	40.00%
VIL3	105	1.83	20.50	27.08	1.09	24.75	0.14	0.149	4.05	4.88%	40.90%	24.10%	35.00%
VIL3	106	2.5	20.50	33.73	1.30	26.01	0.19	0.141	3.86	3.85%	32.95%	34.55%	32.50%
VIL3	107	3	20.50	26.59	1.20	22.23	0.16	0.122	4.40	5.66%	45.45%	24.55%	30.00%
VIL3	108	2.33	20.50	29.51	1.23	24.09	0.16	0.266	4.04	3.16%	47.95%	29.55%	22.50%
VIL3	109	2.33	20.50	42.03	1.91	22.01	0.26	0.250	4.59	9.50%	50.45%	27.05%	22.50%
VIL3	110	4	20.50	36.83	1.62	22.73	0.23	0.204	4.57	5.90%	47.95%	27.05%	25.00%
VIL3	111	1.33	20.50	28.22	1.11	25.42	0.16	0.196	4.50	2.43%	35.45%	17.05%	47.50%
VIL3	112	2.33	20.50	21.41	0.88	24.36	0.12	0.169	4.05	5.12%	45.45%	27.05%	27.50%
VIL3	113	1.5	20.50	12.37	0.58	21.20	0.08	0.086	4.34	5.15%	30.90%	6.60%	62.50%
VIL3	114	3.83	20.50	36.99	1.52	24.27	0.24	0.170	3.67	7.01%	30.45%	14.55%	55.00%
VIL3	115	2.5	20.50	28.57	1.22	23.36	0.18	0.167	4.02	12.60%	42.50%	25.00%	32.50%
VIL3	116	3.33	20.50	26.70	1.15	23.20	0.17	0.142	3.94	12.30%	40.45%	19.55%	40.00%
VIL3	117	3.33	20.50	42.11	1.52	27.65	0.23	0.124	4.05	2.50%	25.45%	49.55%	25.00%
VIL3	118	4.5	20.50	44.61	1.58	28.23	0.25	0.242	3.82	3.35%	25.45%	47.05%	27.50%
VIL3	119	2.5	20.50	37.02	1.59	23.34	0.22	0.143	4.17	14.32%	47.50%	15.00%	37.50%
VIL3	120	7	20.50	45.92	1.63	28.22	0.26	0.094	3.30	11.72%	35.00%	17.50%	47.50%
VIL3	121	3.16	20.50	44.00	1.85	23.73	0.27	0.124	3.88	7.57%	40.45%	29.55%	30.00%
VIL3	122	6.16	20.50	47.61	1.73	27.52	0.26	0.145	4.01	11.28%	33.40%	21.60%	45.00%

VIL3	123	4	20.50	32.02	1.35	23.79	0.20	0.123	3.75	6.30%	17.95%	19.55%	62.50%
VIL3	124	4.66	20.50	47.57	1.76	27.07	0.26	0.177	3.87	5.54%	15.45%	37.05%	47.50%
VIL4	125	2.16	24.10	41.67	1.81	22.97	0.26	0.152	3.78	1.43%	12.95%	19.55%	67.50%
VIL4	126	3.66	24.10	48.43	2.03	23.81	0.33	0.088	3.43	3.26%	15.00%	20.00%	65.00%
VIL4	127	2.83	24.10	46.28	1.96	23.67	0.30	0.215	4.05	14.99%	27.95%	19.55%	52.50%
VIL4	128	3.33	24.10	47.64	1.96	24.34	0.31	0.132	3.82	6.03%	22.95%	24.55%	52.50%
VIL4	129	3.66	24.10	46.54	1.84	25.28	0.27	0.136	3.64	14.60%	27.95%	24.55%	47.50%
VIL4	130	3.16	24.10	47.39	1.87	25.29	0.30	0.172	3.42	2.04%	20.00%	36.60%	43.40%
VIL4	131	4	24.10	46.01	2.13	21.64	0.27	0.207	3.40	1.22%	12.95%	22.05%	65.00%
VIL4	132	3.83	24.10	45.38	1.91	23.80	0.26	0.143	3.50	7.74%	22.95%	22.05%	55.00%
VIL1	133	5.66	17.90	44.09	1.35	32.59	0.20	0.154	3.10	17.85%	50.90%	17.50%	31.60%
VIL1	134	5.5	17.90	43.38	1.22	35.56	0.19	1.261	3.09	19.33%	48.40%	12.50%	39.10%
VIL1	135	7.66	17.90	49.11	1.38	35.54	0.22	0.090	3.07	8.72%	57.95%	19.55%	22.50%
VIL1	136	9.33	17.90	46.53	1.09	42.85	0.17	0.084	2.88	12.91%	57.95%	17.05%	25.00%
VIL1	137	6.16	17.90	46.52	1.36	34.28	0.22	0.105	3.09	7.51%	45.45%	24.55%	30.00%
VIL1	138	7.16	17.90	44.57	1.30	34.21	0.20	0.133	2.77	16.59%	40.45%	9.55%	50.00%
VIL1	139	9.33	17.90	41.79	1.00	42.00	0.16	0.092	2.90	15.41%	45.45%	12.05%	42.50%
VIL1	140	12.5	17.90	40.33	0.85	47.41	0.14	0.054	2.81	14.25%	55.00%	15.00%	30.00%
VIL1	141	9	17.90	43.91	1.31	33.52	0.20	0.097	2.96	28.71%	38.40%	10.00%	51.60%
VIL1	142	10.33	17.90	45.76	1.14	40.07	0.20	0.077	3.01	19.04%	48.40%	15.00%	36.60%
VIL1	143	9.83	17.90	46.73	1.21	38.68	0.21	0.135	3.08	25.10%	38.40%	15.00%	46.60%
VIL1	144	10.5	17.90	46.62	1.07	43.57	0.19	0.080	2.80	17.33%	45.90%	7.50%	46.60%
VIL1	145	6	17.90	32.04	0.85	37.49	0.14	0.096	3.06	17.79%	50.90%	12.50%	36.60%
VIL1	146	12.66	17.90	44.15	0.91	48.74	0.18	0.074	2.96	20.75%	32.95%	22.05%	45.00%
VIL1	147	8.5	17.90	43.45	0.93	46.86	0.18	0.055	2.81	15.34%	57.50%	12.50%	30.00%
VIL1	148	9.16	17.90	34.77	0.71	49.12	0.15	0.066	2.89	13.72%	65.45%	12.05%	22.50%
VIL1	149	10.66	17.90	29.80	0.62	47.81	0.12	0.086	2.88	8.73%	57.95%	17.05%	25.00%

VIL1	150	8.83	17.90	36.05	0.70	51.77	0.13	0.074	2.84	12.33%	52.50%	22.50%	25.00%
VIL1	151	8	17.90	46.10	1.00	46.14	0.17	0.098	3.09	10.76%	55.90%	22.50%	21.60%
VIL1	152	5.83	17.90	31.92	0.56	57.15	0.11	0.075	2.87	12.58%	60.90%	17.50%	21.60%
VIL1	153	7.66	17.90	49.08	1.07	46.04	0.18	0.139	2.91	16.81%	55.90%	17.50%	26.60%
VIL1	154	10.33	17.90	48.79	0.85	57.42	0.16	0.072	2.71	12.79%	57.50%	20.00%	22.50%
VIL2	155	4.66	14.90	31.59	1.05	30.03	0.18	0.133	4.14	11.64%	52.50%	15.00%	32.50%
VIL2	156	3.16	14.90	29.86	1.05	28.55	0.17	0.152	4.54	11.30%	57.50%	22.50%	20.00%
VIL2	157	5.33	14.90	44.51	1.73	25.67	0.26	0.130	3.80	8.59%	52.50%	25.00%	22.50%
VIL2	158	5.16	14.90	42.32	1.46	29.03	0.23	0.156	4.00	8.49%	50.00%	27.50%	22.50%
VIL2	159	3.16	14.90	37.72	1.31	28.75	0.18	0.149	4.63	7.65%	52.95%	19.55%	27.50%
VIL2	160	6	14.90	39.20	1.30	30.11	0.20	0.158	4.15	8.10%	57.50%	25.00%	17.50%
VIL2	161	6.5	14.90	37.75	1.29	29.26	0.19	0.181	4.37	8.51%	42.50%	32.50%	25.00%
VIL2	162	4.5	14.90	34.56	1.08	32.00	0.16	0.184	4.56	9.99%	52.50%	27.50%	20.00%
VIL2	163	4.66	14.90	43.42	1.70	25.60	0.26	0.185	4.53	9.70%	57.50%	25.00%	17.50%
VIL2	164	5.33	14.90	42.50	1.54	27.67	0.24	0.197	4.17	9.12%	50.00%	27.50%	22.50%
VIL2	165	4.16	14.90	32.49	1.21	26.85	0.17	0.143	4.50	7.71%	45.00%	32.50%	22.50%
VIL2	166	6.16	14.90	36.08	1.29	27.90	0.19	0.130	4.67	9.88%	48.40%	32.50%	19.10%
VIL2	167	3.66	14.90	31.42	1.31	24.02	0.17	0.192	4.95	7.27%	55.00%	27.50%	17.50%
VIL2	168	5.83	14.90	34.63	1.29	26.84	0.19	0.130	4.65	8.56%	47.50%	22.50%	30.00%
VIL1	169	13	17.90	46.86	1.82	25.69	0.28	0.165	3.22	9.29%	42.95%	24.55%	32.50%
VIL1	170	11	17.90	47.11	1.63	28.99	0.25	0.164	3.30	12.77%	25.00%	22.50%	52.50%
VIL1	171	12.5	17.90	49.49	1.48	33.48	0.23	0.119	3.14	15.24%	37.50%	25.00%	37.50%
VIL1	172	18.66	17.90	50.13	1.54	32.66	0.26	0.077	2.81	11.15%	35.00%	27.50%	37.50%
VIL2	173	4.66	14.90	34.66	1.27	27.36	0.19	0.150	4.30	10.48%	47.50%	32.50%	20.00%
VIL2	174	4.66	14.90	42.31	1.34	31.50	0.20	0.228	4.67	7.82%	47.50%	27.50%	25.00%
VIL2	175	5.33	14.90	42.32	1.40	30.29	0.22	0.174	4.32	5.60%	42.50%	40.00%	17.50%
VIL2	176	6.33	14.90	40.20	1.31	30.71	0.21	0.137	3.66	7.32%	42.50%	22.50%	35.00%

VIL2	177	4.66	14.90	35.54	1.40	25.35	0.20	0.150	4.68	9.04%	52.50%	20.00%	27.50%
VIL2	178	5.5	14.90	38.55	1.39	27.81	0.21	0.162	4.57	8.58%	47.50%	27.50%	25.00%
VIL2	179	4.83	14.90	42.86	1.61	26.67	0.24	0.113	4.49	7.39%	52.50%	30.00%	17.50%
VIL2	180	5.83	14.90	44.77	1.59	28.21	0.23	0.140	4.55	9.28%	62.50%	10.00%	27.50%
VIL2	181	8	14.90	49.10	1.83	26.80	0.22	0.175	4.25	10.01%	55.00%	17.50%	27.50%
VIL2	182	3.83	14.90	46.05	1.69	27.30	0.22	0.236	4.50	9.50%	55.00%	17.50%	27.50%
VIL2	183	8	14.90	48.80	1.68	29.10	0.24	0.161	4.24	10.04%	45.00%	32.50%	22.50%
VIL2	184	6.16	14.90	47.15	1.69	27.97	0.26	0.151	3.48	6.73%	42.50%	15.00%	42.50%
WAW3	185	2.5	27.80	24.03	1.24	19.35	0.17	0.049	4.30	4.24%	37.95%	32.05%	30.00%
WAW3	186	2.83	27.80	29.21	1.45	20.09	0.20	0.058	4.05	5.36%	35.45%	17.05%	47.50%
WAW3	187	2	27.80	39.45	1.98	19.89	0.27	0.132	4.30	10.68%	37.95%	24.55%	37.50%
WAW3	188	3.33	27.80	39.53	1.66	23.78	0.23	0.108	4.20	9.57%	42.05%	25.45%	32.50%
WAW3	189	1.33	27.80	26.29	1.27	20.70	0.18	0.102	4.70	6.98%	45.45%	24.55%	30.00%
WAW3	190	1.83	27.80	34.63	1.63	21.31	0.22	0.096	4.47	4.83%	42.05%	32.95%	25.00%
WAW3	191	2	27.80	41.16	1.84	22.43	0.25	0.144	4.23	6.72%	42.95%	22.05%	35.00%
WAW3	192	3	27.80	34.88	1.64	21.27	0.23	0.118	4.32	3.30%	40.45%	32.05%	27.50%
WAW3	193	1.5	27.80	30.89	1.58	19.54	0.19	0.092	4.60	4.84%	45.90%	26.60%	27.50%
WAW3	194	2.33	27.80	36.77	1.71	21.57	0.24	0.067	4.08	8.15%	45.90%	24.10%	30.00%
WAW3	195	1.5	27.80	41.82	1.90	22.05	0.25	0.132	4.60	5.33%	47.05%	30.45%	22.50%
WAW3	196	2.33	27.80	38.56	1.81	21.29	0.24	0.122	4.21	3.20%	40.45%	37.05%	22.50%
WAW3	197	1.5	27.80	37.06	2.00	18.54	0.26	0.117	4.41	3.59%	42.05%	40.45%	17.50%
WAW3	198	3.33	27.80	40.80	1.87	21.78	0.25	0.197	4.45	7.52%	50.45%	27.05%	22.50%
WAW3	199	2.5	27.80	45.73	2.42	18.91	0.29	0.114	4.35	5.11%	42.05%	35.45%	22.50%
WAW3	200	2.66	27.80	45.41	2.19	20.70	0.27	0.123	4.80	5.14%	35.45%	34.55%	30.00%
WAW3	201	3.66	27.80	41.28	2.20	18.76	0.28	0.108	4.30	10.78%	45.45%	17.05%	37.50%
WAW3	202	1.83	27.80	42.96	2.27	18.93	0.27	0.166	4.30	7.67%	45.90%	29.10%	25.00%
WAW3	203	2.83	27.80	32.54	1.84	17.67	0.23	0.126	4.25	3.44%	45.00%	34.10%	20.90%

WAW3	204	2.16	27.80	42.75	2.11	20.23	0.26	0.097	4.10	3.93%	45.45%	24.55%	30.00%
WAW3	205	3	27.80	45.09	1.98	22.76	0.24	0.164	4.41	4.73%	42.05%	30.45%	27.50%
WAW3	206	3.16	27.80	44.09	2.00	22.09	0.26	0.131	3.92	5.23%	40.45%	22.05%	37.50%
WAW1	207	9.16	34.10	43.55	1.22	35.78	0.19	0.208	3.35	9.27%	41.35%	24.10%	34.55%
WAW1	208	9.33	34.10	42.22	1.11	37.90	0.17	0.185	3.27	10.33%	48.85%	11.60%	39.55%
WAW1	209	7.33	34.10	46.54	1.27	36.70	0.19	0.262	3.28	7.96%	51.35%	21.60%	27.05%
WAW1	210	16	34.10	46.23	1.14	40.66	0.18	0.191	3.06	6.03%	53.85%	19.10%	27.05%
WAW1	211	7.83	34.10	46.83	1.12	41.92	0.16	0.178	2.95	5.56%	51.35%	24.10%	24.55%
WAW1	212	9.33	34.10	46.29	1.20	38.67	0.17	0.242	3.29	6.30%	46.35%	21.60%	32.05%
WAW1	213	9.5	34.10	46.26	1.13	41.01	0.16	0.162	3.04	8.12%	40.45%	19.55%	40.00%
WAW1	214	10.66	34.10	44.84	1.11	40.54	0.16	0.203	3.20	9.72%	43.85%	14.10%	42.05%
WAW1	215	9	34.10	47.94	1.10	43.66	0.17	0.215	2.90	4.33%	41.35%	29.10%	29.55%
WAW1	216	11.16	34.10	49.21	1.01	48.82	0.16	0.151	2.84	5.31%	40.45%	22.05%	37.50%
WAW1	217	16.83	34.10	49.17	1.01	48.68	0.16	0.125	2.82	7.06%	28.40%	31.60%	40.00%
WAW1	218	12	34.10	48.82	0.94	52.15	0.15	0.115	2.73	4.34%	40.45%	14.55%	45.00%
WAW1	219	13.33	34.10	48.44	0.90	53.69	0.15	0.116	2.78	6.08%	47.95%	27.05%	25.00%
WAW1	220	18	34.10	49.93	0.97	51.47	0.16	0.115	2.88	9.40%	32.95%	17.05%	50.00%
WAW1	221	13.33	34.10	51.49	1.48	34.91	0.19	0.154	2.99	6.90%	50.90%	21.60%	27.50%
WAW1	222	22.66	34.10	46.66	1.00	46.75	0.17	0.101	2.82	10.40%	33.40%	19.10%	47.50%
WAW1	223	9	34.10	51.60	1.37	37.55	0.23	0.196	3.25	4.97%	42.95%	32.05%	25.00%
WAW1	224	12	34.10	51.75	1.16	44.50	0.21	0.134	2.79	6.50%	45.90%	16.60%	37.50%
WAW1	225	10.66	34.10	50.22	1.23	40.96	0.21	0.226	3.09	4.81%	42.95%	24.55%	32.50%
WAW1	226	12.33	34.10	51.20	1.19	43.13	0.21	0.164	2.81	5.60%	42.95%	29.55%	27.50%
WAW1	227	15.33	34.10	48.95	1.16	42.23	0.21	0.146	2.85	6.87%	40.45%	22.05%	37.50%
WAW1	228	15.33	34.10	49.37	1.02	48.40	0.19	0.100	2.79	11.00%	30.90%	19.10%	50.00%
WAW1	229	11.16	34.10	46.94	1.14	41.07	0.20	0.159	3.05	5.37%	52.50%	22.50%	25.00%
WAW1	230	16.5	34.10	49.36	1.01	48.97	0.18	0.144	2.92	7.86%	45.00%	20.00%	35.00%

WAW1	231	9.66	34.10	43.44	0.96	45.02	0.16	0.160	3.13	4.36%	42.50%	27.50%	30.00%
WAW1	232	11.33	34.10	42.24	0.95	44.58	0.16	0.136	3.00	7.93%	45.00%	17.50%	37.50%
WAW1	233	9.33	34.10	50.20	1.27	39.56	0.22	0.126	2.98	5.07%	45.00%	25.00%	30.00%
WAW1	234	10	34.10	48.95	1.23	39.76	0.22	0.173	3.05	9.25%	42.50%	22.50%	35.00%
WAW1	235	9.33	34.10	49.42	1.20	41.05	0.21	0.163	3.02	4.41%	42.05%	32.95%	25.00%
WAW1	236	13.16	34.10	50.41	1.08	46.81	0.19	0.091	2.79	7.92%	42.95%	14.55%	42.50%
WAW1	237	12.16	34.10	47.09	0.98	48.27	0.17	0.077	2.88	12.33%	47.50%	12.50%	40.00%
WAW1	238	19.5	34.10	48.52	0.97	50.03	0.17	0.091	2.73	14.53%	40.00%	7.50%	52.50%
WAW1	239	9.83	34.10	51.45	1.21	42.49	0.21	0.175	3.07	4.03%	37.50%	35.00%	27.50%
WAW1	240	14.33	34.10	52.13	1.06	49.13	0.19	0.100	2.86	4.26%	37.50%	30.00%	32.50%
WAW2	241	4	34.20	39.75	1.96	20.33	0.27	0.129	4.65	4.56%	45.00%	22.50%	32.50%
WAW2	242	5	34.20	40.75	1.81	22.54	0.28	0.132	4.67	5.22%	45.00%	22.50%	32.50%
WAW2	243	2.66	34.20	40.37	1.46	27.59	0.23	0.137	4.22	4.43%	52.50%	22.50%	25.00%
WAW2	244	4.33	34.20	40.06	1.51	26.51	0.25	0.120	4.22	4.84%	52.50%	20.00%	27.50%
WAW2	245	3.66	34.20	38.84	1.46	26.68	0.22	0.208	4.20	3.76%	55.90%	24.10%	20.00%
WAW2	246	4.16	34.20	38.04	1.41	27.07	0.22	0.148	4.11	3.59%	45.90%	24.10%	30.00%
WAW2	247	3.83	34.20	39.97	1.30	30.82	0.21	0.197	4.10	5.91%	62.95%	17.05%	20.00%
WAW2	248	5	34.20	37.40	1.22	30.61	0.20	0.162	3.82	6.98%	45.45%	17.05%	37.50%
WAW2	249	3.5	34.20	41.68	1.56	26.75	0.24	0.214	4.62	8.27%	52.95%	12.05%	35.00%
WAW2	250	4.16	34.20	41.87	1.56	26.93	0.24	0.178	4.19	6.59%	47.95%	19.55%	32.50%
WAW2	251	4.66	34.20	43.42	1.70	25.62	0.26	0.133	4.58	7.49%	47.95%	14.55%	37.50%
WAW2	252	4.66	34.20	40.80	1.75	23.26	0.27	0.193	4.50	4.92%	47.95%	19.55%	32.50%
WAW2	253	3.33	34.20	42.93	2.03	21.12	0.30	0.123	4.53	12.07%	37.05%	10.45%	52.50%
WAW2	254	4.16	34.20	40.75	1.79	22.79	0.27	0.086	4.29	14.60%	32.50%	10.00%	57.50%
WAW2	255	3.33	34.20	43.84	1.80	24.33	0.28	0.197	4.40	4.39%	50.00%	25.00%	25.00%
WAW2	256	4	34.20	43.94	1.59	27.69	0.26	0.154	4.17	6.97%	50.45%	19.55%	30.00%
WAW2	257	4	34.20	45.05	2.09	21.54	0.31	0.149	4.40	9.04%	47.95%	22.05%	30.00%

WAW2	258	3.66	34.20	45.43	2.11	21.53	0.31	0.106	3.96	10.52%	40.45%	9.55%	50.00%
WAW2	259	3.83	34.20	46.35	2.03	22.83	0.28	0.150	4.44	14.32%	29.55%	12.95%	57.50%
WAW2	260	2.83	34.20	44.04	2.08	21.16	0.29	0.209	4.48	13.74%	40.90%	11.60%	47.50%
WAW2	261	6.5	34.20	46.29	2.25	20.58	0.29	0.173	4.17	5.47%	37.05%	22.95%	40.00%
WAW2	262	6.16	34.20	43.90	1.86	23.55	0.29	0.098	4.11	3.07%	46.35%	21.60%	32.05%
WAW2	263	6.16	34.20	46.17	2.00	23.06	0.30	0.171	4.40	10.49%	31.35%	14.10%	54.55%
WAW2	264	5.83	34.20	42.50	1.98	21.44	0.29	0.116	4.10	9.58%	36.35%	14.10%	49.55%
WAW2	265	3.83	34.20	46.52	1.79	25.96	0.28	0.228	4.00	7.33%	54.55%	15.45%	30.00%
WAW2	266	5.5	34.20	45.56	1.65	27.60	0.27	0.172	3.95	6.82%	52.95%	14.55%	32.50%
WAW2	267	4.33	34.20	42.85	1.67	25.69	0.30	0.163	4.08	6.66%	55.45%	14.55%	30.00%
WAW2	268	3.5	34.20	45.34	1.60	28.36	0.27	0.153	4.13	7.43%	50.45%	19.55%	30.00%
WAW2	269	3.66	34.20	42.09	1.62	26.05	0.27	0.202	4.20	8.43%	45.45%	17.05%	37.50%
WAW2	270	4.33	34.20	40.31	1.59	25.30	0.28	0.147	3.91	6.57%	55.45%	17.05%	27.50%
SEL3	271	2.16	28.70	29.97	1.13	26.43	0.19	0.100	3.88	5.75%	40.90%	17.05%	42.05%
SEL3	272	4.66	28.70	29.43	1.01	29.17	0.18	0.127	4.04	6.77%	38.40%	16.60%	45.00%
SEL3	273	2.83	28.70	30.41	1.15	26.42	0.21	0.127	3.66	4.32%	38.40%	24.10%	37.50%
SEL3	274	2.83	28.70	28.71	1.13	25.36	0.20	0.102	3.89	3.27%	38.40%	21.60%	40.00%
SEL3	275	2	28.70	32.33	1.14	28.36	0.20	0.132	4.15	3.01%	37.50%	22.50%	40.00%
SEL3	276	3.16	28.70	29.67	1.07	27.81	0.18	0.107	4.29	3.74%	35.45%	32.05%	32.50%
SEL3	277	2.33	28.70	35.59	1.66	21.47	0.26	0.101	4.04	2.40%	35.00%	25.00%	40.00%
SEL3	278	3.5	28.70	36.82	1.35	27.25	0.23	0.070	3.99	2.30%	35.00%	32.50%	32.50%
SEL3	279	2	28.70	28.63	1.15	25.00	0.18	0.087	4.40	2.85%	37.50%	30.00%	32.50%
SEL3	280	1.5	28.70	30.60	1.30	23.61	0.19	0.129	4.56	2.04%	28.40%	31.60%	40.00%
SEL3	281	1.83	28.70	39.48	1.64	24.12	0.25	0.110	4.38	11.76%	38.40%	16.60%	45.00%
SEL3	282	2.16	28.70	33.78	1.55	21.86	0.25	0.061	4.69	11.39%	20.90%	9.10%	70.00%
SEL3	283	2	28.70	38.35	1.53	25.03	0.22	0.172	4.24	3.69%	40.45%	29.55%	30.00%
SEL3	284	1.83	28.70	38.70	1.55	25.00	0.24	0.158	4.42	4.01%	40.45%	24.55%	35.00%

SEL3	285	1.5	28.70	35.05	1.50	23.34	0.25	0.062	3.84	1.92%	33.40%	24.10%	42.50%
SEL3	286	2.16	28.70	31.11	1.34	23.27	0.22	0.075	4.22	2.35%	30.90%	19.10%	50.00%
SEL3	287	2.83	28.70	38.32	1.66	23.08	0.24	0.236	4.41	5.77%	43.40%	19.55%	37.05%
SEL3	288	3.5	28.70	31.91	1.29	24.76	0.22	0.140	4.14	2.89%	23.40%	14.10%	62.50%
SEL3	289	1.66	28.70	33.85	1.38	24.48	0.23	0.167	4.03	2.85%	40.90%	26.60%	32.50%
SEL3	290	2.5	28.70	37.45	1.54	24.33	0.23	0.216	4.62	2.36%	35.90%	24.10%	40.00%
SEL2	291	5.66	32.20	37.23	1.04	35.80	0.17	0.092	3.83	4.22%	50.45%	29.55%	20.00%
SEL2	292	4.83	32.20	34.35	0.96	35.78	0.19	0.074	3.54	4.07%	47.50%	27.50%	25.00%
SEL2	293	4.5	32.20	37.13	1.17	31.87	0.21	0.119	4.12	5.26%	47.50%	22.50%	30.00%
SEL2	294	6.16	32.20	38.48	1.25	30.76	0.21	0.111	3.96	6.33%	47.50%	15.00%	37.50%
SEL2	295	4.83	32.20	40.69	1.24	32.79	0.18	0.113	4.17	9.60%	50.90%	16.60%	32.50%
SEL2	296	5	32.20	40.91	1.32	30.92	0.20	0.111	3.89	8.84%	53.40%	16.60%	30.00%
SEL2	297	6.5	32.20	34.93	1.10	31.64	0.19	0.098	3.69	6.39%	55.90%	16.60%	27.50%
SEL2	298	6.5	32.20	36.88	1.08	34.21	0.19	0.061	3.32	7.36%	50.90%	19.10%	30.00%
SEL2	299	4.66	32.20	46.20	1.57	29.41	0.23	0.087	4.22	3.13%	42.50%	32.50%	25.00%
SEL2	300	4.66	32.20	42.82	1.45	29.55	0.24	0.060	4.31	2.77%	40.90%	34.10%	25.00%
SEL2	301	6.33	32.20	49.15	1.63	30.10	0.20	0.132	4.20	4.85%	50.00%	29.10%	20.90%
SEL2	302	5.33	32.20	49.43	1.59	31.07	0.23	0.129	4.10	4.08%	47.50%	24.10%	28.40%
SEL2	303	6.83	32.20	50.68	1.59	31.97	0.21	0.116	4.19	2.93%	32.95%	32.05%	35.00%
SEL2	304	6.5	32.20	49.97	1.60	31.29	0.22	0.111	4.06	4.17%	40.45%	32.05%	27.50%
SEL2	305	4.16	32.20	38.92	1.34	29.13	0.17	0.071	4.78	2.02%	30.45%	44.55%	25.00%
SEL2	306	3.5	32.20	45.33	1.57	28.82	0.21	0.092	4.27	2.29%	27.95%	39.55%	32.50%
SEL2	307	2.33	32.20	35.65	1.44	24.83	0.19	0.083	4.44	5.24%	42.50%	25.00%	32.50%
SEL2	308	3.33	32.20	34.87	1.19	29.35	0.16	0.088	4.08	4.61%	37.50%	37.50%	25.00%
SEL2	309	3.16	32.20	36.64	1.44	25.37	0.17	0.079	4.79	5.10%	47.50%	25.00%	27.50%
SEL2	310	3	32.20	35.34	1.14	31.05	0.14	0.086	5.08	5.39%	45.00%	22.50%	32.50%
SEL2	311	3.83	32.20	39.09	1.28	30.56	0.17	0.075	4.88	6.18%	42.50%	21.60%	35.90%

SEL2	312	3.33	32.20	35.02	1.26	27.73	0.19	0.058	4.16	7.86%	40.90%	14.10%	45.00%
SEL2	313	3.83	32.20	46.14	1.71	26.92	0.23	0.077	4.21	2.73%	45.00%	35.00%	20.00%
SEL2	314	3.83	32.20	42.62	1.32	32.29	0.20	0.072	3.85	3.15%	47.50%	32.50%	20.00%
SEL2	315	4.83	32.20	45.90	1.42	32.32	0.20	0.088	3.86	4.25%	42.95%	24.55%	32.50%
SEL2	316	4	32.20	42.87	1.25	34.21	0.19	0.058	3.58	3.53%	52.50%	27.50%	20.00%
SEL2	317	3	32.20	48.42	1.68	28.79	0.21	0.060	5.00	4.67%	40.45%	24.55%	35.00%
SEL2	318	2.83	32.20	47.44	1.64	28.94	0.21	0.083	5.16	5.33%	35.45%	24.55%	40.00%
SEL2	319	4.16	32.20	46.62	1.25	37.39	0.19	0.101	3.83	4.30%	47.95%	24.55%	27.50%
SEL2	320	4.5	32.20	44.21	1.26	35.14	0.18	0.121	3.83	5.21%	53.40%	19.10%	27.50%
SEL2	321	4.16	32.20	37.57	1.17	32.25	0.19	0.068	3.26	2.82%	43.40%	31.60%	25.00%
SEL2	322	3.66	32.20	37.37	1.13	33.10	0.18	0.073	3.31	2.53%	35.90%	26.60%	37.50%
SEL1	323	13	38.20	38.10	1.50	25.35	0.20	0.054	3.98	2.58%	40.00%	41.60%	18.40%
SEL1	324	12.33	38.20	41.64	1.57	26.59	0.20	0.054	4.31	10.03%	20.45%	22.05%	57.50%
SEL1	325	16	38.20	38.45	1.48	26.00	0.21	0.074	3.95	5.17%	40.45%	29.55%	30.00%
SEL1	326	18.66	38.20	38.23	1.34	28.44	0.21	0.037	3.41	9.73%	12.95%	14.55%	72.50%
SEL1	327	21.66	38.20	44.99	1.46	30.82	0.23	0.065	3.25	3.88%	47.50%	41.60%	10.90%
SEL1	328	21.66	38.20	43.77	1.54	28.51	0.23	0.049	3.46	7.24%	30.45%	34.55%	35.00%
SEL1	329	11.66	38.20	43.97	1.09	40.30	0.18	0.055	3.34	3.07%	55.00%	36.60%	8.40%
SEL1	330	20	38.20	47.29	0.86	55.21	0.15	0.054	2.82	2.01%	40.45%	52.05%	7.50%
SEL1	331	14.16	38.20	44.62	0.83	53.46	0.15	0.046	3.61	3.54%	52.50%	36.60%	10.90%
SEL1	332	14	38.20	36.95	0.98	37.85	0.16	0.114	3.98	2.95%	50.00%	36.60%	13.40%
SEL1	333	17.66	38.20	44.27	1.33	33.19	0.21	0.036	3.39	4.90%	50.45%	29.55%	20.00%
SEL1	334	20.5	38.20	45.67	1.21	37.81	0.19	0.037	3.15	6.89%	50.45%	32.05%	17.50%
SEL1	335	14.66	38.20	38.13	1.18	32.23	0.19	0.071	3.67	3.31%	57.95%	32.05%	10.00%
SEL1	336	15.5	38.20	38.95	1.28	30.36	0.20	0.032	3.43	3.30%	55.45%	34.55%	10.00%
SEL1	337	16.16	38.20	38.51	0.97	39.82	0.16	0.077	3.87	3.75%	50.45%	32.05%	17.50%
SEL1	338	17.83	38.20	37.93	0.87	43.77	0.15	0.101	3.62	3.80%	55.00%	30.00%	15.00%

SELI	339	7	38.20	35.47	1.04	34.01	0.16	0.068	4.08	3.12%	52.95%	32.05%	15.00%
SELI	340	10.66	38.20	38.92	0.84	46.48	0.15	0.084	3.21	2.36%	52.95%	37.05%	10.00%
SELI	341	13	38.20	42.80	1.22	35.08	0.20	0.102	3.33	2.28%	42.50%	51.60%	5.89%
SELI	342	14.83	38.20	37.40	1.11	33.79	0.18	0.037	3.91	4.53%	45.45%	34.55%	20.00%

CHAPITRE II

SPECIES-SPECIFIC GROWTH RESPONSES OF BLACK SPRUCE AND ASPEN ENHANCE RESILIENCE OF BOREAL FOREST TO CLIMATE CHANGE

Sylvie Gewehr, Yves Bergeron and Igor Drobyshev

2.1 Abstract

The influence of climate change on tree growth is expected to lead to modifications in future forest composition and productivity. To understand how climate change will affect the boreal forest, climate-growth relationships and growth responses to extreme weather events of two major boreal tree species were determined. Redundancy analysis conducted on black spruce and aspen chronologies showed that growth of the two species was affected differently by climate. Radial growth of black spruce was favoured by cooler temperatures and wetter conditions, while aspen growth was favoured by higher temperatures and drier conditions. These results indicate that black spruce could suffer more from drought stress in the study area than aspen. Black spruce and aspen did not show growth anomalies (pointer years) for the same years or showed opposite growth anomalies for the same year. Climate variables which were associated to black spruce and aspen growth through the redundancy analysis were associated in the same way to growth during pointer years, where extreme values were recorded for those climate variables. Thus black spruce and aspen had species-specific responses to extreme weather events as well. These species-specific growth responses to average climate and climatic anomalies and the temporal niche separation they might induce could make biomass accumulation more even in mixed forests, as compared to pure stands under climatically extreme conditions. Also, whether climate change will benefit black spruce and aspen growth or not, will highly depend on the balance between increasing temperatures and precipitation. However, the species-specific effects of climate change will eventually result in differential growth rates among species, thus keeping both species in mixed stands might reduce the risks of detrimental effects of climate change on forest productivity by enhancing resilience of the boreal forest.

Keywords: *Picea mariana*, *Populus tremuloides*, radial growth, climate change, extreme weather events, mixed stands, resilience.

Résumé

L'effet direct des changements climatiques sur la croissance des arbres mènera à d'importantes modifications de la composition et productivité futures des forêts. Afin de mieux comprendre comment les changements climatiques affecteront la forêt boréale, les relations croissance-climat et les réponses aux extrêmes climatiques deux essences dominantes de la forêt boréale ont été déterminées. L'analyse canonique de redondance des chronologies de croissance de l'épinette noire et du peuplier faux-tremble a indiqué que les deux espèces répondent différemment au climat. La croissance de l'épinette noire était favorisée par des conditions plus fraîches et humides, alors que la croissance du peuplier faux-tremble était favorisée par des conditions plus chaudes et sèches. Ces résultats indiquent que dans cette région l'épinette noire pourrait avoir tendance à plus souffrir de stress de sécheresse que le peuplier faux-tremble. Généralement les deux espèces ne présentaient pas des anomalies de croissance (années caractéristiques) dans les mêmes années ou les deux espèces avaient des anomalies de croissance opposées pour une même année. Les associations entre les variables climatiques et la croissance relevées précédemment se retrouvaient également pour les années caractéristiques. Les deux espèces auraient donc également une réponse spécifique au climat lors d'extrêmes climatiques. Ces réponses spécifiques au climat annuel et aux anomalies climatiques pourraient induire une séparation temporelle des niches écologiques et permettre une accumulation de biomasse plus constante lors d'extrêmes climatiques dans les peuplements mixtes, comparées aux peuplements purs. Les changements climatiques pourront bénéficier ou non à la croissance de l'épinette noire et du peuplier-faux-tremble dépendamment de la balance entre la hausse des températures et l'augmentation des précipitations. Les changements climatiques auront des impacts spécifiques sur chaque espèce, ultimement menant à des taux de croissance différents entre les espèces. En augmentant la résilience de la forêt boréale, conserver des peuplements mixtes pourrait permettre de réduire les risques d'observer des effets néfastes des changements climatiques sur la productivité des forêts.

Mots clés : *Picea mariana*, *Populus tremuloides*, croissance radiale, changements climatiques, extrêmes climatiques, peuplements mixtes, résilience.

2.2 Introduction

In 2007 the Intergovernmental Panel on Climate Change reported that worldwide surface temperatures have increased by 0.74°C between 1906 and 2005, and that in the future temperatures are expected to increase the most at mid to high northern latitudes (IPCC 2007). For western Quebec temperatures are projected to rise by 1.5 to 5.2°C by the middle of the 21st century and to be accompanied by 10-25% more precipitation, except during the summer months for which precipitation is projected to know a slight decrease (2%) or to increase by no more than 15% (Ouranos 2010). Generally, the climate will become moister throughout the year, except during the summers, for which dryer conditions are to be expected. In addition to increasing temperatures and precipitation, extreme weather events are predicted to occur more frequently in the future (Bonsal *et al.* 2001; IPCC 2007; Mailhot *et al.* 2010). Climate change directly affects tree growth and distribution, and consequently, influences the migration potential of tree species and the composition of forests (Hansen *et al.* 2001; Mohan *et al.* 2009).

Growth responses to climate of aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* [Mill.] B.S.P.), the dominant species of the eastern Canadian boreal forest, have been assessed in recent dendroclimatic studies. Black spruce is influenced by temperatures at the start of and during the growing season, while aspen growth is mostly influenced by climatic conditions of the year prior to growth (Hofgaard *et al.* 1999; Tardif *et al.* 2001; Drobyshev *et al.* 2010; Huang *et al.* 2010; see Chapter I). Most dendroclimatic studies have focused on tree growth responses to non-anomalous weather, but recent studies have pointed out the importance of extreme weather events for tree radial growth (Graumlich 1993; Hogg *et al.* 2005, 2008; Leonelli & Pelfini 2008; Drobyshev *et al.* 2010). Depending on the climate sensitivity of tree species, extreme weather events can cause significant growth reductions, and thus a decrease in biomass accumulation in stands where all trees respond negatively to the extreme weather event. Species-specific growth responses to future climate and a higher frequency of what are now climatic anomalies could thus result in differential growth rates among species and ultimately in changing stand composition and structure.

Various studies have pointed out the potential for mixed stands to be more productive than pure stands, given the mixtures including species with different ecological niches or functional traits (e.g. above ground niche separation, temporal niche separation, shade tolerant versus shade intolerant species, etc.) (Man & Lieffers 1999; Chen *et al.* 2003; Bauhus *et al.* 2004; Green 2004; Pretzsch *et al.* 2010; Brassard *et al.* 2011). Black spruce and aspen are known to have distinct functional traits, and above- and belowground niche separation (Burns & Honkala 1990a, 1990b; Légaré *et al.* 2004, 2005; Brassard *et al.* 2011; Cavard *et al.* unpublished). In addition, different growth responses of the two species to climate would allow better use of the resources at a temporal scale and could thus contribute to more constant growth rates of mixed stands.

The aim of this study was to determine the species-specific growth responses to annual climate and to climatic anomalies of black spruce and aspen. The following hypotheses were tested: (1) aspen has different growth-responses to annual climate than black spruce, and (2) extreme weather events cause differential growth responses in the two species. By assessing the importance of species-specific growth responses to annual climate and climatic anomalies, this study should lead to a better understanding of the importance of maintaining mixed black spruce-aspen stands for forest productivity and resilience under a changing climate.

2.3 Methods

2.3.1 Study area

The study area (49°03' – 49°29'N; 78°46' – 79°09'W) was located in the black spruce-feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) bioclimatic domain of western Quebec and the Northern Clay Belt of Quebec and Ontario (Fig.2.1; Simard *et al.* 2008). The Clay Belt consists of thick clay deposits covering the Precambrian Shield left by proglacial Lake Barlow-Ojibway and forms a vast clay plain (Veillette *et al.* 2004). The topography of the study area is rather flat, with a mean altitude of 250 m to 300 m above sea level, and a few bedrock hills breaking the monotony of the clay plain. Half of the glaciolacustrine deposits are covered by thick layers of soil organic layer (SOL), reaching depths of 60 cm or even

more and causing paludification of the forests (i.e. the successional development towards forest peatlands) in some areas. In absence of paludification, the soils found in the Clay Belt are mostly luvisols and gleysols (Groupe de travail sur la classification des sols, 2003).

The climate of the area is continental and characterized by cold and dry winters and by warm summers. During the winter very cold continental arctic air masses coming from the north dominate, whereas the climate of summer months is influenced by moist Atlantic maritime tropical air masses from the south and by dry maritime arctic air masses from the north (Pigott & Hume 2009). According to the climate normals calculated from the data recorded at the La Sarre and Joutel meteorological stations (located 30 km south and about 40 km northeast of the study area respectively) from 1971 to 2000, the mean annual temperature of the area varies between 0.1°C and 0.7°C. Total annual precipitation is around 890mm, with 35% received during growing season and 30% falling as snow (Environment Canada, 2010). Ground frosts are common during the growing season, but the study area is not subject to permafrost (Brown & Gangloff, 1980).

The area is dominated by black spruce stands with variable height and density (Simard *et al.* 2008). Jack pine (*Pinus banksiana* Lamb.) and aspen are common in the region as well and can be found in pure stands or mixed stands with black spruce. Fire is the main natural disturbance in the black spruce-feathermoss domain (Simard *et al.* 2008). The fire cycle in the region has increased from around 100 years before 1850, to 360 years since 1920 (Bergeron *et al.* 2004). In the study area, the spruce budworm (*Chorisonneura fumiferana* Clem.) remains of low impact on black spruce population dynamics, compared to what is observed in most of its range (Gray *et al.* 2000; Lussier *et al.* 2002; Gray, 2008). The forest tent caterpillar (*Malacosoma disstria* Hubner.) is an important defoliator of aspen, but outbreaks in the study area are of short duration, relatively low amplitude and occur less often than south of the 49°N (Cooke & Lorenzetti, 2006; Huang *et al.* 2008).

2.3.2 Data collection

Sampling took place in 2008 and 2009 in three sub-areas with mixed black spruce and aspen stands. A humidity gradient ranging from xeric stands to paludified stands was covered with

ten sampling sites distributed within the three sub-areas of Villebois (VIL), Selbaie (SEL), and Wawagosis (WAW) (Fig. 2.1). A total of 145 plots were established within the 10 sites located in mixed black spruce-aspen stands with different SOL depth varying from 1 to 23 cm (Table 2.1), thus covering the SOL depth limited distribution range of aspen within landscape in the Quebec Clay Belt (see Chapter I). One black spruce and one aspen were sampled in each plot as in Chapter I.

2.3.3 Tree-ring data

The cores and cross-sections taken from black spruce and aspen were prepared and measured following standard methods in dendrochronology (Stokes & Smiley 1968; Speer 2010). The samples were first mounted, sanded and visually cross-dated using the skeleton plot method (Stokes & Smiley 1968). The ring widths were then measured using a Velmex micrometer (Velmex Incorporated, Bloomfield, New York, USA) and TSAP-Win Professional, version 0.55 (Rinntech, Heidelberg, Allemagne) at a precision of 0.01 mm. Measurements were visually verified with TSAP-Win Professional, before the dating of tree-ring series were validated using the program COFECHA (Grissino-Mayer 2001; Speer 2010). Two radii measured for each tree (on the two cores or on two radii on cross-sections) were then averaged.

Raw ring-width series represent growth variability at multiple frequencies. In this study the focus of the analyses was on high frequency variability and the treatment of time series was therefore designed to remove lower frequencies in tree-ring series. To obtain high frequency annual growth chronologies, the cross-dated tree ring series were detrended in the ARSTAN program using a 32 year cubic smoothing spline with a 50% frequency response (Cook 1987; Fritts 1991; Speer 2010). By dividing the original chronology values by the predicted values, ring-width measures were transformed into index values. To remove temporal autocorrelation, the series were prewhitened by autoregressive modelling (Cook 1987). Residual single-tree chronologies were computed (by using the “core series save” option) to analyse climate-growth relationships on single trees for the two species (black spruce $n = 145$ and aspen $n = 143$).

In western Quebec severe defoliation of aspen can occur during insect outbreaks caused by the forest tent caterpillar. Years of severe defoliation, manifested by very narrow and/or white rings (Sutton & Tardif, 2005), were observed in some of the sampled trees in 1980 and 1999-2001. These years were previously identified as years of severe outbreaks (Huang *et al.* 2008). Years of growth suppression in the chronologies can be identified and the impact of defoliation on growth could be potentially removed by using a chronology of a non-host species (Swetnam *et al.* 1985; Speer 2010). However, this procedure requires that the host and non-host species have a similar response to climate. This was not the case for aspen and black spruce (Huang *et al.* 2010), which precluded use of this method in the current study. Therefore, the aspen residual chronologies were not modified prior to analyses.

2.3.4 Dendroclimatic analyses

2.3.4.1 Climate data

Data used for dendroclimatic analyses were generated using BioSIM (Régnière & Bolstad 1994; Régnière 1996). Monthly climate data for the ten sampling sites and for the period 1900-2009 were obtained as in Chapter I. The climate variables included monthly mean temperature (°C), monthly total precipitation (mm), monthly total snowfall (mm), and total degree-days (> 5°C), the sum of all individual degree-days, which are the number of degrees by which the mean daily temperature is above 5°C (Allaby 2007). Finally, the Monthly Drought Code (MDC) was calculated from May to October using monthly maximum temperature and monthly total precipitation generated in BioSIM (Girardin & Wotton 2009). The MDC is a monthly version of the Drought Code developed to capture moisture content of deep and compact organic layers of the forest floor (Turner 1972).

2.3.4.2 Annual weather

The species-specific influence of climate on tree growth was investigated using a redundancy analysis (RDA) in the CANOCO package (version 4.56; Ter Braak & Šmilauer 2002). The RDA was performed on residual chronologies from the two species and for the common

interval 1958-2007 (black spruce $n = 114$; aspen $n = 126$). A correlation matrix where the 240 residual chronologies were considered as response variables and the years as samples (or observations) was used. Climate variables ($n = 48$) were considered as explanatory variables (environmental variables in the CANOCO terminology) and were transformed into ordination axes. These climate variables were: (1) the mean monthly temperatures, monthly total precipitation, and MDC spanning from previous May to August of the year of growth, (2) three multi-month snow variables and (3) the total degree-days above 5°C of the previous and current years.

2.3.4.3 Climatic anomalies

Pointer years are usually defined as years with particularly narrow growth rings present in the majority of trees sampled within a region or site (Schweingruber 1996). In this study, pointer years were defined as years with negative or positive growth anomalies, defined as years with ring width below 5% or above 95% of the ring width distribution of a respective tree. Pointer years were identified in the dataset of all single-tree chronologies. The pointer years were selected by feeding the single-tree chronologies of the two species separately ($n = 145$ for black spruce; $n = 143$ for aspen) to the program XTRSLT of the Dendrochronological Program Library (Holmes 1999). For each species, the number of trees expressing a pointer year was divided by the sample depth for that year in order to assess the signal strength for that pointer year. Only years with growth anomalies present in at least 10% of the trees of one of the species were used for further analyses. The pointer years were identified over the period 1940-2008 because of a low sample depth before 1940. The years of known severe defoliation of aspen due to insect outbreaks (1980 and 1999-2001) were not considered as pointer years. The identified pointer years were analyzed for climatic anomalies in monthly mean temperature, monthly total precipitation, MDC, and degree days above 5°C, by calculating 5% and 95% percentiles for those variables.

2.4 Results

2.4.1 Annual weather

The redundancy analysis revealed that black spruce and aspen growth were differently affected by annual weather (Fig. 2.2). Black spruce and aspen chronologies formed two separated groups along the first ordination axis. The first two ordination axes accounted for 30.5% of the variation in growth. Mean temperature of previous August and current June, as well as MDC of previous August and September were negatively associated with the first axis, whereas previous June and current March precipitation were positively associated with it. The second axis was positively associated with previous May MDC, and negatively with July precipitation and April to May total amount of snowfall. Total number of degree days, temperature of previous November and April MDC were associated with both axes. Only the climate variables which had a $|r| \geq 0.20$ were presented here. All aspen residual chronologies were found on the left part of the first axis, whereas most of the black spruce residual chronologies were found on the right part of the first axis. All of the chronologies are distributed more or less equally along the second axis.

2.4.2 Climatic anomalies

Twenty-three pointer years that showed up in at least 10% of the trees of one of the two species were identified (Table 2.2). Generally the two species did not record the same pointer year or showed opposite growth anomalies. The proportion of trees recording growth anomalies in those pointer years tended to be higher for black spruce than aspen. There was a rather strong negative relationship between expression of a pointer year in black spruce and aspen, well approximated by negative exponential curve, with an $R^2 = 0.38$ (Fig. 2.3). Negative pointer years for black spruce were 1944, 1962, 1970, 1974, 1989, 1994, 2003 and 2008 and positive pointer years were 1951, 1968, 1979, 1985 and 2004. For aspen negative pointer years were 1956, 1969, 1972, 1992, 1998 and 2004, and positive pointer years were 1945, 1960, 1976, 1991, 2003, 2006 and 2008 (Table 2.3).

For each pointer year identified, at least one climatic anomaly was found and generally, at least one of these anomalies was observed in climate variables which were significantly correlated with black spruce or aspen growth in the RDA (Table 2.2). For some pointer years, one or more climatic anomalies could have caused the growth anomalies. In 1969, for example, high mean temperatures in previous September and in January,

precipitation anomalies in previous May and July and in February and August, as well as a low MDC in August could have caused the negative growth anomaly in aspen. The relationship between growth and climatic anomalies appeared to be clearer for some other years like 2004, a year with a very moist summer (extremely low MDC in July and August), which positively affected black spruce growth and negatively affected aspen growth.

2.5 Discussion

2.5.1 Species-specific growth responses to annual weather

The first hypothesis, which stated that the radial growth of aspen would be influenced by other climate variables than that of black spruce, was confirmed by the RDA. The residual aspen chronologies were found on the left part and the black spruce chronologies on the right part of the first ordination axis, which encompassed climate variables specific to differences between the species. The results suggest that aspen growth was favoured by warmer and drier conditions, while black spruce growth benefitted from cooler temperatures and wetter conditions. Mean temperature of previous August and current June, as well as MDC of previous August and September were negatively associated with the first axis, thus aspen growth was positively associated to those climate variables and black spruce was negatively associated to them. On the opposite, previous June and current March precipitation were negatively associated with aspen growth and positively with black spruce growth. Both species also had similar growth responses to some of the climate variables (previous May MDC, July precipitation, April to May total amount of snowfall). The climate-growth associations observed here are similar to results from a previous study conducted on the same trees, which can be consulted for more details on growth responses to climate (see Chapter I).

The differences observed between the two species were expected, as previous studies had shown that boreal coniferous and deciduous tree species were influenced by climate in very different manners (Chapter I; Tardif *et al.* 2001; Huang *et al.* 2010). Temperature, precipitation, and MDC yielded inverse correlations among the two species. These results suggest that black spruce would suffer from moisture stress during the growing season, whereas aspen might be limited by excess moisture. These opposite responses to water stress

have been observed before in similar species, *Picea abies* (L.) Karst. and *Populus tremula* L. (Tatarinov *et al.* 2005). This can be explained by the fact that the shallow root system of black spruce is confined to the unsaturated surface layers of soil organic layer (upper 20 cm), which tend to dry out faster than underlying mineral soil during a summer drought (Lieffers & Rothwell 1987; Rothwell *et al.* 1996).

2.5.2 Pointer years

Pattern of negative growth anomalies in black spruce and aspen were species-specific, which indicated that these species might have responded to different climate anomalies. Generally the two species did not record the same pointer years or showed opposite growth anomalies. Fig. 2.3 showed that there was a rather strong negative relation between those two variables, clearly showing that the two species had different responses to weather anomalies. This relation remained true, even when considering the types of pointer years. Previous studies have shown that growth patterns during non-extreme weather conditions and during the periods of weather anomalies are controlled by a similar set of climate variables (Drobyshev *et al.* 2010; Leonelli & Pelfini 2008). Black spruce and aspen growth each were controlled by different climate variables during non-extreme weather, therefore it was to be expected that they would have different responses to climatic anomalies as well. Climate variables which were associated to black spruce and aspen growth through the RDA were associated to some pointer years. The RDA revealed that June mean temperature was positively related to aspen growth and negatively to black spruce growth. The negative growth anomalies found in black spruce and the positive ones found in aspen in 1976 could thus be related to the extremely high June mean temperature of this year. The same way, extremely low June temperature in 1992 could have caused the negative growth anomalies in aspen. For 1992, as well as for 1956, the total number of degree days also was particularly low, probably causing the negative growth anomalies in aspen. The positive growth anomalies found in black spruce and the negative ones found in aspen in 1979 and 1998 may be related to extremely high March precipitation in those years, while very low March precipitation in 1974 could have caused negative growth anomalies in black spruce.

However, some of the negative growth anomalies in black spruce and aspen could be due to insect outbreaks. The years of severe forest tent caterpillar (FTC) outbreak which could clearly be identified on the aspen samples through white rings (1980, 1999-2001), were not considered as pointer years. If compared to the results of Huang *et al.* (2008), the following pointer years coincide with outbreaks they identified at 49° and/or 50°N: 1956, 1972, 1992, 1998, and 2004. However, the non-host species they used to compare aspen growth to was black spruce, which has very different responses to climate. What OUTBREAK saw as a growth reduction due to the FTC in aspen, could in fact have been due to some extreme weather event which generated a negative growth response in aspen and not black spruce as they respond differently to climate. Only 1972 was confirmed as an FTC outbreak year in the concerned area by Cooke & Lorenzetti (2006), who used defoliation data. Moreover, the spatial patterns and extent of past FTC outbreaks are not well known, so even if some sites were affected by an outbreak others might have remained untouched by the FTC. Negative growth anomalies in black spruce could be due to spruce budworm (SB) outbreaks. According to defoliation data provided by the Ministère des Ressources Naturelles et de la Faune du Québec, no SB outbreak occurred in 1944, but this year is known to have been a year of severe outbreak south of the area, and only one climate variable (January temperature), which is rather unlikely to have caused a negative growth anomaly, displayed extreme values for this year. Another period of outbreak was 1971-1985, during which defoliation caused by SB has been recorded in 1974 which coincides with a negative pointer year identified in this study. However, the temperature of the end of the previous growing season was extremely high and could have caused temperature induced water deficit in black spruce. Only 1944 and 1974 could be related to SB outbreaks in the area, but whether the SB caused these and other negative growth anomalies or not is hard to determine. However it has to be kept in mind that SB reaches its northern distribution limit in this area and that it mainly affects balsam fir and white spruce rather than black spruce (Gray *et al.* 2000; Lussier *et al.* 2002; Gray, 2008).

It would have been necessary to perform Superposed Epoch Analyses (SEAs) in order to determine whether the negative pointer years in aspen and black spruce were related to extreme weather events or insect outbreaks. SEAs would also have allowed identifying the climatic anomalies that really were related to all of the identified growth anomalies in both

species, as a various number of climatic anomalies were detected. Drobyshev *et al.* (2010) performed SEAs on pointer years identified in black spruce in the same area. They identified 1956, 1974, 1989, and 1994 as negative pointer years, which were found in this study too. Through SEAs 1956 was linked to a short growing season, 1974 to a short growing season and a particularly warm August in the previous year, and 1989 to low precipitation during the previous summer. Only 1994 could not clearly be linked to an extreme weather event with the SEAs. In 1956 both aspen and black spruce displayed negative growth anomalies, probably due to the particularly short growing season (Table 2.2; Drobyshev *et al.* 2010), as no insect outbreak has been listed for this year in the study area. Visual examination of the tree samples showed that in both species the tree-ring corresponding to 1956 was paler, as compared to the other tree-rings, in a certain proportion of the samples (black spruce: 46.5%; aspen: 26.4%). Pale tree-rings could therefore also be related to extreme weather events, but this question would need further investigation.

2.5.3 Effects of climate change on mixed black spruce-aspen stand dynamics

Black spruce and aspen growth had different growth responses both to non-extreme weather conditions and climatic anomalies, and thus, are likely to show different responses to future climate variability. According to the Canadian Regional Climate Models (CRCMs) generated and supplied by Ouranos (de Elia & Coté 2010; Ouranos 2010), the mean temperature and total precipitation in western Quebec will increase by 2046-2065, as compared to 1961-1999. Winters are predicted to become much warmer and wetter, while the summers might become drier. Increasing summer temperatures and drier conditions could benefit aspen growth, while inducing drought stress for black spruce. Both species will react individually but whether climate change will benefit their growth or not, will highly depend on the balance between increasing temperatures and precipitation. The species-specific effects of climate change will eventually differentiate species growth rates. Keeping both species in mixed stands may allow reducing the risks of detrimental effects of climate change on forest productivity. Moreover, mixed stands are known to help maintaining biodiversity, and to enhance stand resistance to wind damage, disease, and insect outbreaks (Frivold & Mielikäinen 1990; Kelty 1992).

The species-specific growth responses of black spruce and aspen to non-extreme weather conditions and climatic anomalies and the temporal niche separation they might induce could make biomass accumulation more even in mixed forests, as compared to pure stands under climatically extreme conditions. The different leafing habits between broadleaf and evergreen tree species resulting in different light utilization periods contributes to the temporal niche separation of black spruce and aspen. This temporal niche separation adds to previously demonstrated benefits of spatial niche separation as well as facilitation in mixed stands. Black spruce and aspen occupy different niches above ground, with aspen always overtopping black spruce, and up to a certain proportion, aspen has a facilitation effect on black spruce, by enhancing nutrient cycling (Légaré *et al.* 2004, 2005; Laganière *et al.* 2010; Cavard *et al.* unpublished). The two species also have a spatial belowground niche separation, black spruce roots being rather shallow and aspen roots growing deeper in the soil (Burns & Honkala 1990a, 1990b; Brassard *et al.* 2011). The spatial and temporal niche separation both influence competition for edaphic resources in mixed stands and allow a better use of the available resources (Man & Lieffers 1999; Green 2004; Brassard *et al.* 2009). The reduced demand on edaphic resources by broadleaf trees during their leafless periods, particularly in spring, should help sustain the photosynthetic rates of conifers, which could potentially be high in understory conifers given the enhanced light availability at these times (Man & Lieffers 1997, 1999; Green 2004).

Black spruce and aspen generally had opposed growth responses to climate, leading to a temporal niche separation of black spruce and aspen growth, in addition to the below ground niche differentiation, possibly reducing even more the competition for edaphic resources. Thus one species could use the needed edaphic resources when the climate is favourable to its growth, while the other one's growth might be limited by the same climatic conditions, reducing its use of edaphic resources. This effect of temporal niche separation would be even more pronounced during extreme weather events, which have great impacts on tree growth (Graumlich 1993). Insect outbreaks can have great impacts on tree growth as well (Kulman 1971; Hogg *et al.* 2005; Cooke & Roland 2007), but are species-specific too and thus, cannot cause growth reductions in black spruce and aspen at the same time, adding to the temporal niche separation of the two species. The complementary ecological niches of black spruce and aspen would thus allow a better use of the resources and make biomass

accumulation more constant during extreme weather events or insect outbreaks, as compared to pure stands. Resilience of the boreal forest, which can be defined as the ecosystem's capacity to absorb changes or shocks and still remain functional (Holling 1973), would therefore be enhanced.

2.6 Conclusions

Growth of black spruce and aspen was mostly controlled by different climate variables during the period of both non-extreme weather conditions and weather anomalies. The species-specific growth responses of black spruce and aspen to climate could make biomass accumulation temporally more even in mixed forests, especially during climatically extreme conditions. Extreme weather events, which appeared to have a significant and species-specific effect on tree growth (Graumlich 1993; Leonelli & Pelfini 2008; Drobyshev *et al.* 2010), are predicted to occur more often in the future (Bonsal *et al.* 2001; IPCC 2007; Mailhot *et al.* 2010). Pure stands may be more susceptible to climate change with increased frequency of weather anomalies, as compared to mixed stands with more even patterns of biomass accumulation. In addition to maintaining biodiversity, enhancing stand resistance to wind damage, disease, and insect outbreaks (Frivold & Mielikainen 1990; Kelty 1992), mixed stands may therefore represent a way to reduce economical risks through more even productivity and ultimately, by enhancing resilience of the boreal forest.

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2.9 Figures

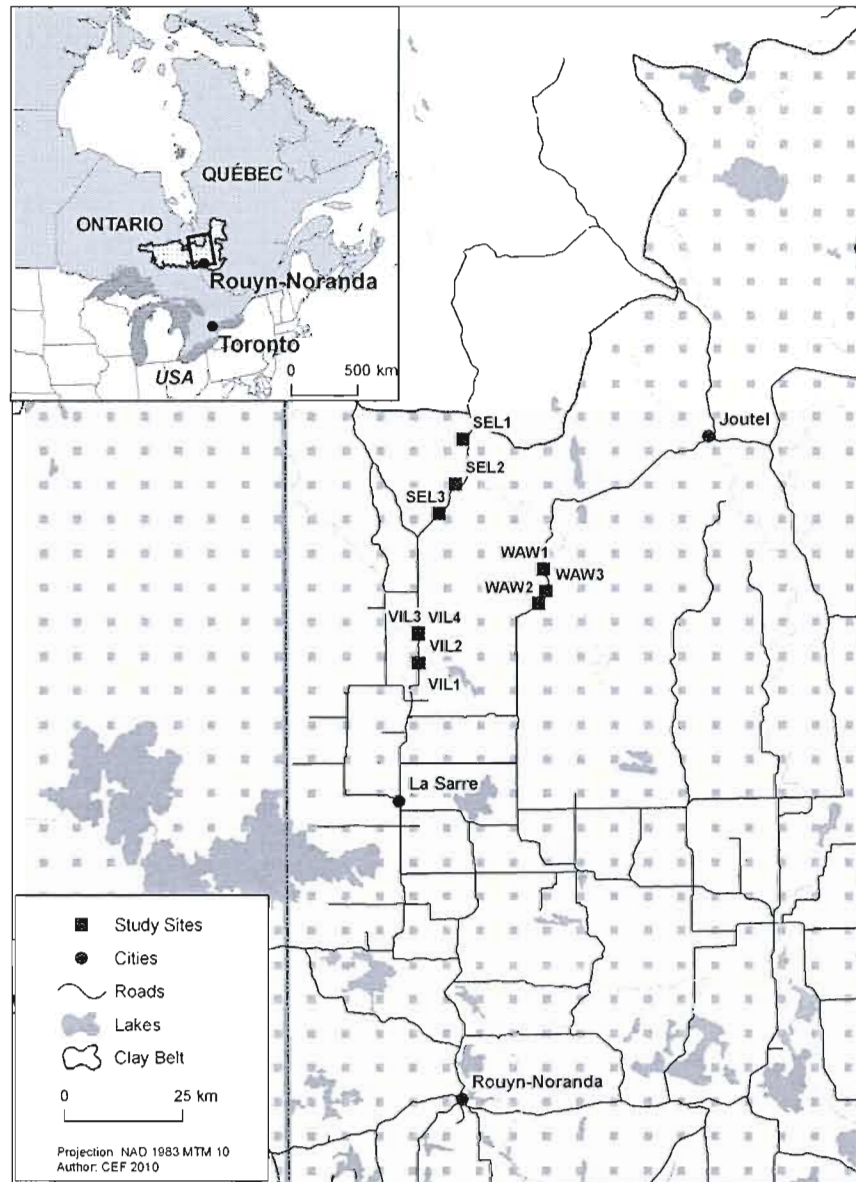


Fig. 2.2 Location map of the study area in western Quebec. The Clay Belt is indicated by the area dotted with grey squares and solid black squares indicate the study sites with their names. VIL1 and VIL2 are indicated by one square only as their locations were very close and so were VIL3 and VIL4 as well.

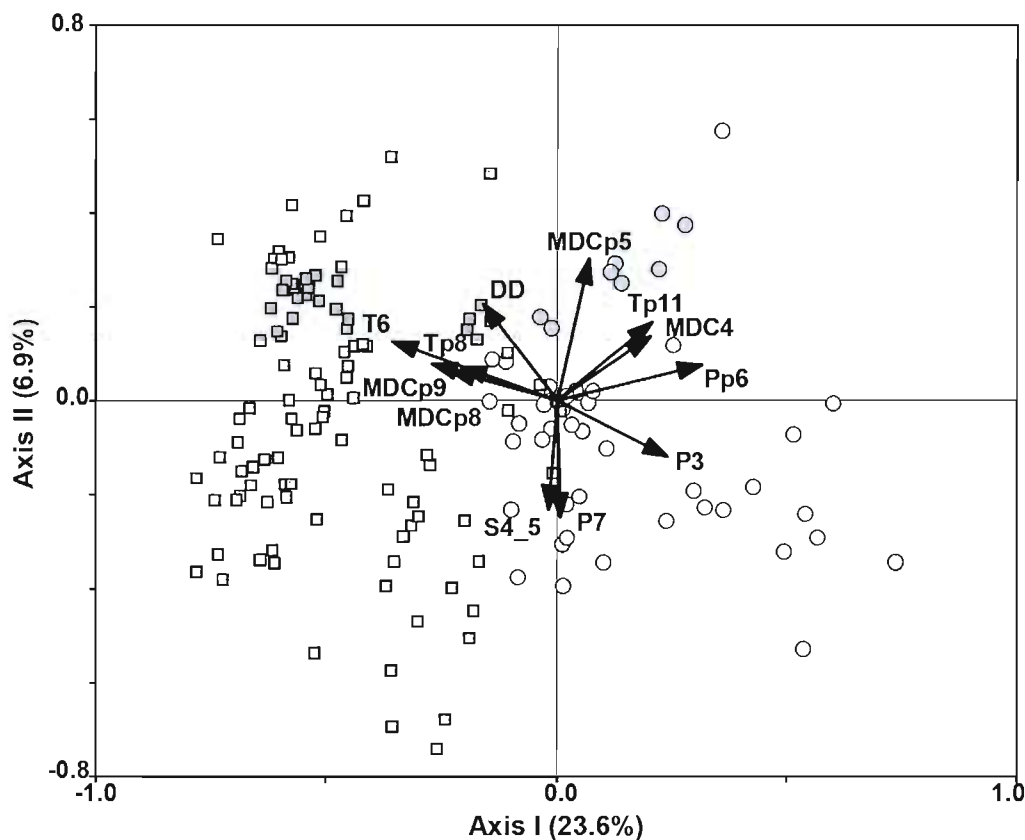


Fig. 2.2 Ordination diagram displaying the first two axes of a redundancy analysis for the data on the tree growth responses to climate variables. Score positions of black spruce (green circles, $n = 114$) and aspen (blue squares, $n = 126$) residual chronologies from 1958 to 2007 are presented. Number of trees had the same scores on the two axes, especially for black spruce, thus one circle or square may represent more than one tree. Explanatory variables are represented by black arrows. Climate variable abbreviations are for monthly mean temperature (T), monthly total precipitation (P), monthly drought code (MDC), total number of degree days (DD), and amount of snowfall (S). Climate variables in the previous year are indicated with a “p”. For example, mean temperature for previous August was indicated by Tp8. The climate variables are positioned in the diagram based on their correlation with the canonical axes, and only climate variables with a $|r| \geq 0.20$ were displayed.

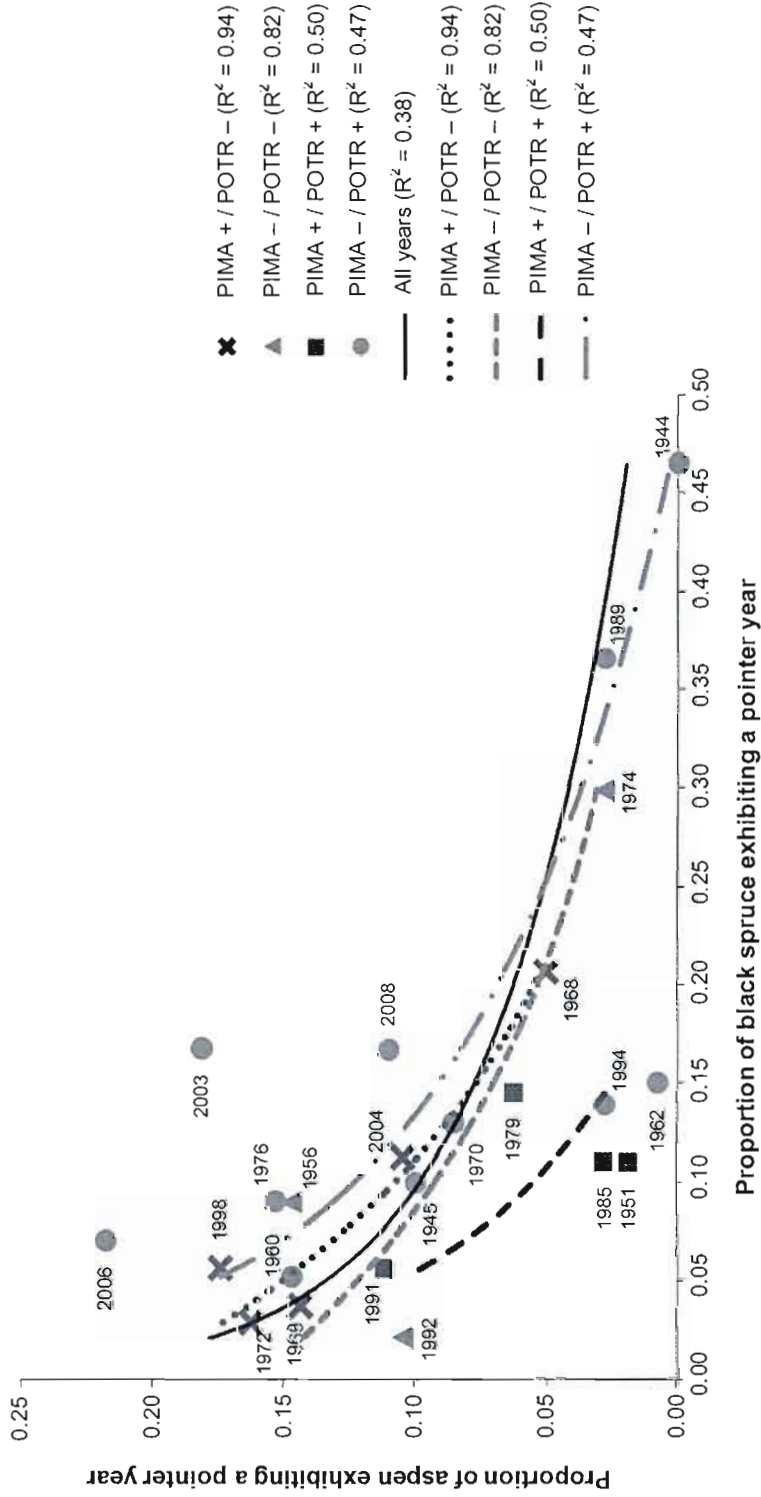


Fig. 2.3 Proportion of aspen exhibiting a pointer year against proportion of black spruce exhibiting a pointer year. Four types of pointer years are identified: negative growth anomalies in both species (PIMA - / POTR -); negative growth anomalies in black spruce and positive in aspen (PIMA - / POTR +); positive growth anomalies in black spruce and negative in aspen (PIMA + / POTR -) and positive growth anomalies in both species (PIMA + / POTR +). R^2 is given for each fit curve and pointer years are labelled.

2.10 Tables

Table 2.1 Characteristics of the 10 sampling sites distributed within three sub-areas: Selbaie (SEL), Villebois (VIL) and Wawagasic (WAW). Type of mineral soil, mean SOL thickness and standard deviation, and number of plots are given for each site. One aspen and one black spruce were sampled in each plot.

Site	Coordinates	Mineral soil	SOL thickness (cm)	Number of plots
SEL1	N49°28.019'; W79°00.867'	Clay	15.55	10
SEL2	N49°22.969'; W79°02.193'	Clay	4.49	16
SEL3	N49°19.732'; W79°05.062'	Clay loam	2.45	10
VIL1	N49°03.100'; W79°08.800'	Clay	9.05	19
VIL2	N49°03.100'; W79°08.660'	Clay	5.07	19
VIL3	N49°06.383'; W79°08.816'	Clay loam	2.84	18
VIL4	N49°06.275'; W79°08.816'	Sandy loam	2.57	10
WAW1	N49°13.434'; W78°46.883'	Clay	12.25	17
WAW2	N49°09.588'; W78°47.801'	Clay	4.29	15
WAW3	N49°10.984'; W78°46.523'	Clay	2.41	11

Table 2.2 Identified pointer years observed in at least 10% of sampled trees of one of the two species. Proportion of trees recording the pointer year in each of the species is given. Type of growth anomaly is shown with a “-“ for negative growth anomalies and “+” for positive growth anomalies. “+ / -“ and “- / +” indicate that both types were observed, the first sign indicating the dominant type of growth anomaly. Climate variables abbreviations are for monthly mean temperature (T), total monthly precipitation (P), monthly drought code (MDC) and total degree-days (DD). Climate variables in the previous year are indicated with a “p”. Climate variables which were associated to aspen and black spruce growth in the previous redundancy analysis the same way they seem to be associated to growth here are bold.

Year	Type of growth anomaly spruce	% of spruces recording	Type of growth anomaly aspen	% of aspen recording	Climatic anomalies
1944	-	46.46%		0.00%	- T Jan > 98% (-12.0°C)
1945	- / +	9.90%	+ / -	10.00%	- T Mar > 99% (-2.5°C) - P May > 99% (140.1 mm)
1951	+	11.01%	+	1.87%	- T Apr > 95% (3.2°C) - P May < 2% (20.8 mm) - MDC May > 95% (107.1)
1956	-	8.93%	-	14.75%	- T pJun, pJul > 98% (17.2°C and 19.0°C) - T Mar, May, Jul, Aug < 5% (-15.1°C, 2.5°C, 13.8°C and 12.9°C) - P pOct > 99% (153.7 mm) - DD < 1% (965.4°C) - MDC May < 5% (43.6)
1960	- / +	5.13%	+ / -	14.73%	- T pNov, Mar, Jul < 5% (-9.3°C, -16.3°C and 14.5°C) - P pJul < 2% (42.2 mm) - P Jun > 95% (158.6 mm) - MDC Jul < 5% (121.9)
1962	-	15.00%	+	0.77%	- T Feb < 1% (-22.5°C) - P pAug, May > 95% (148.2 mm and 124.6 mm)
1968	+	20.59%	- / +	5.04%	- T pMay < 5% (4.4°C) - P Jan, May < 1% (25.4 mm and 13.6 mm) - P Jul > 99% (177.9 mm) - MDC pMay < 5% (44.8) - MDC May > 98% (107.4)
1969	+ / -	3.65%	-	14.39%	- T pSep, Jan > 95% (13.7°C and -12.9°C) - P pMay, Feb < 5% (13.6 mm and 16.0 mm) - P pJul, Aug > 98% (177.9 mm and 153.5 mm) - MDC Jun, Aug < 5% (86.6 and 152.2) - MDC pMay > 98% (107.4)
1970	- / +	12.95%	+ / -	8.57%	- P pAug, pNov > 98% (153.5 mm and 127.4 mm) - MDC pJun, pAug < 5% (86.6 and 152.2)
1972	+ / -	2.82%	-	16.31%	- T pOct > 95% (7.9°C) - P Apr < 1% (6.5 mm) - MDC Apr > 98% (36.5)

1974	-	29.86%	-	2.82%	- T pAug > 99% (18.0°C) - P Mar < 2% (15.7 mm)
1976	-	8.97%	+	15.38%	- T pMay, Jun > 95% (12.0°C and 16.5°C)
1979	+	14.48%	+	6.29%	- P Mar, Jun > 98% (87.1 mm and 173.0 mm) - MDC pJul < 5% (122.0)
1985	+	11.03%	+ / -	2.80%	- T Jul < 5% (14.4°C) - P Jul > 95% (158.7 mm)
1989	-	36.55%	+ / -	2.80%	- P Feb < 1% (8.7 mm) - P pAug > 99% (213.8 mm) - MDC pSep < 1% (84.6)
1991	+	5.56%	+	11.19%	- P pSep > 99% (165.0 mm) - MDC pJul < 1% (113.9)
1992	- / +	2.08%	-	10.49%	- T Jun, Jul < 5% (11.0°C and 13.6°C) - DD < 2% (1051.2)
1994	-	13.89%	+	2.80%	- T pSep, Jan < 5% (7.7°C and -27.3°C) - P Jan < 5% (27.0 mm) - P pMay, pJul > 95% (137.6 mm and 159.7 mm) - T Feb > 99% (-9.0°C)
1998	+ / -	5.59%	-	17.48%	- P Mar > 95% (86.8 mm) - MDC Apr, May > 99% (37.3 and 112.5)
2003	-	16.78%	+	18.18%	- T pSep > 95% (12.9°C) - P pAug < 1% (36.8 mm)
2004	+	11.19%	- / +	10.49%	- MDC Jul, Aug < 2% (121.8 and 140.9)
2006	- / +	6.99%	+	21.83%	- T pJun, Jan > 98% (17.6°C and -11.9°C) - P pNov > 95% (116.7 mm) - DD previous year > 99% (1624.7) - MDC Jun > 95% (196.3)
2008	- / +	16.67%	+ / -	11.02%	- P Jul > 98% (173.5 mm) - MDC Jul < 1% (121.4)

CONCLUSION GÉNÉRALE

L'objectif principal de cette étude était d'évaluer les effets des conditions édaphiques et du climat sur la croissance de l'épinette noire et du peuplier faux-tremble dans l'ouest du Québec. Dans le contexte des changements climatiques, susceptibles d'affecter la composition et la productivité future des forêts, il apparaît nécessaire d'acquérir une meilleure compréhension des facteurs influençant la croissance et la distribution des arbres. Les conditions climatiques sont le principal facteur affectant la distribution des espèces arborescentes à l'échelle continentale et subcontinentale, mais à l'échelle du paysage et du peuplement des facteurs locaux, tels que les conditions de site, jouent un rôle important dans la distribution des arbres (Pearson & Dawson 2003; Hansen *et al.* 2001). Toutefois, très peu d'études considèrent les facteurs édaphiques dans la réponse de croissance au climat et celles-ci restent très spécifiques à la région et aux types de variables de sol étudiés. Aussi, peu d'études ont porté sur l'importance que peuvent avoir des événements climatiques extrêmes sur les essences de la forêt boréale, bien qu'il soit reconnu que la fréquence de ces événements pourrait augmenter avec les changements climatiques (IPCC2007; Mailhot *et al.* 2010; Bonsal *et al.* 2001).

Sur la ceinture d'argile de l'ouest du Québec, où les conditions de sites peuvent être extrêmement variables, les seules études ayant évalué les effets de ces conditions sur la croissance d'essences forestières portent sur l'épinette noire (Drobyshev *et al.* 2010; Simard *et al.* 2007, 2009). Dans ce projet de maîtrise, pour la première fois les effets des conditions de site sur la croissance du peuplier faux-tremble ont été déterminés. Dans cette région, les conditions édaphiques sont directement liées à l'épaisseur de la couche organique, qui a été utilisée dans cette étude pour en exprimer la variabilité. Tout d'abord, les résultats ont démontré que dans l'ensemble de la région, la distribution du peuplier faux-tremble à l'échelle du paysage était limitée aux sites n'ayant pas plus d'environ 20-30 cm de matière organique au sol, alors que l'épinette noire n'était pas limitée dans sa distribution à l'échelle du paysage par l'épaisseur de la couche organique. Par ailleurs, l'accroissement moyen annuel du peuplier faux-tremble diminuait fortement avec une couche organique plus épaisse, ce qui n'était pas le cas pour l'épinette noire sur le gradient d'épaisseur considéré ici (de 1 à environ 25 cm), qui correspond au gradient de distribution du peuplier faux-tremble dans le

paysage. Ces résultats indiquent que l'épaisseur de la couche organique et les conditions édaphiques qu'elle induit limiteraient le peuplier faux-tremble dans cette région. D'autres études par contre, ont démontrées que le peuplier faux-tremble aurait un effet limitant sur l'accumulation de la matière organique (Légaré *et al.* 2005a; Laganière *et al.* 2010). On peut donc conclure, que dans une certaine mesure, le peuplier faux-tremble limite l'épaisseur de la couche organique en ralentissant son accumulation, mais qu'ultimement c'est l'épaisseur de la couche organique qui limite la croissance et la distribution du peuplier faux-tremble dans le paysage. Drobyshev *et al.* (2010) ont montré que les conditions de site trouvées sur la ceinture d'argile pouvaient influencer la réponse de l'épinette noire au climat, les relations croissance-climat variant en fonction de l'épaisseur de la couche organique. La présente étude n'a pas couvert un gradient aussi important que celle de Drobyshev *et al.* (2010), mais s'est concentrée sur le gradient de distribution du peuplier faux-tremble dans le paysage qui correspond également aux conditions de site trouvées dans une grande partie des peuplements de la région. Peu d'effets de l'épaisseur de la couche organique sur les relations croissance-climat de l'épinette noire ont été observées. Pour ce qui est du peuplier faux-tremble, sa réponse au climat était clairement influencée par les conditions de site, démontrant une fois de plus leur importance pour la croissance du peuplier faux-tremble. Ces résultats indiquent que sur la ceinture d'argile, l'épinette noire aura une réponse relativement uniforme aux changements climatiques, alors que la réponse du peuplier faux-tremble variera localement selon l'épaisseur de la couche organique. De plus, la modification des conditions de site causées par l'altération des conditions climatiques et du cycle de feu jouera un rôle primordial pour la distribution future du peuplier faux-tremble dans le paysage forestier de l'ouest du Québec.

L'épinette noire et le peuplier faux-tremble ont présenté des réponses très différentes au climat : leur croissance n'était pas influencée par les mêmes variables climatiques ou présentaient des réponses opposées aux même variables climatiques. Le même phénomène a généralement été observé lors d'extrêmes climatiques, ne générant des anomalies de croissance que dans l'une des deux espèces à la fois ou causant des réponses de croissance opposées dans les deux espèces. D'autres études ont permis de mettre en évidence les différences dans les relations croissance-climat du peuplier faux-tremble et de l'épinette noire (Huang *et al.* 2010; Hofgaard *et al.* 1999; Tardif *et al.* 2001), mais n'ont pas considéré les

événements climatiques extrêmes. Les peuplements mixtes d'épinette noire et de peuplier faux-tremble font partie intégrante du paysage forestier de l'ouest du Québec. La séparation spatiale et temporelle des niches écologiques de ces deux espèces, ainsi que le phénomène de facilitation du peuplier faux-tremble sur l'épinette noire peuvent avantager les peuplements mixtes comparés aux peuplements purs (Brassard *et al.* 2011; Burns & Honkala 1990a, 1990b; Cavard *et al.* non publié; Man & Lieffers 1997, 1999; Green 2004; Légaré *et al.* 2004, 2005a, 2005b; Laganière *et al.* 2010). Les réponses spécifiques à chacune des deux espèces au climat annuel et aux anomalies climatiques peuvent aussi induire une séparation temporelle des niches et ainsi ajouter à la complémentarité des niches écologiques du peuplier faux-tremble et de l'épinette noire. Ainsi une accumulation de biomasse plus constante et une plus grande résilience aux extrêmes climatiques pourraient être assurées dans les peuplements mixtes comparés aux peuplements purs.

L'épinette noire et le peuplier faux-tremble auront des réponses individuelles aux changements climatiques et que les deux espèces en bénéficient ou non dépendra de la balance entre la hausse des températures et l'augmentation des précipitations. Bien qu'il reste plutôt incertain quelle sera l'envergure exacte des changements climatiques à venir, il est évident qu'ils auront des impacts spécifiques sur chaque espèce, qui varieront aussi selon les conditions édaphiques, ultimement menant à des taux de croissance différents entre les espèces et les sites. En augmentant la résilience de la forêt boréale, conserver des peuplements mixtes de peuplier faux-tremble et d'épinette noire pourrait permettre de réduire les risques d'observer des effets néfastes des changements climatiques sur la productivité des forêts.

Bien que les résultats de cette étude restent très spécifiques à la forêt boréale de l'ouest du Québec, ils permettent de faire état de toute l'importance de mieux comprendre le rôle que jouent les conditions de site dans la distribution à l'échelle du paysage, la croissance et les relations croissance-climat des essences forestières, ainsi que de connaître l'importance des impacts spécifiques que peut avoir le climat sur les espèces individuelles. Afin de pouvoir mieux prédire les possibles effets des changements climatiques sur les forêts en allant au-delà de la seule considération des conditions climatiques, des études plus holistiques, mais également adaptées aux spécificités régionales seraient nécessaires.

ANNEXE A

Végétation de sous-bois des 145 placettes d'échantillonnage. Quatre quadrats de 1 m² ont été établis par placette. La proportion de recouvrement de différents types de végétation et d'espèces est donnée par des chiffres de 0 à 7 : 0 = absence; 1 = trace; 2 = 1 à 5%; 3 = 5 à 25%; 4 = 25 à 50%; 5 = 50 à 75%; 6 = 75 à 100%; 7 = 100%. Le type de regeneration est spécifié par le nombre de tiges et l'espèce : ABA = *Abies balsamea*; BPA = *Betula papyrifera*; PMA = *Picea mariana*; PTR = *Populus tremuloides*; SAL = *Salix spp.* Seules les plantes de moins de 1 m de hauteur ont été répertoriées.

Site	Placette	Quadrat	Fougères	Herbacées	Lichens	Litière	Mousses	Régénération	Type de régénération	<i>Alnus rugosa</i>	<i>Chionochloa hispidula</i>	<i>Dicentra uniflora</i>	<i>Equisetum spp</i>	<i>Goodyera repens</i>	<i>Kalmia angustifolia</i>	<i>Linnaea borealis</i>	<i>Lycopodium spp</i>	<i>Pleurozium schreberi</i>	<i>Rhododendron groenlandicum</i>	<i>Ribes glandulosum</i>	<i>Sphagnum spp</i>	<i>Vaccinium spp</i>	<i>Viburnum edule</i>
VIL1	1	1	0	2	0	0	2	1	1xPMA	0	0	0	0	0	0	0	0	6	0	0	0	0	0
VIL1	1	2	0	2	0	3	1	1	1xPTR	0	0	0	0	0	0	0	0	5	0	0	0	0	0
VIL1	1	3	0	1	1	1	1	0		0	0	0	0	0	0	0	0	3	0	0	0	0	0
VIL1	1	4	0	0	1	3	3	0		0	0	0	0	0	0	0	0	6	0	0	0	0	0
VIL1	2	1	0	1	1	5	2	0		0	0	0	0	0	0	0	0	3	0	0	0	0	0
VIL1	2	2	0	1	1	2	2	0		0	0	0	0	0	0	0	0	6	0	0	0	0	2
VIL1	2	3	0	0	0	1	1	0		0	0	0	0	0	0	0	0	6	0	0	0	0	0
VIL1	2	4	0	0	1	3	1	0		0	0	0	0	0	0	0	0	6	0	0	0	1	0
VIL1	3	1	0	0	2	0	1	0		0	0	0	0	0	0	1	0	6	0	0	0	1	0
VIL1	3	2	0	1	1	3	1	0		0	0	0	0	0	0	1	0	6	0	0	0	0	0
VIL1	3	3	0	0	2	2	3	0		0	0	0	0	0	0	0	0	5	0	0	0	1	0
VIL1	3	4	0	0	1	2	1	0		0	0	0	0	0	0	0	0	6	0	0	0	1	0
VIL1	4	1	0	3	1	1	1	0		0	2	0	0	0	3	0	0	4	0	0	4	2	0
VIL1	4	2	0	1	3	3	2	0		0	2	0	0	0	0	0	0	3	0	0	0	1	0

VIL1	4	3	0	2	0	0	2	0	0	0	1	0	0	0	0	0	0	0	2	0	0	6	0	0
VIL1	4	4	0	4	0	1	1	0	0	0	0	1	0	0	0	2	0	0	6	0	0	0	2	0
VIL1	5	1	0	1	1	4	2	0	0	1	0	0	0	0	0	0	0	5	0	0	0	0	0	
VIL1	5	2	0	1	1	4	3	0	0	2	0	0	0	1	1	0	4	0	0	0	2	0	0	
VIL1	5	3	0	0	1	2	1	0	0	0	0	0	0	0	0	0	6	0	0	0	1	0	0	
VIL1	5	4	0	0	2	3	2	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	
VIL2	6	1	0	2	1	4	0	1	5xPTR	0	0	0	0	0	0	2	4	0	0	0	0	0	0	
VIL2	6	2	0	1	1	6	1	0	0	0	0	0	0	0	1	0	3	0	0	0	0	0	0	
VIL2	6	3	0	2	1	6	3	1	1xPTR	0	1	0	1	0	0	0	3	0	0	0	0	0	0	
VIL2	6	4	0	1	2	4	3	1	1xPTR	0	0	0	0	0	0	4	0	0	0	0	0	0	0	
VIL2	7	1	0	2	1	5	1	1	2xPTR	0	0	0	1	0	0	4	0	0	0	1	0	0	0	
VIL2	7	2	0	3	0	2	3	0	0	3	0	0	0	2	2	0	5	0	0	0	3	0	0	
VIL2	7	3	0	1	0	2	1	0	0	2	0	0	0	1	2	0	6	0	0	0	1	0	0	
VIL2	7	4	0	1	0	2	6	0	0	0	0	0	0	0	0	2	0	0	0	2	0	0	0	
VIL2	8	1	0	3	0	3	2	1	1xPTR	0	2	0	0	0	1	0	5	0	0	0	2	0	0	
VIL2	8	2	0	3	2	4	3	0	0	2	0	0	0	2	0	3	0	0	2	0	0	2	0	
VIL2	8	3	0	4	1	5	2	1	2xPTR	0	0	0	0	0	2	0	3	0	0	2	0	0	0	
VIL2	8	4	0	1	1	6	1	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0	0	
VIL2	9	1	0	2	0	3	0	0	0	0	0	0	0	0	2	0	6	0	0	0	0	0	0	
VIL2	9	2	0	1	2	6	2	0	0	0	0	0	0	0	3	0	2	0	0	0	0	0	0	
VIL2	9	3	0	1	0	6	2	0	0	0	0	0	0	0	2	0	3	0	0	0	0	0	0	
VIL2	9	4	0	1	1	6	2	1	1xPTR	0	0	0	0	0	2	0	3	0	0	0	0	0	0	
VIL2	10	1	0	0	1	4	2	0	0	0	0	0	0	0	1	5	0	0	0	0	0	0	0	
VIL2	10	2	0	3	1	4	3	0	0	0	0	0	0	2	3	3	0	0	0	0	0	0	0	
VIL2	10	3	0	4	0	2	4	0	0	0	0	0	0	1	3	3	0	0	0	0	0	0	0	
VIL2	10	4	0	2	0	4	4	0	0	1	0	0	0	1	0	3	0	0	0	0	0	0	0	
VIL3	11	1	0	5	0	4	1	0	0	0	0	0	0	0	3	0	0	0	0	2	0	0	0	

VIL4	17	4	0	3	0	2	1	0	0	0	0	0	0	0	0	1	5	2	0	0	0	2	0
VIL4	18	1	0	3	0	4	1	0	0	0	3	0	0	0	2	3	0	0	0	0	0	2	0
VIL4	18	2	0	3	0	4	1	0	0	0	4	0	0	0	1	3	2	0	0	0	0	1	0
VIL4	18	3	0	2	1	3	4	0	0	2	2	0	0	0	3	3	2	0	0	0	0	3	0
VIL4	18	4	0	3	0	4	1	0	0	0	0	0	0	0	3	5	0	0	0	0	0	2	0
VIL4	19	1	0	4	0	2	1	2	1xBPA	0	1	0	0	0	0	3	4	0	0	0	0	3	0
VIL4	19	2	0	3	0	2	1	1	1xPTR	0	0	0	0	0	2	2	6	0	0	0	0	3	0
VIL4	19	3	0	4	0	2	1	0	0	3	0	0	0	0	3	4	3	0	0	0	0	3	0
VIL4	19	4	0	3	0	3	1	0	0	1	4	0	0	0	1	5	0	0	0	0	0	2	0
VIL4	20	1	0	3	0	2	3	0	1	0	0	0	0	0	4	3	0	0	0	0	0	2	0
VIL4	20	2	0	3	0	4	1	0	0	0	0	0	0	0	2	3	0	0	0	0	0	3	0
VIL4	20	3	0	3	0	4	2	0	0	0	0	0	0	0	0	4	0	3	0	0	0	2	0
VIL4	20	4	0	4	0	3	2	0	0	0	0	0	0	0	1	4	0	0	0	0	0	3	0
VIL4	21	1	0	3	0	4	2	1	1xBABA	0	2	0	0	0	0	3	0	3	0	0	0	3	0
VIL4	21	2	0	3	0	2	4	0	0	0	0	0	0	0	3	2	3	0	0	0	0	4	0
VIL4	21	3	0	4	0	3	1	1	1xPTR	0	0	0	0	0	3	3	1	0	0	0	0	3	0
VIL4	21	4	0	3	1	4	0	0	0	0	0	0	0	0	1	4	1	0	0	0	0	2	0
VIL3	22	1	0	3	0	5	1	1	1xSAL	0	0	0	0	0	1	0	0	0	0	0	0	4	0
VIL3	22	2	0	4	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
VIL3	22	3	0	6	0	3	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	2	0
VIL3	22	4	0	4	0	4	2	0	0	0	0	0	0	0	2	0	0	0	0	0	0	4	0
VIL2	23	1	0	4	1	2	0	2	1xBABA	0	0	0	0	0	3	4	4	0	0	0	0	2	0
VIL2	23	2	0	4	1	4	1	0	0	0	0	0	0	0	3	2	4	0	0	0	0	0	0
VIL2	23	3	0	3	1	5	2	0	0	0	0	0	0	2	3	1	0	0	0	0	0	0	0
VIL2	23	4	0	3	1	2	3	0	0	0	0	0	0	3	0	5	2	0	0	0	0	3	0
VIL1	24	1	0	0	0	1	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
VIL1	24	2	0	2	1	5	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0

VIL3	31	2	0	3	2	3	3	0	0	0	0	0	0	0	1	4	2	0	0	0	0
VIL3	31	3	0	4	1	4	2	0	0	0	0	0	0	0	2	3	3	0	0	0	0
VIL3	31	4	0	4	0	4	2	0	0	0	0	0	0	0	1	0	3	0	0	0	2
VIL3	32	1	0	3	1	4	0	0	0	0	0	0	0	0	1	3	3	0	0	0	0
VIL3	32	2	0	3	1	4	0	0	0	0	0	0	0	0	2	3	4	0	0	0	0
VIL3	32	3	0	4	0	5	0	0	0	0	0	0	0	0	3	2	0	0	0	0	0
VIL3	32	4	0	3	1	2	0	0	0	0	0	0	0	0	1	6	0	0	0	0	0
VIL3	33	1	0	4	1	4	1	0	0	0	0	0	0	0	0	4	0	0	0	0	3
VIL3	33	2	0	2	2	3	1	0	0	0	0	0	0	0	1	4	0	4	0	0	2
VIL3	33	3	0	4	1	3	1	0	0	0	0	0	0	0	1	4	0	3	0	0	2
VIL3	33	4	0	3	0	3	1	0	0	0	0	0	0	0	4	0	0	0	0	0	2
VIL3	34	1	0	4	0	4	2	0	0	0	0	2	0	0	0	3	2	0	0	0	2
VIL3	34	2	0	5	0	3	0	0	0	0	0	2	0	0	1	3	0	0	0	0	0
VIL3	34	3	2	3	1	4	1	0	0	0	0	0	0	0	2	3	0	0	0	0	3
VIL3	34	4	0	3	1	2	1	0	0	2	0	0	0	0	1	5	0	2	0	0	3
VIL3	35	1	0	4	1	5	0	0	0	0	0	0	0	0	1	3	1	0	0	0	3
VIL3	35	2	0	3	1	5	1	0	0	0	0	0	0	0	2	3	2	0	0	0	3
VIL3	35	3	0	3	0	3	0	3	1xPMA	0	0	0	0	0	2	4	1	0	0	0	4
VIL3	35	4	0	5	2	0	1	0	0	0	0	0	0	0	2	3	2	0	0	0	3
VIL3	36	1	0	3	1	3	0	0	0	0	0	0	0	0	2	0	5	0	0	0	3
VIL3	36	2	0	0	2	3	0	3	4xPMA	0	0	0	0	0	1	3	2	0	0	0	3
VIL3	36	3	2	5	0	4	0	0	0	3	0	0	0	0	2	3	1	0	0	0	0
VIL3	36	4	0	5	1	3	1	0	0	0	0	2	0	0	2	3	2	0	0	0	3
VIL4	37	1	0	3	0	2	0	0	0	0	0	0	0	0	0	4	0	4	0	0	2
VIL4	37	2	0	3	1	3	0	0	0	0	0	0	0	0	4	0	4	0	0	0	3
VIL4	37	3	0	2	1	3	0	0	0	0	0	2	0	0	0	5	0	0	0	0	3
VIL4	37	4	2	3	2	3	1	0	0	0	0	0	0	0	4	0	0	0	0	0	4

VIL4	38	1	2	3	0	4	1	0	0	0	0	0	0	0	0	0	0	2	3	3	2	0	0	3	0
VIL4	38	2	0	3	0	3	0	0	0	0	0	1	0	0	0	2	4	2	4	2	0	0	0	3	0
VIL4	38	3	0	3	2	5	1	0	0	0	0	1	0	0	2	3	0	0	0	0	0	0	0	2	0
VIL4	38	4	3	3	0	3	0	0	0	0	0	0	0	0	0	3	0	0	3	0	0	0	0	4	0
VIL4	39	1	0	4	1	4	0	0	0	0	0	0	0	0	0	4	1	0	0	0	0	0	3	0	
VIL4	39	2	0	3	0	5	1	0	0	0	0	0	0	0	0	4	0	0	4	0	0	0	2	0	
VIL4	39	3	0	5	0	3	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	1	0	
VIL4	39	4	0	3	1	3	1	0	0	2	0	0	0	0	1	5	0	0	0	0	0	0	3	0	
VIL4	40	1	0	4	1	3	2	0	0	0	0	0	0	0	2	3	4	0	0	0	0	0	4	0	
VIL4	40	2	0	3	1	3	1	0	0	2	0	0	0	0	0	4	0	0	0	0	0	1	3	0	
VIL4	40	3	0	3	1	2	0	3	1xPMA	0	0	0	0	0	3	4	3	0	0	0	0	3	0	0	
VIL4	40	4	0	3	1	2	0	0	0	0	0	0	0	0	2	5	0	0	0	0	0	0	4	0	
VIL1	41	1	0	2	1	2	0	0	0	1	0	0	0	0	0	6	0	0	0	0	0	2	0	0	
VIL1	41	2	0	0	2	3	2	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	
VIL1	41	3	0	1	3	4	3	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	
VIL1	41	4	0	0	1	3	3	0	0	0	0	0	0	0	0	5	0	0	0	0	0	1	0	0	
VIL1	42	1	0	1	1	3	1	3	2xPMA	0	3	0	0	0	3	0	0	3	0	3	0	3	3	0	
VIL1	42	2	0	1	1	3	1	0	0	0	0	0	0	1	0	0	5	0	0	3	1	0	0	0	
VIL1	42	3	0	0	2	2	2	0	0	0	0	0	0	0	0	6	0	0	0	0	0	2	0	0	
VIL1	42	4	0	1	2	2	0	2	1xPMA	0	0	0	0	0	3	0	0	6	0	0	0	0	0	0	
VIL1	43	1	0	0	1	3	2	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	
VIL1	43	2	0	1	2	6	3	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	
VIL1	43	3	0	0	1	4	2	0	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	
VIL1	43	4	0	3	2	4	0	0	0	0	0	0	0	2	1	0	4	0	0	0	1	2	0	0	
VIL1	44	1	0	2	2	4	2	0	0	0	0	0	0	0	0	4	0	0	4	0	0	2	1	0	
VIL1	44	2	0	2	1	4	1	0	0	0	0	0	0	2	0	0	4	0	0	0	0	0	0	0	
VIL1	44	3	0	2	2	3	1	4	13xPMA	0	0	0	0	1	0	0	5	1	0	0	1	0	0	1	

VIL1	44	4	0	2	1	1	1	1	3	7xPMA	0	0	0	0	0	2	0	0	6	2	0	0	2	0
VIL1	45	1	0	0	2	2	3	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0
VIL1	45	2	0	0	1	2	0	0	0	2	0	0	0	1	0	0	6	0	0	0	0	1	0	0
VIL1	45	3	0	0	2	2	3	0	0	3	0	0	0	0	0	5	0	0	5	0	0	2	0	0
VIL1	45	4	0	0	2	3	3	0	0	0	0	0	0	0	0	5	0	0	5	0	0	0	0	0
VIL1	46	1	0	3	2	2	1	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
VIL1	46	2	0	0	2	4	3	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0
VIL1	46	3	0	0	1	2	1	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0
VIL1	46	4	0	1	1	2	2	0	0	1	0	0	0	0	0	6	0	0	0	0	0	1	0	0
VIL1	47	1	0	0	1	1	1	0	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0
VIL1	47	2	0	0	3	5	3	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
VIL1	47	3	0	0	2	3	1	0	0	0	0	0	1	0	5	0	0	1	2	0	0	0	0	0
VIL1	47	4	0	0	2	3	2	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
VIL1	48	1	0	0	2	3	1	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
VIL1	48	2	0	0	2	3	2	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
VIL1	48	3	0	2	2	0	3	3	3xPMA	0	1	0	0	0	1	0	6	0	0	0	2	0	0	0
VIL1	48	4	0	3	3	0	1	0	0	0	0	1	0	3	0	5	2	0	0	3	0	0	0	0
VIL1	49	1	0	0	1	2	3	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
VIL1	49	2	0	1	3	0	1	0	0	0	0	0	0	2	0	5	0	0	0	2	0	0	0	0
VIL1	49	3	0	1	1	3	5	0	0	0	0	0	1	0	4	0	0	0	0	0	0	0	0	0
VIL1	49	4	0	0	2	3	2	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
VIL1	50	1	0	3	2	0	4	0	0	2	0	0	0	0	5	0	0	1	0	0	0	0	0	0
VIL1	50	2	0	3	1	2	4	0	0	0	0	0	0	0	4	0	0	0	2	0	0	0	0	0
VIL1	50	3	0	3	2	2	3	0	0	0	0	0	0	1	5	0	0	0	2	0	0	0	0	0
VIL1	50	4	0	2	1	2	0	0	0	0	0	0	1	0	6	0	0	0	2	0	0	0	0	0
VIL1	51	1	0	3	2	1	2	0	0	3	0	0	0	0	6	0	0	0	2	0	0	0	0	0
VIL1	51	2	0	3	2	2	0	0	0	0	0	0	0	0	6	0	0	0	0	1	0	0	0	0

VIL1	51	3	0	2	3	3	2	0	0	3	0	0	0	0	0	0	5	0	0	1	1	0
VIL1	51	4	0	0	3	3	3	0	0	1	0	0	0	0	0	0	4	0	0	0	0	0
VIL2	52	1	0	3	1	2	2	0	0	1	0	0	0	1	3	4	0	0	0	4	0	0
VIL2	52	2	0	3	1	4	3	0	0	0	0	0	0	2	3	3	0	0	0	4	0	0
VIL2	52	3	0	2	3	5	2	0	0	0	0	0	0	0	3	3	0	0	0	2	0	0
VIL2	52	4	0	1	2	2	3	1	3xPMA	0	3	0	0	0	0	6	0	0	0	0	0	0
VIL2	53	1	0	3	0	5	2	2	1xPTR	0	0	0	0	0	1	0	4	0	0	0	0	0
VIL2	53	2	0	4	2	4	3	0	0	0	0	0	0	1	0	4	0	0	0	0	0	0
VIL2	53	3	0	3	2	6	3	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
VIL2	53	4	0	3	1	5	3	0	0	0	0	0	0	2	0	3	0	0	0	2	0	0
VIL2	54	1	0	4	1	3	0	0	0	0	0	0	0	3	4	3	0	0	0	0	0	0
VIL2	54	2	0	5	1	3	0	0	0	0	0	0	0	3	4	0	0	0	0	0	0	0
VIL2	54	3	0	5	1	3	2	0	0	0	0	0	0	4	0	3	0	0	0	3	0	0
VIL2	54	4	0	3	3	5	3	0	0	0	0	0	0	3	0	0	0	0	0	2	0	0
VIL2	55	1	0	4	1	5	0	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0
VIL2	55	2	0	3	3	4	3	0	0	3	0	0	0	3	0	3	0	0	0	3	0	0
VIL2	55	3	0	4	1	3	2	0	0	2	0	0	0	3	0	4	0	0	0	3	0	0
VIL2	55	4	0	4	1	4	3	0	0	3	0	0	0	2	0	3	0	0	0	0	0	0
VIL2	56	1	0	3	3	3	2	2	1xPTR	0	3	0	0	0	3	2	4	0	0	0	3	0
VIL2	56	2	0	5	1	3	0	0	0	2	0	1	0	0	3	0	2	0	0	0	2	0
VIL2	56	3	0	5	2	4	2	0	0	0	0	0	0	2	0	3	0	0	0	0	0	0
VIL2	56	4	0	3	3	5	3	0	0	0	0	0	0	3	0	2	0	0	0	0	0	0
VIL2	57	1	0	4	1	3	3	0	4	0	0	0	0	2	2	3	0	0	0	0	0	0
VIL2	57	2	0	6	2	2	2	2	1xPTR	0	0	0	0	0	2	3	2	0	0	0	0	0
VIL2	57	3	0	5	2	1	3	0	0	0	0	0	0	2	3	4	0	0	0	3	0	0
VIL2	57	4	0	4	3	4	3	0	0	0	0	0	0	2	2	3	0	0	0	0	0	0
VIL2	58	1	0	4	2	4	2	0	0	0	0	0	0	3	0	2	0	0	0	3	0	0

VIL2	64	4	0	6	1	3	0	2	1xPTR	0	0	0	0	0	0	0	0	0	0	0	0	0	0
VIL2	65	1	0	3	2	3	1	0		0	0	0	0	0	0	0	3	4	0	0	0	0	0
VIL2	65	2	0	3	2	3	0	0		0	0	0	3	0	0	0	0	3	2	0	0	0	2
VIL2	65	3	0	3	2	3	0	0		0	0	0	2	0	0	4	3	0	0	0	0	0	0
VIL2	65	4	0	4	2	3	0	0		0	0	0	2	0	0	3	3	0	0	0	0	0	0
VIL2	66	1	3	3	2	2	0	0		0	0	0	0	0	0	3	4	2	0	0	0	0	0
VIL2	66	2	0	1	2	3	2	0		0	0	0	0	0	0	3	5	2	0	0	0	0	0
VIL2	66	3	0	2	3	4	3	0		0	0	0	2	0	0	0	0	3	0	0	3	0	0
VIL2	66	4	0	3	1	3	2	0		0	0	0	0	0	0	2	4	3	0	0	0	0	0
WAW3	67	1	5	3	1	3	0	0		0	0	3	0	0	0	0	3	0	0	0	0	0	0
WAW3	67	2	0	3	0	4	0	0		0	0	4	0	0	0	0	3	2	0	0	0	0	0
WAW3	67	3	3	4	0	3	0	0		0	0	4	0	0	0	0	3	0	0	0	0	0	0
WAW3	67	4	3	4	0	3	1	0		0	0	0	0	0	0	0	3	3	0	0	0	0	0
WAW3	68	1	3	4	0	3	0	0		0	0	0	0	0	0	0	3	2	0	0	0	0	0
WAW3	68	2	0	3	0	4	0	3	4xPTR	0	0	3	0	0	0	0	3	0	0	0	0	0	0
WAW3	68	3	5	3	0	3	1	0		0	0	0	0	0	0	0	2	0	0	0	0	0	0
WAW3	68	4	3	4	0	2	0	0		0	0	3	0	0	3	0	3	0	0	0	0	0	0
WAW3	69	1	3	3	0	3	0	0		0	0	5	0	0	0	0	3	0	0	0	0	0	0
WAW3	69	2	0	3	0	3	1	0		0	0	4	0	0	0	0	3	0	0	0	0	0	0
WAW3	69	3	0	5	0	3	0	0		0	0	3	0	0	0	0	3	0	0	0	0	0	0
WAW3	59	4	0	3	0	3	1	0		0	0	3	0	0	0	0	3	2	0	0	0	0	0
WAW3	70	1	2	4	0	2	2	0		0	0	0	0	0	0	2	3	3	0	0	0	0	0
WAW3	70	2	0	3	1	3	0	0		0	0	3	0	0	0	1	4	2	0	0	0	0	0
WAW3	70	3	4	4	0	2	2	0		3	0	0	0	0	0	3	2	0	0	0	0	0	0
WAW3	70	4	5	4	0	2	0	0		0	0	0	0	0	0	1	2	0	0	0	0	0	0
WAW3	71	1	0	4	0	3	0	0		0	0	0	0	0	0	1	4	2	0	0	0	0	0
WAW3	71	2	5	2	0	2	2	0		3	0	0	0	0	0	0	2	0	0	0	0	0	0

WAW3	71	3	0	5	0	3	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0
WAW3	71	4	3	4	0	3	0	2	2xPTR	0	0	0	0	0	0	4	0	0	0	0	0	0	0
WAW3	72	1	3	5	0	3	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
WAW3	72	2	3	3	0	3	2	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0
WAW3	72	3	0	4	3	3	0	0	0	0	4	2	0	0	0	3	0	0	0	0	0	0	0
WAW3	72	4	3	3	0	3	1	3	2xPTR	0	0	3	0	0	0	3	0	0	0	0	0	3	0
WAW3	73	1	2	5	0	3	1	0	0	0	0	3	0	0	3	2	0	0	0	0	0	3	0
WAW3	73	2	0	4	2	4	0	3	3xABA	0	0	0	0	0	0	3	1	0	0	0	0	0	0
WAW3	73	3	2	4	0	4	3	0	0	0	1	0	0	0	3	2	0	0	0	0	0	0	0
WAW3	73	4	0	4	3	4	0	0	0	0	3	0	0	0	3	1	0	0	0	0	0	0	0
WAW3	74	1	3	4	1	4	1	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
WAW3	74	2	3	4	1	4	2	0	0	0	3	0	0	3	0	0	0	0	0	0	0	0	0
WAW3	74	3	0	3	0	5	3	2	2xABA, 1xPTR	0	0	0	0	0	1	0	0	0	0	0	0	0	0
WAW3	74	4	0	4	1	4	2	1	1xABA	0	0	3	0	0	0	2	0	0	0	0	0	0	0
WAW3	75	1	4	5	0	3	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0
WAW3	75	2	3	3	2	3	3	3	2xABA	0	0	0	0	0	3	3	0	0	0	0	0	0	0
WAW3	75	3	4	3	0	3	3	2	1xABA	0	0	4	0	0	1	0	0	0	0	0	0	0	0
WAW3	75	4	0	6	1	3	2	1	2xABA	0	0	0	0	0	2	3	0	0	0	0	0	0	0
WAW3	76	1	1	4	3	4	2	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0
WAW3	76	2	2	5	0	3	2	0	0	0	0	2	0	0	3	2	0	0	0	0	0	0	0
WAW3	76	3	3	5	0	2	0	0	3	0	0	2	0	0	3	3	0	0	0	0	0	0	0
WAW3	76	4	4	3	0	3	3	0	0	0	3	0	0	0	2	0	0	0	0	0	0	0	0
WAW3	77	1	3	3	1	4	2	3	3xABA	0	0	3	0	0	3	3	0	0	0	1	0	0	0
WAW3	77	2	3	3	1	3	2	0	0	0	4	0	0	0	3	3	0	0	0	0	0	0	0
WAW3	77	3	0	4	2	2	0	0	0	0	4	0	0	0	3	2	0	0	0	2	0	0	0
WAW3	77	4	0	3	1	3	1	4	9xABA	0	0	3	0	0	3	1	0	0	0	0	0	0	0

WAW1	78	1	0	3	1	3	1	0	0	1	0	0	0	0	0	1	0	5	3	0	2	0	0
WAW1	78	2	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	2	0	0	0	6	2
WAW1	78	3	0	3	0	2	3	0	0	0	0	2	0	0	2	0	3	3	0	4	3	0	
WAW1	78	4	0	3	1	3	3	0	0	0	0	0	0	0	0	0	4	0	0	3	0	0	
WAW1	79	1	0	3	0	0	0	0	2	0	2	0	0	2	0	0	3	0	6	0	0	0	
WAW1	79	2	0	2	1	0	3	0	0	0	0	0	0	0	0	0	6	0	0	0	2	0	
WAW1	79	3	0	3	2	0	2	0	0	0	0	0	0	0	0	3	3	0	5	2	0	0	
WAW1	79	4	0	3	1	0	2	0	0	0	0	0	0	0	2	0	0	2	0	6	0	0	
WAW1	80	1	0	3	2	2	4	0	2	0	0	0	2	0	0	3	0	0	3	0	0	0	
WAW1	80	2	0	3	1	2	6	0	0	0	0	0	0	0	0	3	0	0	0	3	0	0	
WAW1	80	3	0	3	1	0	5	0	0	0	0	1	0	0	0	3	0	0	3	0	0	0	
WAW1	80	4	0	3	1	3	3	0	2	0	0	0	0	0	0	5	0	0	0	2	0	0	
WAW1	81	1	0	3	2	2	2	0	0	0	0	0	0	2	0	5	2	0	3	3	0	0	
WAW1	81	2	0	3	2	2	4	0	0	0	0	1	0	1	0	5	0	0	0	0	0	0	
WAW1	81	3	0	3	2	2	4	0	0	0	0	2	0	2	0	4	0	0	3	3	0	0	
WAW1	81	4	0	1	2	0	2	0	0	0	0	2	0	0	0	6	0	0	3	0	0	0	
WAW1	82	1	0	3	2	0	3	0	0	2	0	0	1	0	0	5	0	0	0	2	0	0	
WAW1	82	2	0	3	2	2	3	0	0	2	0	0	0	2	0	5	0	0	3	2	0	0	
WAW1	82	3	0	3	3	0	4	0	0	0	0	0	0	0	0	5	0	0	3	2	0	0	
WAW1	82	4	0	3	2	2	3	0	0	3	0	0	3	0	0	3	0	0	4	3	0	0	
WAW1	83	1	0	0	3	0	3	0	0	3	0	0	0	0	0	4	0	0	4	0	0	0	
WAW1	83	2	0	2	2	0	1	0	0	0	0	0	0	0	0	6	0	0	3	0	0	0	
WAW1	83	3	0	2	2	2	4	0	0	3	0	0	0	0	0	5	0	0	0	2	0	0	
WAW1	83	4	0	3	2	0	2	0	0	2	0	0	1	0	0	5	0	0	3	3	0	0	
WAW1	84	1	0	1	2	0	4	0	0	3	0	0	0	3	0	3	0	4	3	0	4	3	0
WAW1	84	2	0	3	1	0	2	0	0	0	0	0	0	0	0	3	0	0	6	0	0	0	
WAW1	84	3	0	1	2	0	2	0	0	2	0	0	1	0	0	6	0	0	0	2	0	0	

WAW1	84	4	0	3	2	2	2	0	0	2	0	0	0	0	0	0	0	5	0	0	3	0	0
WAW1	85	1	0	2	1	2	3	0	0	0	0	0	0	0	0	0	0	5	0	0	0	3	0
WAW1	85	2	0	3	2	0	4	0	0	0	0	0	0	0	0	0	2	0	0	5	0	0	
WAW1	85	3	0	3	1	2	3	0	0	0	0	0	3	0	0	0	0	0	0	5	2	0	
WAW1	85	4	0	3	3	0	2	0	0	0	0	0	0	0	0	2	3	0	6	0	0	0	
WAW1	86	1	0	0	1	2	2	0	0	3	0	0	1	0	2	0	6	0	0	0	1	0	
WAW1	86	2	0	2	2	2	3	0	0	2	0	0	0	0	0	2	0	0	0	0	0	0	
WAW1	86	3	0	0	1	3	1	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	
WAW1	86	4	0	0	1	2	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0	
WAW1	87	1	0	3	2	2	5	0	0	3	0	0	0	3	0	4	0	0	0	0	0	0	
WAW1	87	2	0	3	2	2	3	0	0	3	0	0	1	0	1	0	4	3	0	3	3	0	
WAW1	87	3	0	3	1	2	3	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	
WAW1	87	4	0	3	1	2	3	0	0	2	0	0	0	0	0	6	0	0	0	0	0	0	
WAW1	88	1	0	0	0	2	5	0	0	2	0	0	0	3	0	4	0	0	0	2	0	0	
WAW1	88	2	0	0	2	2	3	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	
WAW1	88	3	0	0	2	3	3	0	0	2	0	0	0	0	0	5	0	0	0	0	0	0	
WAW1	88	4	0	3	1	2	1	0	0	3	0	0	1	2	0	3	0	3	0	5	2	0	
WAW1	89	1	0	4	1	0	3	0	0	3	0	0	0	0	1	0	5	0	0	2	3	0	
WAW1	89	2	0	4	0	0	2	0	0	1	0	0	0	3	0	3	0	3	0	4	0	0	
WAW1	89	3	0	0	1	2	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	
WAW1	89	4	0	3	1	0	0	0	0	0	0	0	3	0	0	5	0	0	0	3	0	0	
WAW1	90	1	0	3	1	0	3	0	0	2	0	0	0	3	0	3	0	3	0	4	2	0	
WAW1	90	2	0	1	1	3	2	0	0	2	0	0	2	0	0	4	0	0	4	0	0	0	
WAW1	90	3	0	3	0	2	5	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	
WAW1	90	4	0	0	2	2	3	0	0	0	0	0	2	0	6	0	0	0	0	0	0	0	
WAW1	91	1	0	0	1	2	2	0	0	1	0	0	0	1	0	6	0	0	2	0	0	0	
WAW1	91	2	0	3	2	2	2	0	0	2	0	0	0	1	2	0	6	0	0	0	0	0	

WAW1	91	3	0	2	1	2	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	3	0
WAW1	91	4	0	3	1	2	0	0	0	2	0	0	1	0	0	0	6	0	0	0	0	2	0
WAW1	92	1	0	0	2	2	2	0	0	0	0	2	0	0	0	6	0	0	0	0	0	0	0
WAW1	92	2	0	0	2	2	3	0	0	0	0	0	0	0	0	6	0	0	2	0	0	0	0
WAW1	92	3	0	0	2	0	3	0	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0
WAW1	92	4	0	0	2	0	2	1	1xPMA	0	0	0	0	2	0	4	0	0	5	0	0	0	0
WAW1	93	1	0	0	2	2	2	0	0	0	0	2	0	0	0	6	0	0	0	0	0	0	0
WAW1	93	2	0	0	2	2	3	0	0	0	0	0	0	0	0	6	0	0	2	0	0	0	0
WAW1	93	3	0	0	2	0	3	0	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0
WAW1	93	4	0	0	2	0	2	1	1xPMA	0	0	0	0	2	0	4	0	0	5	0	0	0	0
WAW1	94	1	0	0	1	2	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	0
WAW1	94	2	0	3	2	2	4	0	0	2	0	0	0	0	0	4	3	0	0	2	0	0	0
WAW1	94	3	0	0	0	2	0	0	0	2	0	0	2	0	0	6	0	0	3	2	0	0	0
WAW1	94	4	0	0	1	0	3	0	0	0	0	0	3	0	0	5	2	0	0	3	0	0	0
WAW2	95	1	0	4	1	4	2	0	2	0	0	0	0	1	1	2	3	0	0	2	0	0	0
WAW2	95	2	0	4	2	4	1	3	2xPTR	0	0	0	0	2	3	1	0	0	0	0	0	3	0
WAW2	95	3	3	5	1	2	2	2	3xPTR	3	0	0	0	0	3	0	0	0	0	0	0	0	0
WAW2	95	4	3	5	0	3	0	2	1xPTR	0	0	0	0	0	4	0	0	0	0	0	0	0	0
WAW2	96	1	0	3	2	6	2	2	1xPTR	0	0	0	0	2	0	2	0	0	0	0	0	0	0
WAW2	96	2	0	3	3	5	3	2	1xPMA	0	0	0	0	2	0	3	0	0	0	0	0	0	0
WAW2	96	3	0	4	2	4	2	0	0	0	0	0	0	3	0	3	0	0	0	0	0	0	0
WAW2	96	4	0	4	1	5	3	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
WAW2	97	1	0	6	1	2	2	2	2xPTR	0	0	0	0	3	0	3	0	0	0	0	0	0	0
WAW2	97	2	0	5	1	2	3	0	0	0	0	0	2	2	3	0	0	0	0	0	0	0	0
WAW2	97	3	0	3	2	3	3	0	0	0	0	0	3	3	3	0	0	0	0	0	0	0	0
WAW2	97	4	0	6	1	0	2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0
WAW2	98	1	0	4	2	2	3	0	0	3	0	0	0	0	0	4	3	0	0	0	0	0	0

WAW2	105	1	0	4	2	3	2	3	2xPTR	2	0	0	2	0	0	3	0	0	0	0	0	0
WAW2	105	2	0	3	3	3	4	2	1xPTR	0	0	0	0	0	0	3	0	0	0	0	0	0
WAW2	105	3	0	3	2	3	3	0		0	2	0	2	0	0	3	0	3	0	0	0	0
WAW2	105	4	3	3	1	0	3	0		2	2	0	0	0	0	3	0	3	0	0	0	0
WAW2	106	1	2	4	1	2	2	0		3	0	0	0	0	0	3	0	2	2	0	3	0
WAW2	106	2	0	5	1	2	3	0		0	0	0	0	0	0	3	0	0	0	0	0	3
WAW2	106	3	0	4	1	2	1	0		0	0	0	0	0	0	3	0	0	4	0	0	3
WAW2	106	4	0	4	2	0	2	0		0	3	0	0	0	0	4	0	3	0	0	0	0
WAW2	107	1	0	3	2	4	3	0		0	3	0	0	2	0	3	0	3	0	0	0	0
WAW2	107	2	0	0	2	4	3	0		0	0	0	0	0	0	2	0	4	0	0	0	0
WAW2	107	3	0	4	1	2	3	3	1xPMA	0	0	0	0	0	0	3	3	4	0	0	0	0
WAW2	107	4	0	3	3	4	2	3	1xPMA, 2xPTR	0	0	0	0	0	0	3	0	4	0	0	0	0
WAW2	108	1	0	6	1	0	1	0		0	0	0	0	0	0	2	0	0	0	0	0	0
WAW2	108	2	0	3	3	2	3	2	1xPTR	0	3	0	0	0	0	2	3	3	0	0	0	0
WAW2	108	3	0	5	1	2	2	0		0	3	0	0	0	0	2	3	3	0	0	0	0
WAW2	108	4	0	6	1	2	0	0		3	0	0	0	0	0	1	2	0	0	0	0	0
WAW2	109	1	0	5	1	3	3	0		0	0	0	0	0	0	3	3	0	0	0	0	0
WAW2	109	2	0	5	2	3	2	0		0	0	0	0	0	0	3	4	2	0	0	1	0
WAW2	109	3	0	3	2	2	1	3	1xPMA	0	0	0	0	0	0	2	5	0	0	0	0	0
WAW2	109	4	0	3	1	4	2	0		0	0	0	0	0	0	2	4	3	0	0	1	0
SEL3	110	1	0	3	1	3	2	2	5xABA	0	0	3	2	0	0	3	2	3	3	0	0	3
SEL3	110	2	0	4	2	2	2	2	1xPTR	0	0	0	0	0	0	3	4	3	0	3	0	3
SEL3	110	3	0	3	3	3	2	0		0	0	0	0	0	0	3	4	3	0	0	0	2
SEL3	110	4	0	4	3	4	2	2	3xABA	0	0	0	2	0	0	3	3	3	2	0	0	2
SEL3	111	1	0	4	2	2	1	0		0	0	0	2	0	0	3	3	2	0	2	0	3
SEL3	111	2	0	5	2	3	2	0		0	0	0	2	0	0	2	3	2	2	0	0	0

SEL3	111	3	0	4	2	4	2	1	1xABA	0	0	0	1	0	0	3	0	2	0	0	0	3	0
SEL3	111	4	0	5	2	4	3	3	1xPTR	0	0	0	0	0	0	0	2	0	0	0	0	2	0
SEL3	112	1	0	5	1	2	3	2	3xABA	0	0	0	0	0	0	2	3	0	0	0	0	3	3
SEL3	112	2	3	3	2	2	3	2	1xABA	0	0	0	0	0	0	2	3	3	0	0	0	2	0
SEL3	112	3	2	4	1	3	1	2	1xABA	0	0	0	2	0	0	3	3	0	2	0	0	3	0
SEL3	112	4	0	3	1	3	2	2	5xABA	0	0	0	0	0	0	2	3	2	0	0	0	3	0
SEL3	113	1	0	5	2	3	1	3	2xABA	0	0	0	2	0	0	0	3	1	2	0	0	0	0
SEL3	113	2	0	5	1	0	1	0		0	0	0	0	0	0	3	3	0	0	0	0	3	3
SEL3	113	3	2	4	0	3	2	0		0	0	4	0	0	0	2	3	0	2	0	0	3	3
SEL3	113	4	0	3	1	3	0	5	9xABA	0	0	0	0	0	0	2	3	0	0	0	0	0	0
SEL3	114	1	0	4	3	4	1	1	1xABA	0	0	0	0	0	0	3	2	2	0	0	0	0	0
SEL3	114	2	0	4	1	2	1	2	1xABA	0	0	3	0	0	0	2	3	2	0	0	0	3	3
SEL3	114	3	0	3	2	3	2	1	1xABA	0	0	3	0	0	0	2	3	2	0	0	0	3	2
SEL3	114	4	0	4	2	4	1	1	1xABA	0	0	3	0	0	0	0	0	2	0	0	0	3	0
SEL3	115	1	2	3	2	5	2	3	5xABA	0	0	0	0	0	0	3	3	0	0	0	0	0	0
SEL3	115	2	3	4	2	2	2	2	2xABA	0	0	0	0	0	0	3	2	3	0	0	0	3	0
SEL3	115	3	0	5	0	2	0	2	1xABA	0	0	0	0	0	0	3	3	2	0	0	0	0	3
SEL3	115	4	0	5	0	2	1	0		0	0	0	2	0	0	3	3	2	0	0	0	0	3
SEL3	116	1	0	4	0	3	2	0		0	0	4	0	0	0	2	2	2	0	0	0	3	0
SEL3	116	2	0	3	0	0	2	0		0	0	5	0	0	0	2	0	2	0	0	0	3	0
SEL3	116	3	0	4	1	3	2	0		0	0	4	2	0	0	0	3	3	0	0	0	3	0
SEL3	116	4	0	3	1	2	2	2	2xABA	0	0	5	0	0	0	0	3	0	0	0	0	3	0
SEL3	117	1	0	3	0	2	2	0		0	0	5	0	0	0	2	2	2	0	0	0	2	3
SEL3	117	2	2	4	0	3	1	0		0	0	3	0	0	0	3	3	2	0	0	0	3	0
SEL3	117	3	0	3	2	6	1	1	1xABA	0	0	0	0	0	0	0	0	0	0	0	0	2	0
SEL3	117	4	0	4	1	4	2	2	3xABA	0	0	3	0	0	0	2	2	2	0	0	0	0	3
SEL3	118	1	0	3	1	3	3	0		0	0	4	0	0	0	2	3	3	0	0	0	2	3

SEL2	124	4	0	3	1	5	3	2	7xABA	0	0	0	0	0	0	0	0	2	0	0	0	0	0	0
SEL2	125	1	0	3	1	3	3	3	1xABA	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0
SEL2	125	2	0	4	1	2	3	1	2xABA	0	0	0	0	0	3	0	4	0	0	0	0	0	0	0
SEL2	125	3	0	3	1	4	3	3	12xABA	0	0	0	0	0	2	0	4	0	0	0	0	0	0	0
SEL2	125	4	0	4	2	3	4	0		0	0	0	0	0	2	0	3	0	0	0	0	0	0	
SEL2	126	1	0	3	1	5	3	2	2xABA	0	0	3	2	0	0	0	3	0	0	0	0	0	0	0
SEL2	126	2	0	2	3	6	3	3	5xABA	0	0	0	0	1	0	2	0	0	0	0	0	0	0	0
SEL2	126	3	0	3	2	6	3	0		0	0	0	0	0	2	0	2	0	0	0	0	0	0	0
SEL2	126	4	0	1	1	6	3	1	1xABA	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0
SEL2	127	1	0	2	2	5	3	3	15xABA	0	0	0	0	0	3	0	2	0	0	0	0	0	0	2
SEL2	127	2	0	4	2	4	3	3	16xABA	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0
SEL2	127	3	0	3	2	6	2	3	10xABA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SEL2	127	4	0	3	1	4	3	3	18xABA, 1xPMA	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
SEL2	128	1	0	3	2	6	2	0		0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
SEL2	128	2	0	4	1	5	2	0		0	0	0	0	2	0	3	0	0	0	0	0	0	0	0
SEL2	128	3	0	3	2	3	3	0		3	0	0	0	0	0	3	0	0	0	0	0	0	0	3
SEL2	128	4	0	5	2	4	2	0		0	0	0	0	2	0	2	0	0	0	0	0	0	0	0
SEL2	129	1	0	3	2	5	3	0		0	3	0	0	0	0	2	0	0	0	0	0	0	0	3
SEL2	129	2	0	5	2	2	3	2	2xPTR	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
SEL2	129	3	0	3	2	4	2	4	6xABA, 3xPMA	0	0	3	0	0	0	0	3	0	0	0	0	0	0	0
SEL2	129	4	0	4	1	5	0	0		0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
SEL2	130	1	0	3	1	6	1	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SEL2	130	2	0	3	0	5	3	1	2xABA	0	0	0	0	0	3	0	2	0	0	0	0	0	0	0
SEL2	130	3	0	4	1	5	3	2	2xABA	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
SEL2	130	4	0	5	2	3	3	0		0	0	3	0	0	0	3	0	0	0	0	0	0	0	3
SEL2	131	1	0	3	2	3	3	0		0	0	3	0	0	0	1	0	5	0	0	0	0	0	2

SEL2	131	2	0	3	1	3	2	1	1xABA	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
SEL2	131	3	0	3	1	4	2	2	1xPTR	0	0	3	0	0	0	3	0	0	0	0	0	0	0	2	3
SEL2	131	4	0	4	2	2	3	0		0	0	3	0	0	0	3	0	4	0	0	0	0	0	2	0
SEL2	132	1	0	3	0	2	3	0		0	0	3	0	0	0	2	0	5	0	0	0	0	0	2	0
SEL2	132	2	0	3	2	0	4	2	1xABA	0	0	0	0	0	0	3	0	5	0	0	0	0	0	3	0
SEL2	132	3	0	3	1	0	3	0		0	0	0	0	0	0	3	0	6	0	0	0	0	0	3	0
SEL2	132	4	0	3	1	2	2	0		0	0	0	0	0	0	3	0	6	0	0	0	0	0	2	0
SEL2	133	1	0	3	2	5	2	1	1xABA	0	0	3	0	0	0	3	0	0	0	0	0	0	0	3	0
SEL2	133	2	0	3	1	5	3	2	1xABA	0	0	0	0	0	0	2	0	0	0	0	0	0	0	2	0
SEL2	133	3	0	3	1	5	1	0		0	0	0	0	0	2	0	2	0	0	0	0	0	0	0	0
SEL2	133	4	0	3	2	6	1	2	1xABA, 1xPTR	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
SEL2	134	1	0	0	2	5	3	0		0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
SEL2	134	2	0	3	1	2	5	0		0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0
SEL2	134	3	0	3	1	3	3	0		0	0	0	0	0	0	3	0	5	0	0	0	0	0	0	0
SEL2	134	4	0	3	1	2	3	0		0	0	0	0	0	2	0	6	0	0	0	0	0	0	0	0
SEL2	135	1	0	0	1	3	3	0		0	0	0	0	0	0	6	0	0	0	0	0	0	0	0	0
SEL2	135	2	0	0	1	6	1	0		0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0
SEL2	135	3	0	0	1	7	0	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SEL2	135	4	0	3	1	0	4	0		0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0
SEL1	136	1	0	3	3	2	4	0		0	3	0	2	0	0	3	0	3	2	0	0	0	3	0	0
SEL1	136	2	0	3	3	3	4	3	1xPMA	0	0	0	0	0	2	0	3	0	0	0	0	0	0	3	0
SEL1	136	3	0	0	2	0	2	0		2	2	0	3	0	0	3	0	3	5	0	3	0	0	0	0
SEL1	136	4	0	3	2	0	2	0		3	0	0	2	0	3	3	0	3	0	0	0	0	0	0	0
SEL1	137	1	0	3	2	0	4	0		3	3	0	3	0	0	3	0	4	0	0	0	0	0	0	0
SEL1	137	2	0	3	2	2	0	0		3	0	0	3	0	0	3	0	5	0	0	0	0	0	0	3
SEL1	137	3	0	3	2	3	4	3	1xPMA	0	0	0	0	0	0	4	0	4	0	0	0	0	0	0	3

SEL1	137	4	0	3	3	0	3	0	3	0	3	0	0	3	0	4	0	0	0	0	0	0	
SEL1	138	1	0	3	2	2	3	3	1xPMA	3	3	0	0	0	3	0	3	0	0	0	3	0	
SEL1	138	2	0	3	1	3	5	0		3	0	0	3	0	3	0	2	0	0	0	0	0	
SEL1	138	3	0	0	1	2	2	0		3	0	0	2	0	0	0	0	5	0	3	3	0	
SEL1	138	4	0	2	2	0	3	4	2xPMA	0	0	0	2	0	0	0	4	3	0	0	3	0	
SEL1	139	1	0	0	0	2	0			3	2	0	2	0	0	0	3	5	0	2	2	0	
SEL1	139	2	0	3	3	2	3	3	3xPMA	0	1	0	3	0	0	0	4	0	0	3	0	0	
SEL1	139	3	0	0	2	0	2	0		4	0	0	3	0	0	0	4	0	0	3	0	0	
SEL1	139	4	0	3	3	2	4	0		0	2	0	0	0	0	0	3	2	0	0	0	0	
SEL1	140	1	0	3	2	0	3	0		0	3	0	3	0	0	2	0	5	3	0	0	3	0
SEL1	140	2	0	2	1	0	4	0		0	3	0	3	0	0	1	0	3	4	0	0	3	0
SEL1	140	3	0	2	2	0	2	3	1xPMA	0	0	0	2	0	0	3	0	4	0	0	3	0	0
SEL1	140	4	0	0	1	0	3	5	10xPMA	0	2	0	3	0	0	2	0	3	3	0	0	0	0
SEL1	141	1	0	0	2	3	0	0		2	2	0	2	0	0	0	3	3	0	4	3	0	0
SEL1	141	2	0	2	1	2	3	0		2	0	0	3	0	0	2	0	2	5	0	0	2	0
SEL1	141	3	0	0	3	0	3	3	1xPMA	3	1	0	2	0	0	0	0	4	0	0	3	0	0
SEL1	141	4	0	2	2	0	4	0		0	2	0	2	0	0	0	3	4	0	3	3	0	0
SEL1	142	1	0	3	2	0	3	0		0	0	0	3	0	2	2	0	5	0	2	0	0	0
SEL1	142	2	0	2	3	3	4	3	1xPMA	3	0	0	3	0	0	2	0	3	0	0	3	0	0
SEL1	142	3	0	3	3	0	4	2	2xPMA	3	0	0	2	0	0	3	0	4	0	0	3	0	0
SEL1	142	4	0	0	0	2	2	3	3xPMA	0	3	0	3	0	0	0	3	0	0	4	3	0	0
SEL1	143	1	0	1	2	2	5	3	3xPMA	0	0	0	3	0	2	3	0	3	0	0	3	0	0
SEL1	143	2	0	2	2	0	5	3	2xPMA	0	3	0	2	0	0	2	0	3	3	0	0	3	0
SEL1	143	3	0	0	3	3	4	0		0	0	0	0	0	0	0	3	0	0	0	0	0	0
SEL1	143	4	0	3	2	0	6	2	1xPMA	0	0	0	2	0	0	0	0	0	0	0	0	0	0
SEL1	144	1	0	0	2	0	4	4	6xPMA	0	0	0	0	0	0	0	4	4	0	0	3	0	0
SEL1	144	2	0	0	3	3	2	2	3xPMA	0	0	0	2	0	0	0	5	0	0	0	3	0	0

SEL1	144	3	0	3	3	0	2	3	0	0	0	2	0	0	3	0	4	0	0	0	3	0
								6xPTR														
SEL1	144	4	0	3	3	2	3	0	0	0	0	0	0	0	2	0	5	3	0	0	3	0
SEL1	145	1	0	0	3	3	4	0	0	2	0	3	0	0	0	0	0	4	0	0	0	0
SEL1	145	2	0	0	2	0	5	0	0	0	0	0	0	0	0	0	3	3	0	0	0	0
SEL1	145	3	0	3	0	0	3	2	1xPMA	0	0	3	0	0	3	0	4	3	0	0	3	0
									1xABA, 3xPMA													
SEL1	145	4	0	2	2	3	3	3	0	2	0	0	0	0	2	0	4	3	0	3	0	0

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