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Avant-propos

Cette thèse est organisée en cinq chapitres, dont le premier et le dernier représentent l'introduction et la conclusion générale, respectivement. Les trois autres chapitres sont présentés sous forme d'articles scientifiques, dont un est publié et les deux autres sont en cours d'évaluation.

Le chapitre 2 est publié sous la référence : Ropars P, Boudreau S (2012) Shrub expansion at the forest-tundra ecotone: spatial heterogeneity linked to local topography. *Environmental Research Letters* 7 : 015501. Cet article a été publié dans le cadre d'un numéro spécial intitulé : *Recent dynamics of arctic and subarctic vegetation*.

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En tant qu'auteure principale des trois articles, j'ai élaboré les objectifs de recherche, planifié et organisé la récolte des données, effectué les analyses statistiques et rédigés les manuscrits. Stéphane Boudreau, mon directeur de thèse, a contribué activement à toutes les étapes de la réalisation de ces trois articles. Esther Lévesque a contribué à l'écriture des articles relatant les principaux résultats des chapitres 3 et 4.

CHAPITRE 1 Introduction générale

1.1 Les changements environnementaux récents

Le réchauffement planétaire ne fait maintenant plus l'objet de controverses au sein de la communauté scientifique. Les nombreux indicateurs utilisés afin d'inférer les variations du climat arrivent tous à la même conclusion : les températures annuelles moyennes au cours du dernier siècle ont non seulement connu une hausse marquée, mais cette dernière s'est faite à un rythme accéléré (IPCC 2013). En effet, les trois dernières décennies ont successivement enregistré les températures les plus chaudes depuis 1850. Outre l'augmentation de la température atmosphérique, l'augmentation de la température des masses d'eau océaniques, l'augmentation du niveau des océans, le raccourcissement de la période de gel des lacs et des rivières, la diminution de la quantité de glace et de neige ainsi que le changement dans la phénologie de nombreuses espèces témoignent d'une planète en pleine mutation (Parmesan 2006, IPCC 2013). Ces nombreux constats appuient tous la thèse qu'un réchauffement climatique est en cours et qu'il aura sans contredit de nombreuses conséquences sur l'ensemble du monde vivant.

Bien que certains sceptiques tentent toujours de le nier, tout indique que la majeure partie du réchauffement observé est attribuable aux émissions anthropiques de gaz à effet de serre (GES ; IPCC 2013). La concentration atmosphérique de ces derniers n'a cessé de croître depuis l'avènement de l'aire industrielle, permettant à certains gaz comme le CO₂ et le CH₄ d'atteindre des sommets inégalés au cours des derniers 650 000 ans (IPCC 2013). De 1750 à 2011, les concentrations de CO₂ et de NO₂ ont augmenté de 40 % et 20 %, respectivement, tandis que celle de CH₄ a enregistré une augmentation de plus de 150 %. Par conséquent, l'effet combiné de ces GES a augmenté le budget énergétique planétaire de 2,29 W/m² au cours de cette période, tandis que l'effet de l'activité solaire n'aurait augmenté que de 0,05 W/m² (IPCC 2013). De ce fait, la majeure partie du réchauffement climatique actuel serait expliquée par l'augmentation de la concentration des GES d'origine anthropique, plutôt que par des variations naturelles de l'activité solaire.

Les observations effectuées sur le terrain ainsi que la grande majorité des modèles développés afin de prédire les variations futures du climat suggèrent fortement que les régions arctiques et subarctiques sont et seront les plus affectées par le réchauffement

climatique (Serreze *et al* 2000, IPCC 2013). En effet, il est prédit que ce dernier se fera ressentir plus hâtivement, se fera à un rythme plus élevé et aura des effets plus importants dans les hautes latitudes de l'hémisphère nord (IPCC 2013).

1.2 La limite latitudinale des arbres

Au cœur de ces régions nordiques, l'écotone forêt boréale toundra (EFT) revêt un intérêt particulier. Cette vaste zone de transition entre la forêt boréale continue et la toundra arbustive (Payette *et al* 2001) pourrait en effet être le théâtre de profondes modifications. Certains changements, comme la dégradation du pergélisol et la formation de mares de thermokarst qui lui est associée (Allard et Séguin 1987) ainsi que l'augmentation de l'activité des micro-organismes du sol et, par conséquent, l'accélération de la minéralisation des nutriments (Grogan et Chapin 2000) sont d'ailleurs déjà observées. Une autre conséquence potentielle d'une élévation des températures est le déplacement vers le nord de l'aire de répartition des espèces végétales. En effet, le lien étroit entre le climat et la répartition des différents types de végétation est connu depuis fort longtemps. Les bases scientifiques de cette association ont été établies par Alexander von Humboldt au début du 19^e siècle lorsque ce dernier a montré la concordance entre certaines isothermes et les limites des grandes zones de végétation. Or, avec le réchauffement climatique observé et appréhendé, ces isothermes devraient se déplacer vers les pôles, tout comme les grandes zones de végétation. Par exemple, la limite des arbres en Amérique du Nord et en Eurasie, qui correspond selon Larsen (1980) à la position de l'isotherme de 13 °C en juillet, devrait se déplacer vers le nord avec un adoucissement des températures. Ces prédictions sont en accord avec de nombreuses études paléoécologiques ayant montré des déplacements de la limite des arbres associés à des variations du climat (MacDonald *et al* 1993, Tinner et Lotter 2001, Shuman *et al* 2004). De plus, des travaux récents relatent que de nombreuses espèces arborescentes sont limitées physiologiquement par la température à leur limite septentrionale de répartition (Sveinbjörnsson 2000, Sveinbjörnsson *et al* 2002), suggérant ainsi qu'un adoucissement du climat pourrait leur permettre d'étendre leur limite de répartition vers le nord.

Malgré ces évidences, la réponse de la limite latitudinale des arbres aux changements climatiques actuels ne semble pas être uniforme à l'échelle circumpolaire. En effet, une synthèse d'une quarantaine d'études traitant de la dynamique récente de nombreuses limites latitudinales des arbres montre que seulement la moitié de celles-ci se sont déplacées vers les pôles en réponse au réchauffement climatique récent (21 sur 40), alors qu'aucun changement n'a été détecté pour les autres (Harsch *et al* 2009). Ce résultat laisse supposer que la dynamique des espèces arborescentes présentes à l'EFT ne serait pas contrôlée uniquement par la température, mais plutôt par un ensemble de variables climatiques et écologiques. Notons, par exemple, l'influence de la microtopographie sur les caractéristiques édaphiques locales (quantité de matière organique, humidité ; MacDonald et Yin 1999) ainsi que celle du pergélisol sur l'épaisseur de la couche active du sol (Camill et Clark 1998, Frost *et al* 2012). Ces deux facteurs ont le potentiel de freiner l'avancée de la limite des arbres en limitant l'établissement ou la croissance de certaines espèces arborescentes (Frost et Epstein 2014). Quoi que la remise en circulation des nutriments qu'entraîne la dégradation du pergélisol soit généralement favorable à la croissance et à l'établissement des espèces ligneuses (Lantz *et al* 2009), une étude récente présente un fort déclin du couvert forestier suite aux changements hydriques au centre de l'Alaska, États-Unis (Jorgenson *et al* 2001). De plus, la présence d'un décalage entre le début du réchauffement et la réponse des espèces végétales est souvent énoncée pour expliquer l'apparente immobilité de la limite des arbres (Chapin et Starfield 1997, Lloyd *et al* 2002), notamment celui nécessaire à la production de graines viables (Lescop-Sinclair et Payette 1995, MacDonald *et al* 1998). L'inertie de certaines limites septentrionales des arbres pourrait donc être que transitoire.

Outre les exemples présentés ci-dessus, les interactions entre les espèces arborescentes et celles de sous-étage, dont les arbustes, pourraient elles aussi influencer la réponse des espèces arborescentes au réchauffement climatique actuel (Lloyd et Fastie 2003). En effet, de plus en plus de recherches suggèrent que certains arbustes ont une influence sur le recrutement et la croissance des espèces arborescentes des forêts boréales (*Empetrum hermaphroditum* : Nilsson *et al* 2000, DeLuca *et al* 2002, Wardle *et al* 2003 ; *Kalmia angustifolia* : Krause 1986, Mallik 1994, 1995) ainsi qu'à la limite septentrionale des arbres

(Senfeldr *et al* 2014). Parmi les hypothèses avancées, les arbustes pourraient limiter la croissance de certaines espèces arborescentes par la libération de composés allélopathiques (Nilsson et Wardle 2005) ou en modifiant les conditions de croissance (humidité, durée du couvert de neige, accès à la lumière ; Soukupova *et al* 2001, Dullinger *et al* 2005, Senfeldr *et al* 2014). D'un autre côté, le couvert arbustif pourrait aussi protéger les jeunes plantules arborescentes des dommages causés par le vent et le froid (Senfeldr *et al* 2014) et diminuer la pression exercée par les herbivores (Dullinger *et al* 2005). Qu'elle soit positive ou négative, l'influence des arbustes sur la strate supérieure pourrait s'accroître au cours des prochaines années puisque certaines espèces de la strate arbustive sont considérées comme étant plus promptes à réagir à l'augmentation des températures (Epstein *et al* 2004a, Tape *et al* 2006, Frost et Epstein 2014).

1.3 La strate arbustive

La strate arbustive, dont le rôle fonctionnel dans la dynamique des écosystèmes subarctiques a longtemps été ignoré, suscite maintenant un intérêt grandissant au sein de la communauté scientifique. De nombreuses études, utilisant diverses méthodologies et indicateurs, se sont intéressées depuis le début des années 2000 à la dynamique récente de la strate arbustive. L'augmentation souvent importante de la biomasse, du couvert et de l'abondance de différentes espèces arbustives a piqué la curiosité de plusieurs et moussé l'intérêt pour découvrir les causes de ce phénomène et en mesurer les conséquences. Je détaillerai donc dans cette section les changements observés dans la dynamique de la strate arbustive à l'échelle circumpolaire, exposerai les différentes méthodes pour les quantifier et présenterai les causes potentielles ainsi que les conséquences sur leur environnement biotique et abiotique.

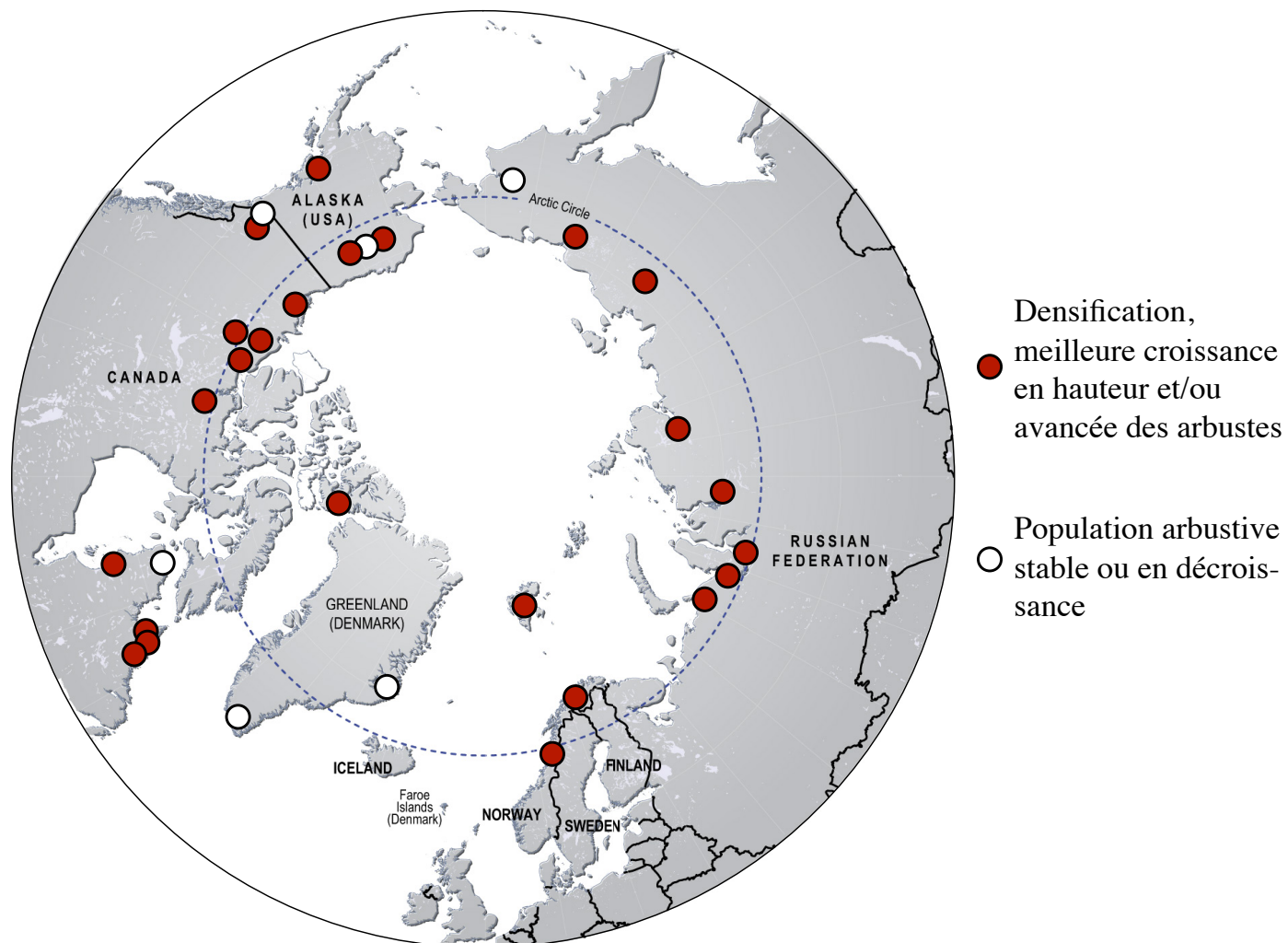


Figure 1.1 État des populations arbustives à l'échelle circumpolaire. La figure a été modifiée et mise à jour à partir d'une recension des études traitant de la dynamique récente de la strate arbustive présentée dans l'article de Myers-Smith et collaborateurs (2011a).

1.3.1 Changements récents

Dans bon nombre de régions arctiques et subarctiques, la strate arbustive a connu une expansion importante au cours des dernières décennies (Figure 1.1). Cette expansion se manifeste généralement de trois façons différentes : (1) une densification des arbustes déjà en place grâce à une croissance latérale accrue, (2) une augmentation de la croissance verticale des arbustes ou (3) une avancée latitudinale ou altitudinale de la limite des arbustes, impliquant de ce fait la colonisation de nouveaux milieux (Myers-Smith *et al* 2011a).

Parmi les régions où la dynamique de la strate arbustive a été étudiée, notons par exemple le nord de l'Alaska où l'aulne semble être le principal responsable de la densification récente (Sturm *et al* 2001a, Tape *et al* 2006), l'Arctique canadien où le saule, l'aulne et certaines espèces sempervirentes se sont récemment densifiés (Hudson et Henry 2011, Lantz *et al* 2009, 2010, Hill et Henry 2011, Mackay et Burn 2011) et le nord du Québec où le bouleau a été identifié comme principale espèce responsable de l'augmentation du couvert arbustif (Tremblay *et al* 2012). La situation est similaire en Europe et en Russie, où la grande majorité des études ont montré que la strate arbustive était en expansion (Forbes *et al* 2010, Hallinger *et al* 2010, Senfeldt *et al* 2014). La plupart de ces études ont recensé une densification des arbustes déjà en place grâce à une croissance latérale accrue, mais certaines ont observé une avancée de la limite latitudinale ou altitudinale des arbustes (Alaska : Dial *et al* 2007, Yukon : Myers-Smith 2011, Suède subarctique : Hallinger *et al* 2010, Alpes : Dullinger *et al* 2003, Anthelme *et al* 2007, Cannone *et al* 2007) et une augmentation de la croissance en hauteur de plusieurs espèces arbustives (Myers-Smith *et al* 2011b, Elmendorf *et al* 2012a). Notons également que plusieurs habitants de ces régions nordiques ont observé une augmentation du couvert arbustif sur leur territoire dans les dernières décennies (Thorpe *et al* 2002, Forbes *et al* 2009, Spiech 2014).

Bien que la plupart des régions étudiées aient enregistré une densification récente de leur strate arbustive, certaines n'ont recensé aucun changement dans cette dernière (Figure 1.1). Dans deux régions du Groenland par exemple, le couvert arbustif n'a subi aucun changement significatif dans les dernières décennies (Daniëls *et al* 2010, Boulanger-

Lapointe *et al* 2014), tout comme dans un site de l'est de la Russie (Frost et Epstein 2013). De plus, Tape et collaborateurs (2012) ont montré que dans une même région, certains milieux peuvent supporter une densification importante de la strate arbustive en place tandis que d'autres milieux adjacents peuvent n'enregistrer aucun changement de couvert pour cette même strate. Bien que l'étendue de la densification de la strate arbustive suggère un contrôle global, les exemples énoncés ci-dessus soulignent l'importance de certaines caractéristiques locales pour expliquer, du moins en partie, le phénomène.

Afin de quantifier la densification de la strate arbustive, deux types d'analyses descriptives ont été utilisés : l'analyse comparative de photographies aériennes ou obliques ainsi que l'analyse d'indices d'activité photosynthétique évalués à partir d'images satellitaires. L'analyse comparative de photographies aériennes permet d'apprécier l'évolution récente du couvert végétal en effectuant un examen visuel direct. Pour ce faire, différents ensembles de photographies d'une région sont comparés. Les photographies anciennes proviennent notamment des vastes campagnes de reconnaissance du territoire nordique québécois (Tremblay *et al* 2012) ainsi que des campagnes d'exploration pétrolière américaine (Sturm *et al* 2001a, Tape *et al* 2006) effectuées au milieu du 20^e siècle. Ces campagnes ont permis de photographier le territoire avec une qualité et une résolution exceptionnelles permettant ainsi leur comparaison avec des photographies ou des images satellitaires récentes. Jumelé à un traitement approprié des photographies (orthorectification), ce type d'analyse permet de quantifier les changements observés dans la strate arbustive avec une grande précision. De ce fait, cette technique permet non seulement de quantifier l'augmentation du couvert arbustif, mais également de distinguer la réponse de la strate arbustive dans différents types de milieux à travers le paysage. Bien qu'elle ait donné des résultats fiables, cette technique comporte son lot de désavantages qui peuvent, pour certains, être contournés. Parmi ces désavantages, notons par exemple le fait que son utilisation est limitée aux régions pour lesquelles des photographies anciennes sont disponibles et de bonne qualité, que cette technique nécessite un traitement relativement long, restreignant ainsi l'étendue des régions étudiées et qu'elle doit être accompagnée d'une validation exhaustive sur le terrain afin de s'assurer de la validité des résultats obtenus et d'identifier les espèces responsables du changement observé. De plus, cette

technique ne permet pas d'identifier la ou les causes des changements enregistrés. Une bonne connaissance des régions à l'étude est donc nécessaire (historique des perturbations, caractéristiques édaphiques, climat, etc.) afin d'avancer des hypothèses écologiquement valables.

L'analyse d'images satellitaires via différents indices tels que le *Normalized Difference Vegetation Index* (NDVI) permet elle aussi d'apprécier les changements du couvert végétal. Le NDVI est un rapport des réflectances dans le rouge (R) et dans le proche infrarouge (IR ; $NDVI = (IR - R) / (IR + R)$) qui permet de distinguer entre la présence d'une végétation saine et d'une végétation moribonde. En effet, la chlorophylle contenue dans les feuilles des plantes saines absorbe le rouge, tandis qu'elle réfléchit l'infrarouge qui augmenterait inutilement la température interne de la plante. Pour une même période, la comparaison de ces indices d'une année à l'autre permet de suivre l'évolution de l'activité photosynthétique, liée au développement et à l'augmentation de l'abondance des espèces végétales dans une région donnée. À l'échelle circumpolaire, l'interprétation de tels indices a permis de constater une augmentation de la biomasse photosynthétique dans les dernières décennies qui serait principalement attribuable à l'expansion de la strate arbustive (Myneni *et al* 1997, Silapaswan *et al* 2001, Stow *et al* 2004, Goetz *et al* 2005, Raynolds *et al* 2006). Toutefois, ces conclusions sont bien souvent peu supportées par des données terrain. Bien que cette méthode permette d'analyser de vastes territoires, il est donc essentiel de garder à l'esprit qu'elle est une mesure indirecte de la performance des communautés végétales et qu'elle a peu de valeur sans une validation rigoureuse sur le terrain. De plus, tout comme pour l'analyse de photographies aériennes, cette méthode ne permet pas de déterminer les causes des changements enregistrés.

1.3.2 Cause principale de la densification de la strate arbustive : l'augmentation récente des températures

La densification de la strate arbustive a été recensée dans différentes régions arctiques et subarctiques au cours des dernières décennies. Bien que non uniforme, l'étendue de ce phénomène suggère qu'il est contrôlé par un facteur agissant à l'échelle planétaire, du

moins en partie. De ce fait, l'augmentation récente des températures est le facteur le plus fréquemment proposé pour expliquer ce phénomène. Comme les études descriptives utilisées pour quantifier la densification de la strate arbustive ne peuvent nous éclairer sur les causes de ce phénomène, il devient nécessaire de s'appuyer sur d'autres évidences. Parmi ces dernières, les études paléoécologiques suggèrent que les arbustes ont le potentiel de répondre positivement à des conditions climatiques plus clémentes. En effet, des espèces arbustives appartenant aux genres *Salix*, *Betula* et *Alnus* étaient présentes en plus grande abondance en Arctique après le dernier maximum glaciaire, période où les conditions climatiques sont connues pour avoir été plus chaudes et plus humides qu'actuellement (Anderson et Brubaker 1994, Kullman 1995, Naito et Cairns 2011). Afin de confirmer ou d'infirmer le lien entre le climat et la densification des arbustes, deux autres types d'études ont été entreprises : des études expérimentales utilisant des serres expérimentales (« open-top chambers ») d'une part et des études dendrochronologiques d'autre part. Je présenterai donc dans cette section ces deux types d'analyses ainsi que les principales conclusions qu'elles nous permettent de tirer sur les liens unissant la densification de la strate arbustive et le climat.

L'utilisation de serres expérimentales permet de simuler l'augmentation des températures et d'évaluer la réponse d'une espèce d'intérêt. En suivant la réponse de cette dernière au fil des saisons de croissance subséquentes, il est possible d'inférer les changements dans la performance de l'espèce sous de nouvelles conditions climatiques. Parmi les différents indicateurs de performance mesurés, notons par exemple le pourcentage de recouvrement (Wahren *et al* 2005), la croissance en hauteur (Chapin *et al* 1995, Elmendorf *et al* 2012a) et l'effort reproducteur (Arft *et al* 1999). Bien que cette méthode soit souvent utilisée sur de courtes périodes et donc qu'elle ne permette pas de tirer des conclusions à long terme (Elmendorf *et al* 2012b), les résultats obtenus semblent montrer l'effet positif d'un adoucissement du climat sur la performance globale de différentes espèces arbustives. Cette réponse est toutefois maximale dans le Bas-Arctique, comparativement au Haut-Arctique où les espèces semblent investir davantage dans la reproduction (Dormann et Woodin 2002, Walker *et al* 2006). Une des hypothèses avancées pour expliquer cette réponse différentielle entre les deux régions est liée à la compétition pour la lumière et les

nutriments. Comme ces derniers sont en quantité nettement supérieure dans le Bas-Arctique, une meilleure croissance conférerait un avantage compétitif dans ce milieu (Arft *et al* 1999). La diminution du nombre d'individus et donc de la compétition apparente dans le Haut-Arctique favoriserait quant à elle un plus grand investissement dans la reproduction sexuée. Cependant, certains indices nous laissent croire que la compétition pourrait également être importante dans ces régions (N. Boulanger-Lapointe, communication personnelle). Parmi les arbustes du Bas-Arctique, les espèces décidues sont celles pour lesquelles la réponse au réchauffement est la plus marquée. L'augmentation de leur pourcentage de recouvrement (Chapin *et al* 1995, Bret-Harte *et al* 2002, Wahren *et al* 2005) ainsi qu'une meilleure croissance en hauteur (Chapin et Shaver 1985, Jónsdóttir *et al* 2005, Elmendorf *et al* 2012a) ont toutes deux été observées lors de telles études. Cette tendance est d'autant plus prononcée lorsque l'utilisation des serres expérimentales est couplée à l'ajout de nutriments (Chapin et Shaver 1996, Bret-Harte *et al* 2001). De plus, la germination des graines de certaines espèces arbustives (*Empetrum nigrum* ssp. *hermaphroditum* et *Vaccinium uliginosum*) et, par conséquent, l'établissement de nouveaux individus semblent être favorisés par une augmentation des températures (Graae *et al* 2008).

En plus de confirmer le lien entre le climat et la croissance, les études dendrochronologiques nous permettent d'identifier les différents paramètres climatiques associés à une meilleure croissance. Cependant, bien que leur propension à former des cernes annuels de croissance soit connue depuis le début du 20^e siècle, les espèces arbustives sont demeurées largement ignorées en dendrochronologie. Leur faible intérêt économique, leur courte longévité (Schweingruber 2007) ainsi que les nombreuses embûches encourues lors de leur traitement ne sont que quelques raisons pouvant expliquer leur absence prolongée des analyses dendrochronologiques. Par exemple, le collet des arbustes (c'est-à-dire la partie la plus vieille) est difficile à identifier sur le terrain et il est souvent nécessaire de traiter les échantillons afin de distinguer leurs cernes annuels de croissance (Au et Tardif 2007, Bår *et al* 2008). Ces derniers sont souvent étroits, incomplets ou complètement absents (Callaghan 1973, Liang et Eckstein 2009, Hallinger *et al* 2010). L'utilisation des arbustes en dendrochronologie est d'autant plus problématique

dans les régions arctiques et subarctiques, où les courtes saisons de croissance ne permettent parfois pas au collet des vieux individus d'enregistrer une croissance radiale. En effet, la croissance des arbustes est initiée dans les parties apicales des individus grâce à la libération d'une hormone nommée auxine (Forest *et al* 2006). Cette hormone migre par la suite le long des branches pour finalement se rendre au collet. Comme les branches deviennent de plus en plus longues au fil des années, la croissance prend de plus en plus de temps à être initiée dans les parties les plus vieilles de l'arbuste. Dans les années où les conditions sont difficiles, le collet peut donc ne pas former de cellules et, par conséquent, ne pas enregistrer de croissance radiale (Hallinger *et al* 2010). Néanmoins, le besoin criant d'approfondir nos connaissances sur les variations récentes du climat des régions arctiques et subarctiques où peu d'espèces arborescentes sont en mesure de croître a fortement encouragé la communauté scientifique à développer des outils et techniques afin d'utiliser les arbustes comme modèles d'études dendrochronologiques. Une revue de littérature récente révèle que 76% des chronologies recensées sont sensibles à certaines variables climatiques (Myers-Smith *et al* 2015). En effet, plusieurs espèces arbustives répondent positivement aux températures estivales (Bär *et al* 2008, Liang et Eckstein 2009, Forbes *et al* 2010, Hallinger *et al* 2010, Hantemirov *et al* 2011, Boudreau et Villeneuve-Simard 2012, Jorgensen *et al* 2015), corroborant de ce fait les résultats obtenus grâce aux études expérimentales détaillées plus haut. Dans les milieux arctiques et subarctiques où la saison de croissance est courte, une amélioration des conditions climatiques estivales pourrait en effet favoriser les réactions enzymatiques de la photosynthèse et permettre une meilleure croissance. Cependant, les variations de croissance radiale des espèces arbustives ne sont pas toutes expliquées par les températures de la saison de croissance en cours. Certaines semblent en effet contrôlées par les températures printanières (Xiao *et al* 2007, Au et Tardif 2007) ou par les précipitations hivernales (Liang et Eckstein 2009; Hallinger *et al* 2010; Schmidt *et al* 2010) ou estivales (Blok *et al* 2011). De plus, la relation croissance-climat semble varier en fonction de la position géographique, de la hauteur des espèces arbustives considérées et de la disponibilité en eau du sol (Myers-Smith *et al* 2015). Les espèces arbustives érigées croissant à la limite entre le Haut-Arctique et le Bas-Arctique et dans un milieu où la disponibilité en eau n'est pas limitante semblent être les plus sensibles au climat (Myers-Smith *et al* 2015).

1.3.3 Autres causes potentielles de la densification de la strate arbustive

Bien que l'augmentation récente des températures soit le plus souvent invoquée comme cause principale de la densification de la strate arbustive, il n'en demeure pas moins que plusieurs autres facteurs peuvent être impliqués dans ce phénomène. Parmi ceux-ci, notons par exemple les différents régimes de perturbations que subissent les environnements nordiques. En permettant le relâchement de nutriments dans ces régions où les sols sont reconnus comme étant pauvres, les perturbations favorisent généralement une meilleure performance des arbustes en place et permettent ainsi une densification accrue. Par exemple, des milieux récemment brûlés ont connu une densification plus importante de leur strate arbustive ainsi qu'une meilleure croissance en hauteur des individus en place que les milieux non brûlés (Racine *et al* 2004, Lantz *et al* 2010). En plus d'augmenter la quantité de nutriments disponibles, les feux créent des sites de germination favorables pour différentes espèces arbustives, permettant ainsi une colonisation plus efficace de ces dernières. En Alaska, les milieux où les nutriments sont fréquemment remis en circulation tels que les plaines inondables et les abords de cours d'eau ont permis une plus grande densification de la strate arbustive en place (Tape *et al* 2012). De plus, une augmentation du couvert et de la croissance de plusieurs espèces arbustives ont été observées sur des glissements de terrain associés à la dégradation du pergélisol (« retrogressive thaw slumps » ou « cryogenic landslide » ; Lantz *et al* 2009, Frost et Epstein 2014), dans des lacs de fonte drainés (Marsh *et al* 2009), sur des pingos (Mackay et Burn 2011) et dans les traces laissées par le passage répété de véhicules motorisés (Kemper et MacDonald 2009). Ces exemples appuient tous la thèse que les perturbations d'origine naturelle ou anthropique peuvent contribuer à la densification de la strate arbustive. D'un autre côté, il existe des situations où certaines perturbations ont eu un effet négatif sur la strate arbustive. Par exemple, en modifiant considérablement le régime hydrique de la région à l'étude, la dégradation du pergélisol a réduit la quantité de sites propices à l'établissement et à la croissance des espèces arbustives de grande taille (bouleaux et saules) en Alaska (Lloyd *et al* 2003).

Outre les perturbations, la pression exercée par les herbivores pourrait elle aussi moduler la

réponse des espèces arbustives. L'effet des herbivores dépendra cependant de la taille et de la densité des troupeaux et de l'intensité du broutement (Speed *et al* 2010). Par exemple, il est raisonnable de croire que le caribou migrateur (*Rangifer tarandus* L) a le potentiel de moduler l'effet du climat sur la croissance des espèces arbustives parce qu'il fait généralement partie de grands troupeaux (ex. 430 000 individus dans le troupeau de la Rivière-aux-Feuilles en 2011 : décompte aérien du Gouvernement du Québec, données non publiées) et qu'il peut ingérer une grande quantité de tissus végétaux. En effet, des études expérimentales ont montré que l'effet positif du réchauffement des températures semble être largement contrebalancé par le broutement chez différentes espèces arbustives dont *Betula nana* (Post et Pederson 2008, Olofsson *et al* 2009), *Salix glauca* (Post et Pederson 2008) et *Vaccinium myrtillus* (Rinnan *et al* 2009). Cette pression exercée peut de ce fait favoriser la productivité des taxons non consommés, telles les poacées, et limiter la croissance des espèces préférées par les herbivores (Manseau *et al* 1996, Brathen et Oksanen 2001, Eskelinen et Oksanen 2006). En contrepartie, le passage répété des caribous peut mettre à nu le sol minéral (Boudreau et Payette 2004, Vistness et Nellemann 2008), créant de ce fait des lits de germination favorables pour différentes espèces arbustives (Forbes *et al* 2001).

À l'échelle locale, les différences observées dans l'étendue de la densification arbustive sont probablement associées à la topographie du terrain. En ayant une influence sur l'exposition au vent, le couvert de neige (son épaisseur et sa persistance dans la saison de croissance : Sonesson et Callaghan 1991, Shaver *et al* 1996), la disponibilité en nutriments (Shaver *et al* 1996) ainsi que l'humidité (Schimel *et al* 1999) et la température du sol (Romanovsky et Osterkamp, 1995), la topographie du paysage peut avoir un impact important sur la croissance et le recrutement des espèces végétales. En effet, Tremblay et collaborateurs (2012) ont mesuré une augmentation différentielle du couvert arbustif en fonction de l'altitude et de la pente (degrés et orientation).

1.3.4 Effets de la densification de la strate arbustive sur les communautés végétales

Malgré le récent engouement pour les effets du réchauffement climatique sur les

écosystèmes nordiques, il demeure toutefois de nombreuses lacunes dans notre capacité à prévoir les changements auxquels devra faire face l'EFT. Or, la compréhension de la dynamique de cette région est primordiale afin de prédire l'évolution du paysage subarctique. Parmi les différents impacts que la densification de la strate arbustive pourrait avoir sur son environnement, notons par exemple son influence sur la neige et le pergélisol. En effet, la hauteur et la densité de la strate arbustive peuvent sensiblement modifier l'accumulation, la durée ainsi que les propriétés physiques de la neige (Liston *et al* 2002, Pomeroy *et al* 2006, Marsh *et al* 2010). De ce fait, la neige s'accumule préférentiellement à proximité des peuplements arbustifs, permettant ainsi de limiter la pénétration du froid dans le sol (Sturm *et al* 2001b) et d'augmenter l'activité microbienne et la décomposition de la litière (Sturm *et al* 2001b). À l'été cependant, l'ombre générée par un couvert arbustif important diminuerait les températures du sol (Marsh *et al* 2010) et la profondeur de la couche active (Blok *et al* 2010). Même si les processus hivernaux semblent plus importants, il est nécessaire de considérer les effets de la strate arbustive en été et en hiver afin de déterminer un bilan net sur le pergélisol. De plus, une densification des peuplements arbustifs dans les régions arctiques et subarctiques pourrait augmenter la quantité de litière (Cornelissen *et al* 2007) et le taux de minéralisation de l'azote (Buckeridge *et al* 2010). Finalement, quoi que l'ombre produite par la strate arbustive puisse diminuer la pénétration de la lumière jusqu'au sol et donc limiter l'évaporation (Walker *et al* 2003), la présence de cette strate est généralement associée avec une augmentation de l'évapotranspiration, asséchant de ce fait le sol (Myers-Smith *et al* 2011a, Cranston et Hermanutz 2013).

En modifiant leur environnement immédiat, les arbustes ont le potentiel d'influencer les autres espèces végétales présentes dans les régions nordiques. Plusieurs études expérimentales ont montré qu'une augmentation du couvert arbustif réduisait l'abondance de plusieurs taxons végétaux (Pajunen *et al* 2012) ainsi que la richesse spécifique des sites étudiés (Klein *et al* 2004). En effet, la plupart des espèces vasculaires et cryptogames sont désavantagées lorsque la densité de la strate arbustive augmente (Cornelissen *et al* 2001, Walker *et al* 2006, Pajunen *et al* 2011, 2012), tandis que les poacées sont plus abondantes dans cette même situation (Walker *et al* 2006, Pajunen *et al* 2012). De plus, une forte densité d'arbustes est généralement associée à un faible établissement des plantules

d'espèces arborescentes (Anschlag *et al* 2008, Pérez-Devesa *et al* 2008). Au Québec subarctique, il a été montré que l'établissement des plantules d'épinette noire, principale espèce présente à l'EFT, est largement favorisé par la mise à nu du sol minéral (Greene *et al* 2004 ; Dufour-Tremblay et Boudreau 2011). Le rôle potentiel des espèces arbustives dans la régénération des espèces arborescentes de l'EFT pourrait ainsi limiter la transgression vers le nord de la limite des arbres, du moins à court terme.

En plus d'affecter la performance des autres espèces végétales, la densification de la strate arbustive pourrait influencer différentes populations animales. Par exemple, la densification de la strate arbustive peut avoir un effet négatif sur le caribou migrateur et les rennes en diminuant significativement le couvert lichénique (Joly *et al* 2007) ainsi qu'en augmentant les coûts associés au déplacement et à la quête de nourriture en hiver (Schmitz *et al* 2003). Par ailleurs, un plus grand couvert arbustif peut être avantageux pour certaines espèces s'en nourrissant, tels les orignaux, les lièvres et les lagopèdes (Tape *et al* 2010).

Un changement dans la structure des communautés végétales de l'EFT pourrait également avoir des impacts qui dépasseraient largement les frontières de cette région. En effet, les écosystèmes arctiques et boréaux sont connus pour leur grande influence sur la dynamique de l'atmosphère (Chapin *et al* 2000). Un changement dans la répartition des espèces arborescentes et arbustives pourrait entraîner une diminution de l'albédo et une augmentation subséquente de la température de l'atmosphère (boucle de rétroaction positive ; Bonan *et al* 1992, Chapin *et al* 2005, Sturm *et al* 2005). Des niveaux plus bas d'albédo au printemps et à l'été ont d'ailleurs déjà été enregistrés pour des régions où le couvert arbustif a augmenté (Chapin *et al* 2005, Loranty *et al* 2011). De plus, un couvert arbustif important augmente les températures du sol en hiver et accélère les processus de décomposition, permettant ainsi un relâchement important du carbone séquestré dans les couches profondes du sol (Mack *et al* 2004, Schuur *et al* 2007). En contrepartie, une augmentation du couvert arbustif pourrait aussi augmenter la quantité de carbone stocké dans la biomasse végétale (Mack *et al* 2004). Bien que le bilan net de ces effets ne soit pas connu, il va sans dire qu'une augmentation du couvert arbustif dans les régions nordiques aura des conséquences à l'échelle planétaire. Le rôle de la strate arbustive dans la

dynamique de cette région a été très peu étudié jusqu'à maintenant, et ce malgré le fait qu'elle occupe une part prépondérante de l'EFT. Son abondance ainsi que sa capacité à répondre rapidement aux changements environnementaux ont pourtant le potentiel de faire de cette strate un acteur de premier plan.

1.4 Le bouleau glanduleux : espèce structurante de l'EFT

Au Québec subarctique, le bouleau glanduleux (*Betula glandulosa* Michx) est sans contredit l'espèce arbustive la plus abondante. Dans cette région, il forme de larges peuplements denses où s'accumule une quantité importante de matière organique (de Groot *et al* 1997). De plus, on reconnaît à cette espèce une grande plasticité morphologique (Weis et Hermanutz 1988). Cette dernière lui permettrait de coloniser une vaste gamme de milieux, mais aussi d'avoir une aire de répartition atteignant l'île de Baffin (Porsild et Cody 1980). Dans la partie méridionale de son aire de répartition, le bouleau glanduleux arbore un port érigé et semble s'établir majoritairement par graines (13 332 graines/m²; taux de germination de 15 %; Weis et Hermanutz 1988). Par contre, à sa limite nordique, il dépasse rarement 20 cm et la production de graines y est largement diminuée (670 graines/m²; taux de germination de 2 %; Weis et Hermanutz 1988). La plasticité du bouleau glanduleux est également invoquée pour expliquer sa réponse rapide lors d'expérimentations simulant une augmentation des températures ou l'ajout de nutriments (ex. Bret-Harte *et al* 2001). Bien que plusieurs études s'attardent à la réponse des bouleaux arbustifs aux changements climatiques actuels, peu ont tenté d'établir un lien entre la croissance annuelle et la température. Pourtant, ce type d'analyse a montré des résultats intéressants dans le cas de *Betula emmanii* dans la péninsule du Kamtchatka (Dolezal *et al* 2010), où une corrélation entre les températures estivales et la largeur des cernes de cette espèce a été mise en évidence. L'adoucissement des températures estivales a également été bénéfique pour la croissance de *Betula nana* dans la partie nord-est de la Sibérie (Blok *et al* 2011) et en Alaska (Tape *et al* 2012). Si une telle relation entre la croissance du bouleau glanduleux et le climat pouvait être établie, les possibilités de reconstitution climatique dans l'Arctique canadien pourraient s'accroître considérablement.

1.5 Objectifs de la thèse

Les études descriptives (analyses de photographies aériennes et interprétation du NDVI), expérimentales (augmentation simulée des températures de l'air) et dendrochronologiques suggèrent que les environnements arctiques et subarctiques sont en pleine mutation. Au cœur de ces environnements, les espèces de la strate arbustive semblent avoir la capacité de répondre rapidement à un réchauffement des températures. L'objectif principal de cette thèse est donc d'étudier la dynamique récente de la strate arbustive dans un contexte de réchauffement climatique, en mettant l'accent sur l'étude du bouleau glanduleux. Le corps de cette thèse se divise en trois chapitres (chapitres 2 à 4), chacun ayant des objectifs spécifiques qui nous permettront de dresser un portrait global de la dynamique de la strate arbustive à l'écotone forêt boréale-toundra au Nunavik.

Le chapitre 2 a pour objectif spécifique de quantifier la densification de la strate arbustive depuis les 50 dernières années dans la région d'étude à l'aide de la comparaison de photographies aériennes datant de 1957 à une image satellitaire de 2008. Afin de distinguer d'éventuelles différences dans l'étendue de cette densification, celle-ci a été évaluée dans deux types d'environnement largement répandus dans l'aire d'étude : les terrasses sablonneuses et les sommets rocheux de faible altitude. De plus, une validation exhaustive sur le terrain nous permettra d'identifier la ou les espèces responsables de la densification de la strate arbustive.

Le chapitre 3 vise à identifier les variables environnementales responsables de l'hétérogénéité de la densification de la strate arbustive à l'échelle du paysage. Pour ce faire, une approche par sélection de modèles avec critère d'information d'Akaike a été utilisée. De surcroît, ce chapitre veut évaluer l'influence de cette densification sur l'abondance et la diversité des espèces arbustives non impliquées dans ce phénomène.

L'objectif spécifique du chapitre 4 est d'identifier les facteurs climatiques contrôlant la croissance radiale et axiale du bouleau glanduleux, principale espèce arbustive présente dans la région d'étude. À l'aide de techniques dendrochronologiques, la relation entre le climat et la croissance de cette espèce arbustive a été évaluée dans trois types

d'environnement différents (terrasses sablonneuses, sommets rocheux et combes à neige). Pour terminer, ce chapitre vise également à évaluer si l'augmentation de l'activité photosynthétique inférée par le NDVI (« Normalized Differential Vegetation Index ») dans la région d'étude est expliquée par l'augmentation de la croissance du bouleau glanduleux.

Le chapitre 5 consiste en une conclusion générale où les résultats probants ainsi que les perspectives qui en découlent seront exposés.

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CHAPITRE 2 Shrub expansion at the forest-tundra ecotone: spatial heterogeneity linked to local topography

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2.1 Résumé

La densification récente de la strate arbustive a été documentée dans plusieurs régions arctiques. Cependant, peu d'études se sont intéressées aux variations de ce phénomène à l'échelle locale. Cette étude a pour objectif de quantifier la densification de la strate arbustive à l'écotone forêt boréale-toundra (Québec, Canada) dans deux types d'environnements : les terrasses et les sommets (qui couvrent 70% de la superficie terrestre de la région) et d'identifier les espèces impliquées dans ce phénomène. La comparaison d'une mosaïque de photographies aériennes de 1957 (137 km²) et d'une image satellitaire de 2008 (151 km²) nous a permis de constater une densification de la strate d'intérêt pour les deux types d'environnement. La densification est cependant plus importante sur les terrasses que sur les sommets (21.6% vs 11.6%). Une validation terrain exhaustive révèle que *Betula glandulosa* Michx. est la principale espèce responsable de la densification arbustive dans la région. De plus, les nombreuses plantules observées sur les sites d'études suggèrent que le phénomène pourrait se poursuivre dans les prochaines années.

2.2 Abstract

Recent densification of shrub cover is now documented in many arctic regions. However, most studies focus on global scale responses, yielding very little information on the local patterns. This research aims to quantify shrub cover increase at northern treeline (Québec, Canada) in two important types of environment: sandy terraces and hilltops (which cover *ca.* 70% of the landscape) and to identify the species involved. The comparison of a mosaic of two aerial photographs from 1957 (137km²) and one satellite image taken in 2008 (151km²) revealed that both hilltops and terraces recorded an increase in shrub cover. However, the increase was significantly greater on terraces than on hilltops (21.6% vs 11.6%). According to ground truthing, the shrub cover densification is associated mainly with an increase of *Betula glandulosa* Michx. The numerous seedlings observed during the ground truthing suggest that shrub densification should continue over the next few years.

2.3 Introduction

Arctic and subarctic regions have been subjected to important changes over the last few decades (IPCC 2007a). Among the rapid changes observed, Myneni and collaborators (1997, 1998) were the first to report evidence of the pan-Arctic increase in vegetation cover. By analysing worldwide NDVI trends between 1981 and 1991, they showed that the greatest increase in photosynthetic activity occurred in regions above 50° N. Since then, this phenomenon has been observed for different regions (Alaska: Silapaswan *et al* 2001, Jia *et al* 2003, Verbyla 2008; Russia: Forbes *et al* 2010; Western Canada: Olthof and Pouliot 2010), over a longer time span (≥ 20 years: Jia *et al* 2003, Goetz *et al* 2005, Verbyla 2008, Forbes *et al* 2010, Olthof and Pouliot 2010), and at a better resolution ($= 1\text{km}^2$: Jia *et al* 2003, Olthof and Pouliot 2010). Moreover, recent NDVI studies revealed that the increase in photosynthetic activity is more important in regions dominated by erect shrub species (Raynolds *et al* 2006), a result corroborated by the comparison of aerial photographs and satellite images which reported an increase in shrub cover in Alaska (Sturm *et al* 2001a, Tape *et al* 2006) and northern Québec (Tremblay *et al* 2012).

Changes in shrub cover in arctic and subarctic regions are however likely to be spatially heterogeneous. In these regions, minor differences in the abiotic environment could translate into important differences in shrub survival, growth and reproduction. Local topography, one of the most influential features at the landscape level (Shaver *et al* 1996), will influence variables such as snow accumulation, duration of the snow cover (Sonesson and Callaghan 1991, Shaver *et al* 1996), nutrient availability (Shaver *et al* 1996), soil moisture (Schimel *et al* 1999) and soil temperature (Romanovsky and Osterkamp 1995), which can all have major impacts on plant growth and recruitment. Increase in shrub cover could then be a function of the different topographic features of the landscape. Such observations have been reported in northern Alaska (Tape *et al* 2006), where shrub cover increase was more important on hill slopes, in valleys and south-facing slopes. However, most of the studies used a spatial scale that does not provide insights on the importance of the local topography for shrub densification. Temporal NDVI analyses use NOAA-AVHRR (National Oceanic and Atmospheric Administration-Advance Very High Resolution Radiometer) satellite images with, at best, a 1km^2 -resolution (Jia *et al* 2003,

Olthof and Pouliot 2010). Furthermore, the NDVI reflects the change in photosynthetic activity without any distinction of the taxa implied. As the shrub cover increases in many arctic and subarctic regions (ACIA 2005, IPCC 2007b), it becomes necessary to understand how and where the changes occur. A better understanding of the importance of the local topography on the response of shrub communities is therefore important to refine our ability to predict future response of shrub communities to climate change.

The objective of this study was to quantify the change in shrub cover in subarctic western Québec over the last 50 years, if any. Specific objectives were (1) to determine if shrub cover has increased, (2) to identify the species implied in the cover change, and (3) to determine if the intensity of the change varies with the local topography (hilltops and terraces). Based on current knowledge, we hypothesized that there has been a non-uniform increase in shrub cover in the studied area, which is mostly attributable to *Betula glandulosa* Michx., the main erect shrub species.

2.4 Methods

2.4.1 Study area

The study area is located near the Boniface River research station (57°45'N, 76°20'W), 35km east of Hudson Bay and 10km south of the treeline in subarctic Québec, Canada (Figure 2.1). The region is located in the shrub subzone of the forest-tundra ecotone (Payette 1983), where black spruce (*Picea mariana* (Mill.) B.S.P.) is the main tree species and dwarf birch (*Betula glandulosa* Michx.) dominates the shrub layer. At the regional scale, shrub-lichen tundra is the dominant community, covering approximately 70% of well-drained sites (Payette *et al* 2008). This vegetation type is found mainly on slopes and exposed hilltops along with spruce-lichen woodlands. The forested stands, confined to more mesic environments, are remnants of a once more extensive forest cover (Payette and Morneau 1993). Fires were frequent during the Holocene period (Payette *et al* 2008), but were rather scarce over the last millennium due to cooler and wetter climatic conditions (Filion 1984). More recently, trampling from the Leaf River Caribou Herd (*Rangifer tarandus* L.) exposed mineral soil over substantial areas. Browsing evidence was however mostly observed on *Salix* species.

The nearest weather station (Inukjuaq Meteorological Station, 58° 28' N, 78° 05' W) recorded an annual mean temperature of -7°C for the 1970-2000 period, with the highest and lowest mean monthly temperatures recorded in July (10.2°C) and February (-25.2°C), respectively (Environment Canada 2010). Over this period, annual precipitation averaged 460mm, of which 44% fell as snow (Environment Canada 2010). The temperature trend in the region has however changed considerably over the last 50 years. Between 1969 and 1993, the region experienced a cooling trend at a rate of -0.03 °C yr⁻¹ while a warming trend (+0.09 °C yr⁻¹) was observed afterwards. This rapid change in temperature was also recorded for most of northern Québec (Chouinard *et al* 2007).

2.4.2 Ortho-photo analyses

Change in shrub cover was evaluated through the comparison of two aerial photographs

and a satellite image taken in July 1957 and 2008, respectively. The 2008 image is a Worldview-1 Standard Ortho-Ready panchromatic satellite image taken on July 15th, which covers 151km². The 1957 photos are two adjacent 9" x 9" aerial photos produced from high quality negatives stored at the National Air Photo Library of Canada and covering an area of 137km² (taken on July 29th, 1:40 000). Aerial photos were scanned at 1200 dpi for further analysis.

Aerial photographs and the satellite image were orthorectified in order to remove topographic distortions and to project them in the UTM 18 NAD 83 map projection. The orthorectification of the 2008 satellite image was carried-out with PCI GEOMATICS V.10.3 software and resulted in a 0.5m-resolution ortho-photo. The latter was then used as a template to rigorously match the 1957 aerial photos to the UTM projection. A 15m-resolution digital elevation model (DEM) of the study region generated by Natural Resources Canada was used as an elevation output. These manipulations were performed with the ALTA Photogrammetry Suite 7 software and resulted in a 1m-resolution 1957 ortho-photo. The spatial lag between the two ortho-photos is <1m. From here on, the satellite image and aerial photos are both referred to as ortho-photos.

In general, erect shrub species were easily detected by their darker shade and the roundish aspect of each individual (Figure 2.2), while trees were recognized by the triangular shape of their projected shade. Pale areas were mostly characterized by lichen and graminoid vegetation. Therefore, shrub cover identification was based on both the pixel colour and the texture of the ortho-photo. Preliminary observations of both ortho-photos suggested that the analyses should be restricted to non-forested, well-drained sites, because shrub cover was difficult to evaluate with accuracy in-between trees and in wetlands, riparian ecosystems and snowbeds. Of these non-forested well-drained sites, which cover *ca.* 70% of the landscape, two broad categories were retained: hilltops and sandy terraces. Hilltops are characterized by the presence of arctic-alpine species and exposed mineral soil. Sandy terraces, located on the river's margin, are low altitude sites dominated by shrub, lichen and herbaceous species. Prior to the field season, the 113km² overlapping zones of the two ortho-photos were scrutinized to identify potential sites belonging to either category. Once

in the field, 59 of the 106 pre-identified sites were selected to evaluate shrub cover change from 1957 to 2008 (26 hilltops and 33 terraces, Appendix A). Sites were excluded when they: *i.* did not correspond with the given definition of one of the two environments, and/or *ii.* were not easily accessible by foot from the river. On average, exposed hilltops and terraces covered 1.2 ha and 1.1 ha, respectively. The 59 sites covered a total area of 671.7 ha, *i.e.* 58.2% of the total well-drained non-forested area of the study area.

In the laboratory, each of the 59 study sites was delimited in respect to the ground truthing and drawn using ArcGIS 9.3 (by ESRI; see section 2.3; Figure 2.3). The analyzed area for each site, ranging from 0.5 ha to 2.1 ha, reflects the natural variability in site sizes. Then, a grid consisting of a series of 16m²-cells (4m x 4m) was overlaid on both ortho-photos. Inside the site's perimeter, shrub cover was estimated within each cell and assigned to one of the following cover classes: (1) 0%, (2) 1-25%, (3) 26-50%, (4) 51-75%, and (5) 76-100%. For every given site, shrub cover was calculated for both ortho-photos by averaging the median value of the cover class assigned to each cell. Shrub cover change over the last 50 years (delta) was then calculated as the difference in shrub cover between 2008 and 1957. The evaluation of shrub cover was carried-out by the same observer for every site and was recorded in Excel tables with respect to the spatial position of each cell.

Rather than degrading the 2008 ortho-photos to match the resolution of the 1957 ortho-photo, we decided to conduct the analyses at the finest resolution for each ortho-photo (1m and 0.5m for 1957 and 2008, respectively) in order to retain as much information as possible. However, to evaluate if different resolutions could influence shrub cover evaluation, we conducted a supplemental analyses for ten sites after having degraded the 2008 ortho-photo to a 1.0m resolution (Aggregate tool in ArcGIS, which uses cubic convolution resampling). Shrub cover evaluations for both the degraded and non-degraded 2008 ortho-photos were compared.

2.4.3 Ground truthing

An extensive ground truthing was carried-out in order to identify which species were

implicated in the shrub cover change, if any, and to evaluate our accuracy in evaluating shrub cover on the 2008 ortho-photo. At each of the 59 sites, four 60m transects were delimited from the centre of the site and extended respectively towards the four cardinal points (N, E, S, W; Figure 2.3). The position of each transect was determined with a high-precision GPS (Leica, Model GS20, ± 30 cm). Tree and shrub species were recorded at every centimetre along the transects. Each species cover could then be calculated for each site by dividing the number of centimetres on which it was recorded by the total number of centimetres surveyed (24 000cm).

To determine our accuracy in evaluating shrub cover on the 2008 ortho-photo, we conducted an additional photo-interpretation analysis. We overlaid a 1m²-cell grid over the 2008 ortho-photo (5 hilltops and 5 terraces) and we evaluated the shrub cover in every single cell touching the linear transects surveyed in the field. We used 1m² cells to optimize the comparison with the results from the ground truthing exercise, as larger cell size would include more variability.

2.4.4 Statistical analysis

Differences in shrub cover between terraces and hilltops (in 1957, in 2008 and for the delta values) and in dwarf birch cover from ground truthing data were tested using one-sample *t*-tests. Changes in shrub cover from 1957 to 2008 in both environments and between the different validation procedures (resolution and field and ortho-photo results) were evaluated using paired *t*-tests. The delta frequency distribution of terraces and hilltops were compared using a Kolmogorov-Smirnov test.

2.5 Results

2.5.1 Shrub cover change

In 1957, hilltops had a greater shrub cover than terraces (35.3% vs 28.6%; Table 2.2; $t(57) = -2.39$, $P < 0.05$; Figure 2.4, Table 2.1). From 1957 to 2008, shrub cover increased in most of the studied sites (31/33 terraces, 23/26 hilltops), with a substantial increase ($>15\%$) in 27 terraces and 10 hilltops. This increase resulted in a significant difference in shrub cover between 1957 and 2008 in both environments (terraces: 28.6% vs 50.2%; $t(32) = -10.27$, $P < 0.01$; hilltops: 35.3% vs 46.9%; $t(25) = -6.67$, $P < 0.01$). Moreover, terraces showed a greater increase than hilltops (21.6% vs 11.6%; $t(57) = -3.52$, $P < 0.05$) and, as a result, shrub cover in 2008 did not significantly differ between hilltops and terraces (46.9% vs 50.2%; $t(57) = 1.68$, $P = 0.10$; Figure 2.4). There was no significant difference between the delta frequency distribution of terraces and hilltops (Kolmogorov-Smirnov test: $P = 0.96$). However, terraces tended to have a higher proportion of cells showing a large increase in shrub cover ($\text{delta} = 2, 3$, and 4 ; Figure 2.5).

Differential resolution between the 2008 and 1957 ortho-photos did not have a major impact on shrub cover evaluation. On hilltops, 68.2% of the cells were assigned to the same cover class, while 14.3% and 17.1% were assigned respectively to the cover classes directly above or below. On terraces, 62.5% of the cells were assigned to the same cover class, while 22.2% and 14.4% were respectively assigned to the cover classes above or below. For both environments, $<1\%$ of the cells were assigned to other cover classes (± 2 classes). Overall, the observed differences in shrub cover at the site scale ranged from -4.8% to 4.1% , shrub cover being under-evaluated for 6 sites and over-evaluated for 4 sites. Differences in shrub cover were not statistically significant ($t(9) = 0.89$, $P = 0.39$).

2.5.2 Species implicated

Dwarf birch was the major shrub species recorded during ground truthing. On average, dwarf birch covered 36.7% of the surveyed area. The cover of this species ranged from 13.2% to 58.6% and was significantly higher on terraces than on hilltops (40.1% vs 32.5%;

$t(57) = 2.48$, $P < 0.05$). Dwarf birch was the only species found at every site. Moreover, several dwarf birch seedlings not detected on the ortho-photos were found in open areas in both terraces and hilltops. The other most abundant species on terraces were *Rhododendron tomentosum* Harmaja, *Empetrum nigrum* L., and *R. groenlandicum* Oeder, with a cover of 7.0%, 6.3% and 4.9%, respectively. On hilltops, *R. tomentosum*, *E. nigrum*, and *Vaccinium uliginosum* L. were the other most abundant species, with a cover of 10.0%, 8.7% and 2.5%, respectively. *Salix planifolia* Pursh, *S. glauca* L., *S. uva-ursi* Pursh, *Alnus viridis* ssp. *crispa* (Ait.) Turrill, *Diapensia lapponica* L., *Kalmia procumbens* L., *Arctous* sp., and *Rubus chamaemorus* L. were also recorded in the vegetation surveys on both terraces and hilltops, but covered less than 2.1% of the surveyed area.

Shrub cover evaluation inside the 1m² cell touching the transects used for ground truthing closely matched the dwarf birch cover evaluated in the field (differences ranging from - 5.5% to 5.5%, $t(9) = 0.71$, $P = 0.49$). However, it was lower than the total shrub cover recorded in the field for 9 of the 10 sites (Table 2.2; $t(9) = 5.16$, $P < 0.01$). Such results strongly suggest that the perceived shrub cover on the ortho-photos corresponds to the dwarf birch cover and not to the total shrub cover.

2.6 Discussion

Our results indicate an increase in shrub cover over the past 50 years at the northern limit of the forest-tundra ecotone in subarctic Québec. This finding corroborates other studies using a similar method conducted in different regions of the Arctic (Alaska: Sturm *et al* 2001a, Tape *et al* 2006; northern Québec: Tremblay 2010; Russia: Forbes *et al* 2010) and studies which revealed a major increase of the NDVI over the last few decades (Jia *et al* 2003, Verbyla 2008).

2.6.1 *Betula glandulosa*, a key species for shrub expansion

The observed increase in shrub cover is mainly attributable to dwarf birch, a species previously identified as one of the key species in pan-arctic shrub densification (Tape *et al* 2006). Dwarf birch was found at all sites and was the dominant shrub species at 56 out of 59 sites.

Dwarf birch's fast response to environmental change could be linked to its growth plasticity, clonal growth and reproduction potential. As shown by Bret-Harte *et al* (2001), dwarf birch generates numerous leaf-producing long shoots, which allows it to rapidly take advantage of experimental fertilization and warming treatments. It can also reproduce asexually via clonal growth, with stems producing adventitious roots when over-grown by adjacent vegetation (Shaver and Cutler 1979). It also produces an abundant seed rain (>13 000 seeds/m²; Weis and Hermanutz 1988), and seed germination is higher under experimental warming (Vaartaja 1959). In fact, several seedlings were observed in the field, which suggest that the densification should continue in the upcoming years.

2.6.2 Potential causes of shrub expansion: climate change, fire or caribou?

The recent increase in temperature is the most likely factor explaining the shrub expansion in the Boniface River region. To the best of our knowledge, climate warming is the only large-scale disturbance recorded in the region over the last few decades and, therefore, the only one able of promoting a regional response of such intensity. The warming trend

observed since the 1990s has already triggered an increase in black spruce seed viability in the region (Dufour-Tremblay and Boudreau 2011) and preliminary dendrochronological analyses revealed an important increase in radial growth since the mid 1990s. Many studies have demonstrated a similar growth increase for other shrub species under extensive warming (*Hippophae rhamnoides* L.: Xiao *et al* 2007, *Empetrum nigrum* ssp. *hermaphroditum* Hagerup: Bär *et al* 2008, *Artemisia tridentata* Nutt.: Poore *et al* 2009, *Salix lanata* L.: Forbes *et al* 2010, *Juniperus nana* Willd.: Hallinger *et al* 2010).

Besides improving radial and vertical growth, climate warming has many indirect effects that can be beneficial for shrub species. For example, an increase in temperature is known to enhance decomposition rate and nutrient cycling (Chapin and Shaver 1996, Hobbie 1996, Bret-Harte *et al* 2001, 2002, Wahren *et al* 2005). Combined with the capacity of birch litter to promote nitrogen availability (Buckeridge *et al* 2010), shrub growth can be largely enhanced (Jonasson *et al* 1999, Gordon *et al* 2001, Sturm *et al* 2005).

Winter events could also play a major role in the observed pan-Arctic shrub densification. The abrasive effect of windblown ice particles may limit the vertical growth of erect species (Sonesson and Callaghan 1991). Thicker snow cover under large shrub patches enhances decomposition during winter because of its insulating effect (Liston *et al* 2002) and may also result in greater water availability at the beginning of the growing season. In fact, differential snow accumulation, one of the most important environmental factors for plant growth in subarctic regions (Payette *et al* 1973), could at least partially explain why shrub cover increased significantly more on terraces than on hilltops. As they are more exposed to wind, hilltops have thinner snow cover, which could result in greater winter damage to aboveground biomass because of mechanical breakage of exposed tissues (Marchand and Chabot 1978) and winter desiccation (Sonesson and Callaghan 1991). On the other hand, individuals established on terraces are protected by a thicker snow cover and the reduced importance of wind is believed to allow dwarf birch individuals to grow rapidly and to expand.

Fire and large herbivores are among other disturbances that could be considered to explain

this shrub densification. The Boniface River area has experienced massive deforestation in the last few millennia because of the combined effects of fire and climate. The climatic cooling of the last 3000 years prevented black spruce from producing viable seeds that would have ensured its regeneration after the frequent fires of the Holocene period (Payette and Gagnon 1985, Gajewski *et al* 1993, Payette *et al* 2001). Fires are however unlikely to have triggered the recent shrub densification, as few fires occurred over the last millennium in the study region (Payette *et al* 2008). In fact, some of the study sites did not burn for at least 1300 years.

On a shorter time scale, the role of large herbivores in shrub expansion might also be given some consideration. Caribou (*Rangifer tarandus* L.) activity in the study area was high from the mid-1990s to the mid-2000s. Although caribou browsing can inhibit shrub performance, caribou trampling creates suitable seedbeds for dwarf birch by exposing the mineral soil. In fact, numerous newly established seedlings were observed in old caribou trails. The absence of suitable seedbeds was hypothesized by Parnikoza and collaborators (2009) to explain the halted expansion of two shrub species in Antarctica. However, because dwarf birch expansion was observed on sites with or without caribou activity evidence, it strongly suggests that caribou activity did not trigger shrub expansion.

2.7 Conclusion

This research shows an increase in shrub cover in the last 50 years for the studied region. Exhaustive ground truthing allowed us to identify dwarf birch as the main species implicated in this phenomenon. We also demonstrated that the shrubification is non-uniform across the landscape, with terraces promoting a higher shrub densification during the last decades. Further studies are now warranted to understand the processes at play in subarctic shrub densification. Does expansion rely mainly on clonal growth or on sexual reproduction? What is the spatial pattern of shrub expansion? Our ability to predict changes at the landscape level depends on our ability to understand the ecological processes underlying the observed changes.

2.8 Acknowledgments

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2.9 Tables

Table 2.1 Shrub cover change results for terraces (33 sites) and hilltops (26 sites).

Terraces				Hilltops			
Site	Shrub cover 1957 (%)	Shrub cover 2008 (%)	Change (%)	Site	Shrub cover 1957 (%)	Shrub cover 2008 (%)	Change (%)
1	16.0	32.1	16.1	11	20.8	44.7	23.9
2	12.5	27.8	15.3	28	22.5	46.0	23.5
3	10.0	38.2	28.2	29	33.0	40.5	7.4
4	8.2	55.6	47.4	30	35.6	44.3	8.7
5	24.6	45.7	21.2	31	36.0	47.0	11.0
6	11.3	49.6	38.3	32	31.5	34.9	3.4
7	29.7	50.1	20.4	34	39.1	59.2	20.1
8	25.6	60.5	34.9	36	38.4	45.2	6.8
9	26.6	43.7	17.1	38	41.6	44.8	3.2
10	30.0	46.8	16.8	42	50.4	46.1	-4.3
12	43.0	62.7	19.8	43	43.6	52.9	9.3
13	40.8	57.2	16.4	45	45.8	57.3	11.4
14	27.3	48.8	21.5	48	42.6	41.6	-1.1
15	38.9	57.6	18.7	52	46.7	47.8	1.1
17	25.2	50.7	25.5	55	48.8	47.6	-1.2
33	27.4	63.5	36.1	56	40.8	49.5	8.8
37	41.4	35.5	-5.9	59	39.3	49.3	10.0
41	51.9	44.9	-7.0	88	31.5	40.1	8.6
46	42.9	64.2	21.3	90	33.7	51.6	17.8
47	19.1	49.7	30.6	97	28.6	44.8	16.1
49	25.0	45.4	20.4	98	22.5	49.4	26.9
50	27.4	49.0	21.6	99	30.9	50.2	19.3
51	48.2	56.9	8.7	100	31.5	49.6	18.1
58	45.0	58.4	13.4	102	29.7	45.1	15.4
86	39.9	50.2	10.3	103	19.9	48.6	28.7
87	44.1	55.4	11.4	106	33.2	42.3	9.1
89	33.9	57.4	23.5				
91	31.6	50.0	18.4				
94	14.8	52.7	37.8				
95	11.2	51.4	40.2				
96	16.7	56.6	39.9				
101	30.5	47.3	16.8				
105	23.0	40.6	17.6				
Mean	28.6	50.2	21.6		35.3	46.9	11.6

Table 2.2 Results of the validation analyses. First, shrub cover was evaluated on the non-degraded (0.5m resolution) and the degraded (1m resolution) 2008 ortho-photos. Second, shrub cover evaluated on the 2008 ortho-photo (1m² cell) was compared to ground thruthing results (total shrub cover and dwarf birch cover).

Type of environment	Site	Shrub cover estimated from ortho-photos		Cover estimated with 2008 ortho-photo (%)	Observer over- or underestimation			
		1957 (%)	2008 (%)		Cover estimated from linear releves (%)			
					Total shrub cover (%)	Dwarf birch cover (%)	Cover ortho-photo - total cover (%)	Cover ortho-photo - birch cover (%)
Terrace	10	30.0	46.8	21.2	43.9	22.8	-22.7	-1.6
	12	43.0	62.7	48.9	64.4	45.6	-15.5	3.3
	14	27.3	48.8	34.7	42.5	33.0	-7.8	1.7
	91	31.6	50.0	48.7	85.5	53.6	-36.8	-4.9
	95	11.2	51.4	30.2	28.3	27.6	1.9	2.6
Hilltop	36	38.4	45.2	44.4	90.4	44.3	-46.0	0.1
	43	43.6	52.9	31.6	53.6	33.2	-22.0	-1.6
	56	40.8	49.5	47.5	65.7	47.7	-18.2	-0.2
	98	22.5	49.4	29.2	53.8	23.7	-24.6	5.5
	106	33.2	42.3	28.0	49.8	33.5	-21.8	-5.5

2.10 Figures

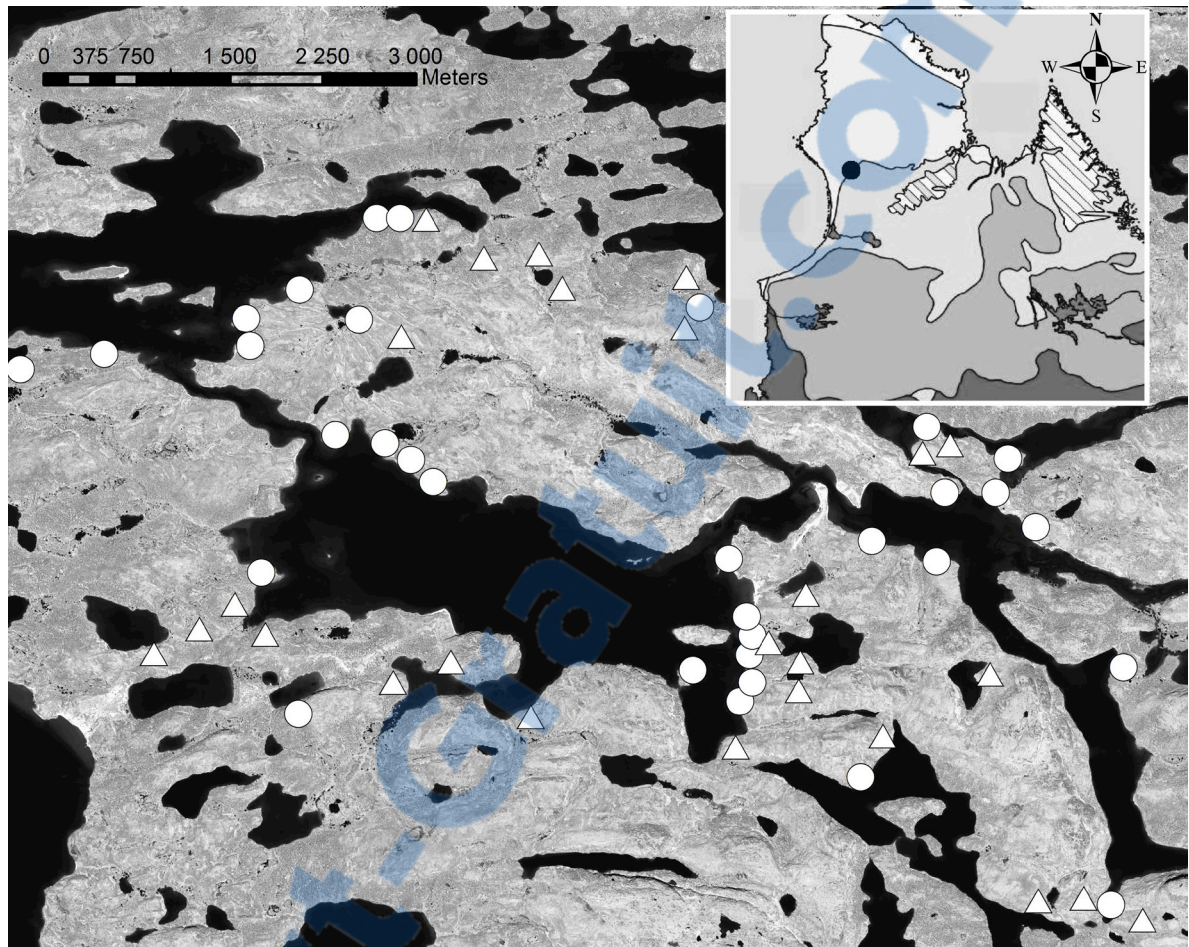


Figure 2.1 Satellite image of the Boniface River region at the forest tundra ecotone in subarctic Québec. The terraces (circles, 33) and hilltops (triangles, 26) used in this study are identified on the map. The study region is located at the forest-tundra ecotone, *ca.* 10km south of the treeline.

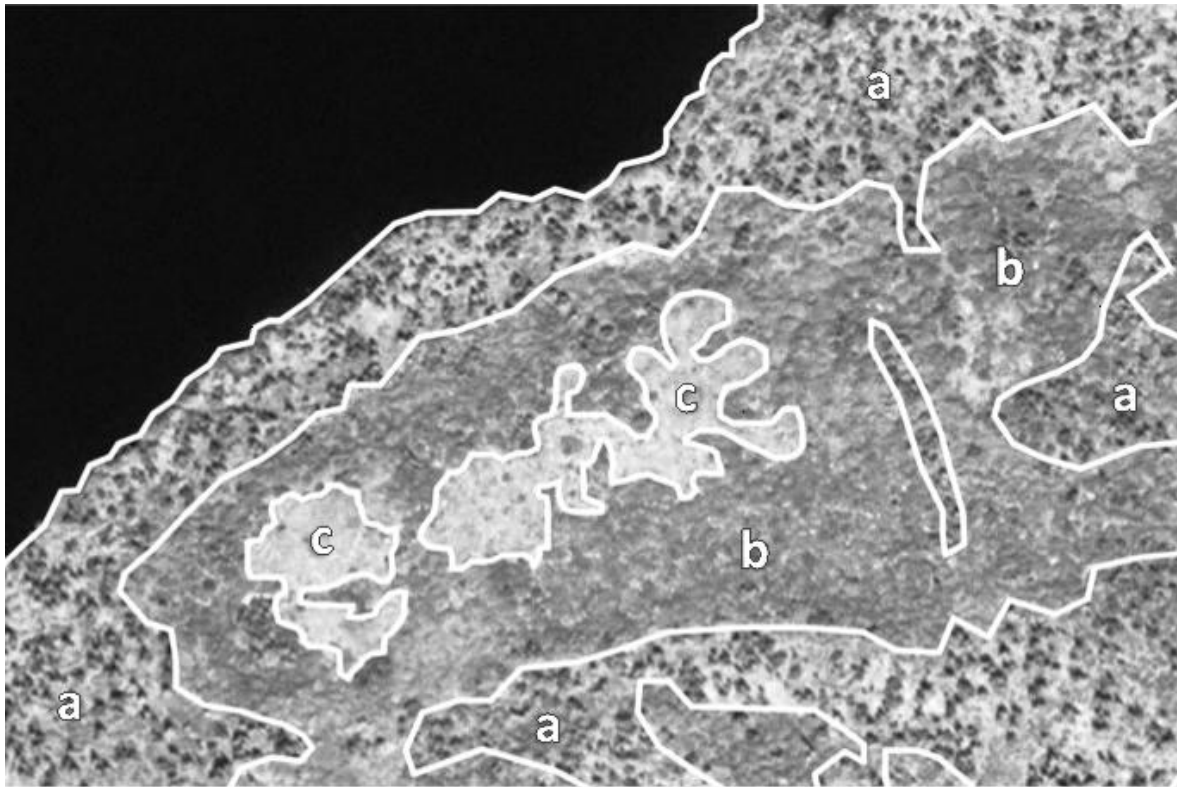


Figure 2.2 Detail of the 2008 ortho-photo showing (a) tree-covered areas, (b) shrub-covered areas, and (c) open areas mostly colonized by lichens, herbaceous species and some shrubs.

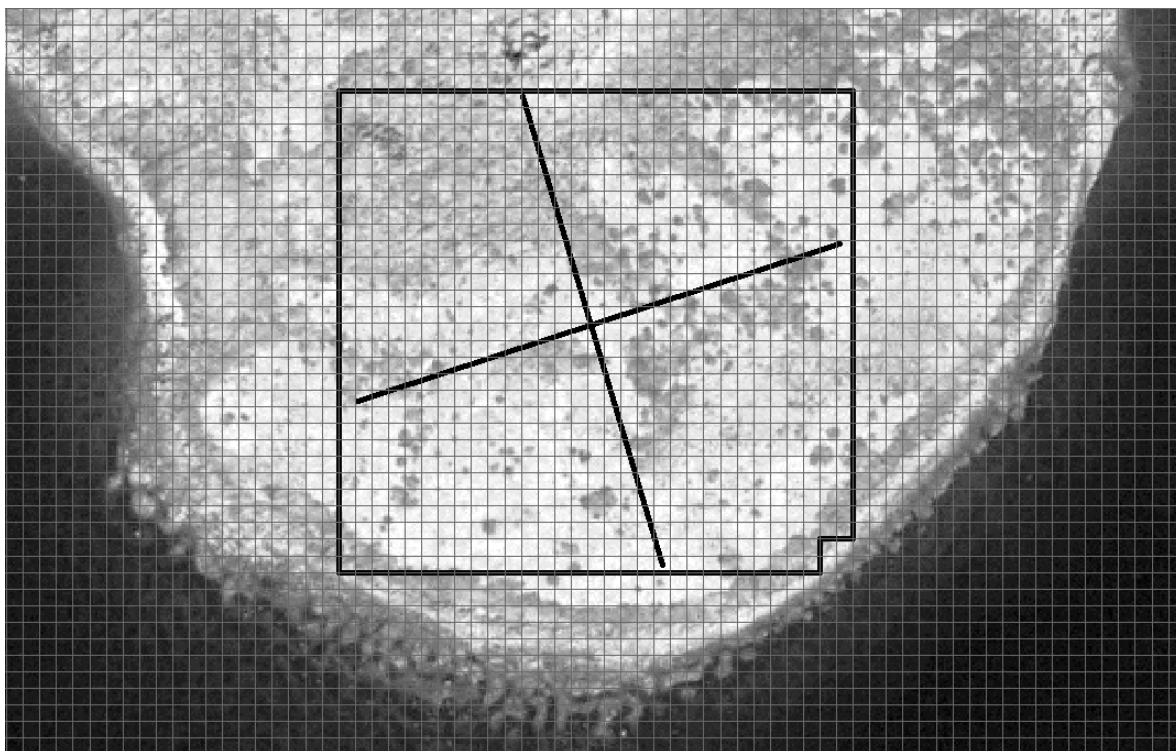


Figure 2.3 Satellite image of a sandy terrace (Site 1) over which a 16m²-cell grid was overlaid. The two perpendicular lines represent transects along which linear surveys were conducted. Outer black line shows the site's perimeter.



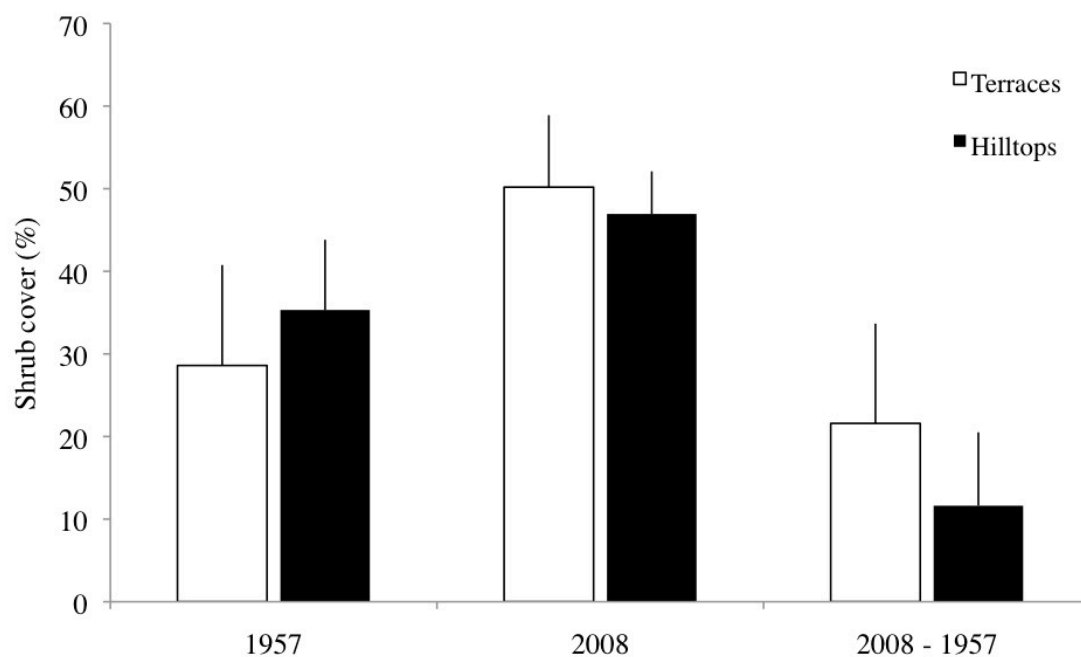


Figure 2.4 Shrub cover on terraces and hilltops in 1957, in 2008 and the increase from 1957 to 2008 as evaluated on the two ortho-photos. Mean $\pm$ 1 st. dev.

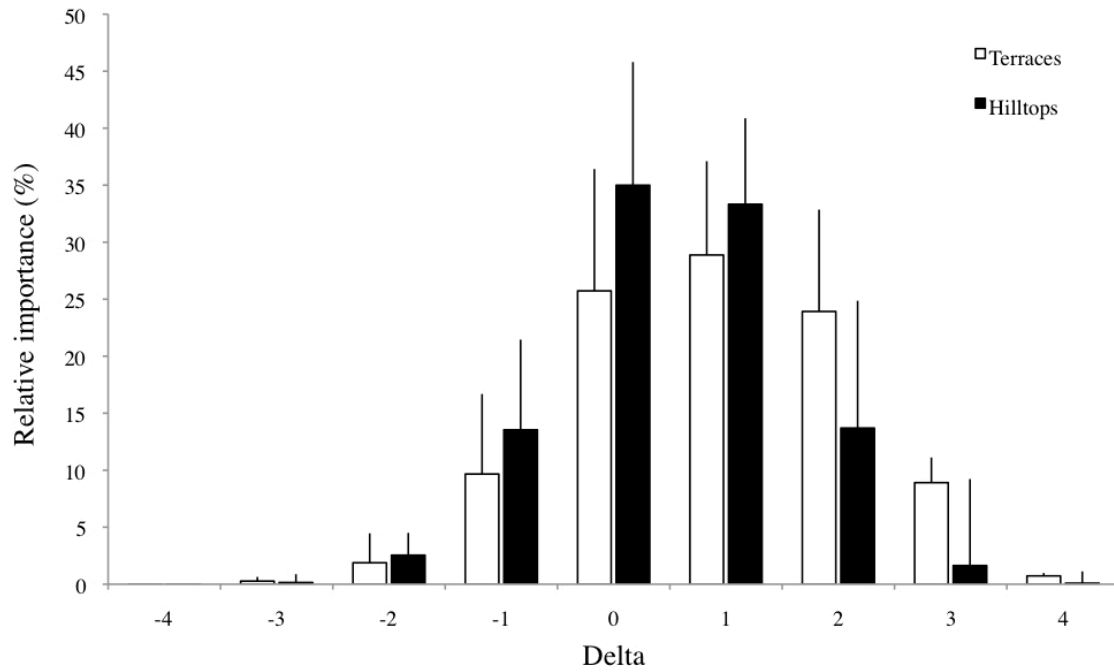


Figure 2.5 Frequency distribution of each delta value (2008 cover - 1957 cover) for terraces and hilltops. Percentage represents the average of the 33 terraces and 26 hilltops, respectively.

CHAPITRE 3 Shrub densification heterogeneity in subarctic regions: the relative influence of historical and topographic variables

Soumis sous :

Ropars P, Lévesque E & Boudreau S (2015) *Ecoscience*

3.1 Résumé

Bien que la densification de la strate arbustive soit un phénomène fréquemment observé dans les régions nordiques, son ampleur varie à l'échelle du paysage. Au Québec subarctique (Canada), où le bouleau glanduleux (*Betula glandulosa* Michx.) est la principale espèce responsable de ce phénomène, les causes et les conséquences de l'hétérogénéité de la densification de la strate arbustive sont méconnues. Cette étude a pour objectifs d'identifier les facteurs environnementaux expliquant la densification différentielle du bouleau glanduleux et d'évaluer l'influence de cette densification sur l'abondance et la diversité des autres espèces arbustives présentes. Nous avons utilisé la sélection de modèle avec critère d'Akaike pour classer différents modèles écologiquement valables incluant des variables topographiques, historiques et édaphiques. L'influence de la densification du bouleau glanduleux a été évaluée à l'aide de régressions linéaires. Nous avons trouvé que le modèle le plus plausible pour expliquer l'hétérogénéité de la densification du bouleau glanduleux dans l'ouest du Nunavik incluait des variables historiques (couvert arbustif initial, temps écoulé depuis le dernier feu) et topographique (type d'environnement). Parmi ces facteurs, seul le couvert initial d'arbustes avait une influence significative et positive sur la densification du bouleau glanduleux. Une augmentation du couvert de bouleau glanduleux a eu une influence négative sur le couvert des autres espèces arbustives. Cependant, aucune relation n'a été trouvée entre la densification du bouleau glanduleux et la richesse spécifique des autres espèces arbustives, suggérant que la densification observée n'est pas suffisamment importante pour exclure d'autres espèces moins compétitives.

3.2 Abstract

Expansion of erect shrub species is widely reported in northern regions, though its extent varies across the landscape. In subarctic Québec (Canada), where dwarf birch (*Betula glandulosa* Michx.) is the main species responsible for shrub expansion, little is known about the causes and consequences of this phenomenon. This study aims to identify the drivers of dwarf birch densification heterogeneity at the landscape level and to evaluate the influence of this densification on other shrub species' abundance and diversity. We used model selection using Akaike's information criterion to rank ecologically relevant predefined models that includes topographic, historical and edaphic variables. The influence of dwarf birch densification was evaluated through regression analysis. We found that the best model explaining the heterogeneity in dwarf birch densification in western Nunavik includes factors related to both historical conditions (initial shrub cover, time elapsed since last wildfire) and topography (type of environment). Among these factors, only the initial shrub cover had a significant positive influence on the shrub densification. Increase in dwarf birch cover was found to negatively influence the cover of other shrub species. However, no relation was found between dwarf birch densification and other shrub species richness, suggesting that the densification did not yet lead to the exclusion of less competitive shrub species.

3.3 Introduction

Greening of terrestrial ecosystems in response to climate change has been observed throughout the northern circumpolar region (Myers-Smith *et al* 2011a and references cited therein). Repeated aerial photograph comparisons (Sturm *et al* 2001a, Tape *et al* 2006, Beck and Goetz 2011, Ropars and Boudreau 2012, Tremblay *et al* 2012) and NDVI analyses derived from satellite images (Raynolds *et al* 2006, Forbes *et al* 2010, McManus *et al* 2012, Fraser *et al* 2014) revealed that this greening trend is mainly associated with the rapid expansion of erect shrub species. This expansion occurs either via (1) densification of pre-existing shrub patches, (2) increase in vertical growth or (3) northward/upward advance of the shrubline (Myers-Smith *et al* 2011a). These results are in accordance with numerous experimental studies that identified deciduous shrubs as one of the most responsive plant functional groups to warmer temperatures (Bret-Harte *et al* 2001; Jónsdóttir *et al* 2005; Wahren *et al* 2005, Elmendorf *et al* 2012b).

An increase in the abundance (i.e. densification) of erect shrub species can lead to changes in the abiotic environment, which in turn alters the dynamics of plant communities. In winter for instance, erect shrubs favor greater snow accumulation and modify snow properties, thereby influencing soil thermal regime, growing season length, soil humidity and microbial activity (Sturm *et al* 2005), even if the link between the latter and shrub abundance seems weaker than previously thought (Myers-Smith and Hik 2013). Experimental studies showed that an increase in shrub cover resulted in a decrease in understory plant species richness (Klein *et al* 2004) and cover (Cornelissen *et al* 2001, Walker *et al* 2006, Pajunen *et al* 2011). On the other hand, forbs and graminoids were positively correlated with shrub cover in other studies (Walker *et al* 2006, Pajunen, *et al* 2012), a phenomenon likely associated with their higher tolerance to light limitation (Oksanen and Virtanen 1997). While other studies have focused on the impact of shrub encroachment on understory plant species (Baez and Collins 2008, Pajunen *et al* 2011; Pajunen *et al* 2012), few focus specifically on its influence on other shrub species (but see Lavallée, 2013).

Although observed at several sites throughout the northern regions, shrub densification is heterogeneous at both regional and local scales. At the regional scale, shrub expansion heterogeneity is likely associated with species-specific responses to non-uniform warming trends (Epstein *et al* 2004b), since species showing greater morphological plasticity appear to be more responsive to improved environmental conditions (Bret-Harte *et al* 2001). Spatial heterogeneity may also be associated with different herbivory pressures since large herbivores can significantly reduce the abundance or, at least, inhibit the expansion of their preferred species (Brathen and Oksanen 2001, Post and Pedersen 2008, Plante *et al* 2014).

At the local scale, the extent of shrub densification is likely associated with small differences in local topography that result in site-specific abiotic environments. Indeed, Tremblay *et al* (2012) showed that shrub densification occurred at varying degrees across the landscape near Kangiqsualujjuaq (north-eastern Nunavik) in response to differences in altitude, slope and aspect, while Ropars and Boudreau (2012) reported a greater increase in shrub cover on low altitude terraces (21.6%) compared to exposed hilltops (11.6%) in the Boniface River area (western Nunavik). In Northern Alaska, Tape *et al* (2012) explained the differences observed in shrub densification with variable nutrient supply, which is closely related to topography. Local topography modulates wind exposure, snow cover (depth and duration; Sonesson and Callaghan 1991, Shaver *et al* 1996), nutrient availability (Shaver *et al* 1996), soil moisture (Schimel *et al* 1999), as well as soil temperature (Romanovsky and Osterkamp 1995) and, therefore, might have major impacts on plant growth and recruitment. Recent disturbances, such as wildfire, have also been found to facilitate shrub densification and vertical growth in Northwestern Alaska (Racine *et al* 2004) and in the Mackenzie Delta region, Northwest Territories (Lantz *et al* 2010). In the shrub and forest tundra, wildfires expose new seedbeds, releasing nutrients trapped in the living vegetation and creating opportunities for seedling establishment in communities where recruitment is otherwise limited (Zasada *et al* 1983, Hobbie and Chapin 1998, Gough 2006). Like wildfires, caribou trampling may also expose mineral soil (Boudreau and Payette 2004, Vistness and Nellemann 2008) and therefore create suitable seedbeds for shrub individuals.

In order to better predict the impacts of climate change on subarctic plant communities, it becomes necessary to understand the causes and consequences of erect shrub species densification. Therefore, this study aims to identify the abiotic variables driving the local scale heterogeneity in the densification of *Betula glandulosa* Michx. (hereafter referred to as dwarf birch), the main species responsible for shrub densification in Nunavik (Ropars & Boudreau 2012). In addition, we aim to evaluate the influence of dwarf birch densification on abundance and diversity of other shrub species. Based on current knowledge, we hypothesize that (1) topographical variables will explain the heterogeneity in dwarf birch densification and that (2) dwarf birch densification will negatively influence the abundance and diversity of other shrub species.

3.4 Methods

3.4.1 Study area

The study area is located in subarctic Québec (Canada), 35 km east of Hudson Bay and 10 km south of the Arctic treeline (Figure 1, 57° 45' N, 76° 20' W). The area belongs to the shrub subzone of the forest-tundra ecotone (FTE; Payette 1983). Dominant at the regional scale, the shrub-lichen tundra community covers *ca* 70% of the well-drained sites (Payette *et al* 2008) and is mainly found on sandy terraces and low altitude hilltops. Dwarf birch, the most abundant shrub species, is mainly responsible for the recent shrub expansion in the region (Ropars and Boudreau 2012) as well as in eastern subarctic Québec (Tremblay *et al* 2012). The remaining well-drained sites are colonized by lichen-spruce woodland and krummholz (*Picea mariana* (Mill.) B.S.P), whereas spruce-moss stands are confined to protected and well-watered areas (Payette and Morneau 1993). More widely distributed at the beginning of the Holocene, these stands have been gradually decimated by the combined effect of wildfires and harsher climatic conditions over the last 3000 y. Wildfires were frequent in the region between 2040 and 890 cal. BP (Arseneault and Payette 1997a, Arseneault and Sirois 2004), but the cooler and wetter conditions of the last 1000 y as well as the reduced forested cover resulted in a lower wildfire frequency over the last millennium (Filion 1984). Migratory caribou (*Rangifer tarandus* L.) were frequently encountered until *ca* 2005 and their repeated trampling exposed patches of mineral soils (Dufour-Tremblay and Boudreau 2011). While dwarf birch is part of the caribou diet (Crête *et al* 1990, Manseau *et al* 1996), browsing evidences are mostly restricted to *Salix* species in the studied region.

The nearest weather station (Inukjuag Meteorological Station, 58° 28' N 78° 05' W; 130 km northwest of the study site) recorded an annual mean temperature of -7°C for the 1971-2000 period, with the highest and lowest mean monthly temperatures recorded in July (9.4°C) and February (-25.8°C), respectively (Environment Canada 2013). Annual precipitation averages 460 mm, of which 42% falls as snow (Environment Canada 2013). Known for its relatively stable temperature during most of the 20th century, the region has experienced extensive warming since the early 1990's (Chouinard *et al* 2007).



3.4.2 Site selection

For this study, we focused on 2 types of well-drained non-forested sites, exposed hilltops and sandy terraces. We focused on terraces and hilltops because they are widespread in the study area, covering approximately 70% of the landscape. Sandy terraces (hereafter referred to as terraces) are well-drained sites located along the Boniface River covered by lichens and graminoids with large patches of shrub species. Low-altitude hilltops are characterized by the presence of arctic-alpine plant species and evidence of periglacial processes such as frost heaves. Prior to the field season, we pre-selected 106 potential sites (53 terraces and 53 hilltops) using a 113-km² Worldview-1 Standard Ortho-Ready panchromatic orthorectified satellite image (resolution 0.5 m). Once in the field, 59 of these sites were selected for further analysis (33 terraces and 26 hilltops; Figure 1). Sites were excluded when they did not correspond with the given definition of one of the 2 environments and/or because they were not within walking distance (> 3km) of the river. Initial shrub cover and shrub densification for these 59 sites were published in a previous paper (Ropars and Boudreau 2012). Initial cover was evaluated on an aerial photograph mosaic taken in July 1957, whereas shrub densification was calculated as the difference between shrub cover inferred from the analysis of a satellite image taken in July 2008 and the aerial photograph mosaic taken in 1957 (Table SI in Supplemental material section, see Ropars and Boudreau 2012 for more details).

3.4.3 Data collection

During summer 2009, the geographic position of the 59 sites (latitude, longitude) was determined at its central point, corresponding to the intersection of two 120 m perpendicular linear transects (extending North-South and East-West) sampled to determine shrub species composition and abundance at each site (adapted from Mueller-Dombois and Ellenberg 1974). Shrub species were recorded at every centimeter along the transects (total number of centimeters surveyed per site = 24 000 cm). Percentage cover of a species was then calculated by dividing the number of centimeters on which it was recorded by the total number of centimeters surveyed. If a species was seen but not recorded during the

vegetation surveys, it was given a cover of 1 cm to account for its presence on the site.

For a subset of 27 sites, mineral soil cover was visually estimated in 10 systematically located 1-m² quadrats (1 m x 1 m) and assigned to one of the following cover classes: 0-1%, 2-5%, 6-10%, 11-25%, 26-50%, 51-75%, 76-90%, and 91-100%. Using the mean value of each class, these 10 measurements were subsequently averaged to obtain a mean value for each site. Organic horizon depth in each site was evaluated in 18 systematically located dug holes and then averaged. As direct snow measurements are unavailable for the studied region, we used the mean dwarf birch height to approximate the minimal snow cover for each site (see Arseneault and Payette 1992). Indeed, erect shrub vertical growth is limited to the snow-air interface because drifting ice particles abrade vegetal tissues above the protecting snow cover (Marchand and Chabot 1978). Mean dwarf birch height for a given site was averaged from ten height measurements on randomly selected living individuals.

Back from the field, we derived the slope (in degrees), the slope aspect (in degrees), and the altitude for each of the 59 sites from a 15 m-resolution digital elevation model (DEM) of the study region (<http://geogratis.cgdi.gc.ca/geogratis/en/index.html>) generated by Natural Resources Canada. We also determined the age of 44 of the 59 sites as the time elapsed since the last wildfire based on the exhaustive wildfire cartography reported in Payette *et al* (2008). The 15 remaining sites were located outside of the area covered by the cartography.

The shrub densification and site-specific environmental information are summarized in Table I of the supplemental material section. The mean surface of the sites surveyed is 1.14 ha and ranges from 0.44 to 2.08 ha. All sites are less than 10 km apart from each other.

3.4.4 Statistical analyses

For each site, total shrub cover, species richness, species diversity and species evenness were calculated (including dwarf birch). Species richness was defined as being the total number of shrub species per site, while total shrub cover was obtained by adding every species' cover for each site. As 2 or more different shrub species can overlap, total shrub

cover could be > 100% for one site. Shrub species diversity and evenness were calculated with the Shannon's diversity and evenness indexes (as described in Magurran 1988). We assessed the differences between terraces and hilltops in terms of diversity, evenness, total shrub cover and species richness using the non-parametric Kruskal-Wallis test.

We built ecologically relevant statistical models that could explain the heterogeneity in shrub densification between 1957-2008 in the study area using the environmental variables we measured. Because we did not have all variables for the 59 sites, we divided our modelisation effort in three steps. First, we built 8 models with the variables available for all 59 sites (type of environment, 1957 cover, altitude, slope, aspect). Five models were built with a single variable, one with 2 variables (1957 cover + type of environment), one with 3 variables (1957 cover + type of environment + altitude). The last model includes all five variables. Secondly, we added the age of the site to each of the models identified as plausible in the first step. We also built a model with the age of the site as the only variable. These models were run using the 44 sites for which the time elapsed since the last fire was available. Lastly, in order to reduce the number of models tested in the third step, we chose the plausible models identified in the second step that includes the more variables and built four new models. The first three models were built by adding respectively one variable (organic matter depth, the mineral soil cover and the dwarf birch height - used as a proxy of snow depth) to the previously identified model while the last one was built by adding all three variables. These individual variables were also used to build three models with a single variable. These models were run using the 27 sites for which the organic matter depth, the mineral soil cover and the dwarf birch height were available.

To determine the most plausible model(s) at each step, we used model selection based on Akaike's information criterion corrected for small sample size (AICc; Sugiura 1978). AICc considers the fitting quality and the number of variables included in each competing model and ranks them in terms of loss of information. The best model, i.e. the one having the lowest AICc value, is therefore the one for which the loss of information is minimal (Mazerolle 2006). Using the *aictab* function of the AICcmodavg package (Mazerolle 2014), we calculated the AICc for each of the competing models. The *aictab* function also

calculates delta AICc (ΔAICc), AICc weight ($w\text{AICc}$) and the cumulative AICc weight. The ΔAICc is calculated as the difference between the AICc of one model and the lowest AICc value, the best model having therefore a ΔAICc equals to 0. The AICc weight is the likelihood of a given model to be the best one among a set of competing models (Johnson and Omland 2004) whereas the cumulative AICc weight corresponds to the $w\text{AICc}$ of one model plus the $w\text{AICc}$ values and all better models. Burnham and Anderson (2002) suggest basing our conclusions on the best model only if it has a $w\text{AICc} > 0.90$. Otherwise, they suggest basing the conclusions using the multimodel inference. This approach allows us to compute a weighted average of the estimates of the variables of interest instead of relying solely on the estimates of the best model. Using the *modavg* function of the *AICcmodavg* package, we obtain the model-averaged estimate of the parameters, the unconditional standard error and the 95% confidence interval. We can conclude that one variable has an effect on densification when the confidence interval excludes 0.

The influence of dwarf birch densification (difference in dwarf birch cover between 1957 and 2008; independent variable) on other shrub species cover (total and individual cover, as well as for evergreen and deciduous species), species richness, Shannon diversity index and evenness index (dependant variables) was evaluated through generalized linear models (GLMs). For this section, dwarf birch data were excluded to calculate the 4 variables of interest. The dependent variables were tested for normality using the Shapiro-Wilk test and appropriate distribution was assigned to the variables for which we rejected the null hypothesis (binomial and Poisson distribution for species cover and richness, respectively). The influence of dwarf birch densification on each species cover was evaluated using the same procedure. All statistical analyses were performed in the R Environment (R Development Core Team, version 3.0.2, <http://www.r-project.org/>).

3.5 Results

3.5.1 Shrub communities

Over the 59 sites surveyed, a total of 13 shrub species were recorded (Table I). Dwarf birch, *Rhododendron tomentosum*, *Empetrum nigrum* and *Vaccinium uliginosum* were ubiquitous, being found in > 95% of the sites, regardless of the environment. Other species were mainly confined to hilltops, despite being recorded at least once on terraces (*Diapensia lapponica*, *Kalmia procumbens*, *Salix uva-ursi*).

Shrub cover ranged between 28.7 and 119.1% (and between 20.1 and 52.4% when excluding overlapping shrub species) and was not significantly different between terraces and hilltops (Kruskal-Wallis, $p = 0.55$; Figure 2). On terraces, total shrub cover averaged $63.0\% \pm 21.7$ (mean $\pm$ SD) and was largely dominated by *B. glandulosa* ($40.1\% \pm 12.5$) followed by *R. tomentosum* ($7.0\% \pm 6.2$) and *E. nigrum* ($6.3\% \pm 9.0$). On hilltops, shrub cover averaged $58.9\% \pm 17.0$ and was also dominated by *B. glandulosa* ($32.5\% \pm 10.4$) followed by *R. tomentosum* ($10.1\% \pm 4.9$), and *E. nigrum* ($8.7\% \pm 9.0$). There were no significant differences in species richness (Kruskal-Wallis, $p = 0.08$; Figure 2) or in Shannon diversity (Kruskal-Wallis, $p = 0.17$; Figure 2) between terraces and hilltops (Figure 2). However, the evenness index (Kruskal-Wallis, $p < 0.01$) was significantly higher on terraces than on hilltops (Figure 2).

3.5.2 Candidate models to explain shrub densification

Given the 8 candidate models we built in the first step for model selection using AIC, we found that the model including the 1957 shrub cover and the type of environment (terrace or hilltop) was the most plausible one (Table II). This model was 3 times more plausible than the second best model (evidence ratio: $wAICc_{\text{best model}}/wAICc_{\text{2nd best model}}$: 0.66/0.22). However, the best model had a $wAICc < 0.90$, suggesting that we should use multimodel inferences to obtain more accurate estimates (Burnham and Anderson 2002). We therefore calculated the model-averaged estimate of the 3 variables included in the plausible models (1957 shrub cover, type of environment and altitude). Among them, the 1957 shrub cover

(estimate: -0.7662, unconditional SE: 0.0891, 95% conf. int.: -0.9508, -0.6015) and the type of environment (estimate: -4.5596, unconditional SE: 2.1976, 95% conf. int.: 0.2524, 8.8669) had significant impacts on shrub densification of dwarf birch.

For the second step, we found that the model including the 1957 shrub cover and the time elapsed since the last fire was the most plausible one (Table II). However, this model was only 1.3 times more plausible than the second best model (evidence ratio: $wAICc_{\text{best model}}/wAICc_{\text{2nd best model}}$: 0.46/0.36). Because the best model had a $wAICc < 0.90$, we calculated the model-averaged estimate of the 4 variables included in the plausible models (1957 shrub cover, type of environment, altitude and age). Among them, only the 1957 shrub cover (estimate: -0.7432, unconditional SE: 0.0985, 95% conf. int.: -0.9361, -0.5502) had a significant negative effect on the recent densification of dwarf birch.

Lastly, in the third step, we found that the most plausible model was the one including the 1957 shrub cover, the type of environment, the altitude, the time elapsed since the last fire and the organic matter depth. This model was 1.1 times more plausible than the second best model (evidence ratio: $wAICc_{\text{best model}}/wAICc_{\text{2nd best model}}$: 0.46/0.41). Once again, we calculated the model-averaged estimate of the 7 variables included in the plausible models (1957 shrub cover, type of environment, altitude, age, organic matter depth, mineral soil cover, dwarf birch height) because the best model had a $wAICc < 0.90$. Only the 1957 shrub cover (estimate: -0.5521, unconditional SE: 0.1351, 95% conf. int.: -0.8169, -0.2874) and the time elapsed since the last fire (estimate: 0.0116, unconditional SE: 0.0038, 95% conf. int.: 0.0041, 0.0191) had respectively significant negative and positive effects on the recent densification of dwarf birch (Figure 3b). The opposite effect of the 1957 shrub cover and the time elapsed since the last fire could be explained by the negative relationship between the two (Figure 3c).

3.5.3 Influence of shrub densification on the shrub community

Dwarf birch densification had a negative effect on the shrub cover of other species (GLM, $p = 0.02$; Figure 4) but not on individual species cover (GLM, $p > 0.46$). The negative influence of dwarf birch densification on the cover of evergreen shrub species was

significant (GLM, $p = 0.02$) and marginally significant for deciduous species (GLM, $p = 0.05$). Dwarf birch densification had no significant effect on shrub species richness (GLM, $p = 0.34$; Figure 4) or on Shannon diversity (GLM, $p = 0.40$; Figure 4). The evenness index was positively influenced by dwarf birch densification (GLM, $p = 0.04$; Figure 4).

3.6 Discussion

Shrub densification in subarctic and arctic ecosystems has been mainly associated with an increased performance of shrub species in response to higher temperatures (Myers-Smith *et al* 2011a). However, the observed densification of dwarf birch in North America over the last decades is non-uniform across the landscape (Tape *et al* 2006, 2012 Ropars and Boudreau 2012, Tremblay *et al* 2012), emphasizing the importance of local and historical conditions on the performance of shrub species. Soil properties (Tape *et al* 2012) as well as disturbances (Landhausser and Wein 1993, Racine *et al* 2004, Lantz *et al* 2010) were shown to influence shrub densification. In this study, we found that variables best explaining dwarf birch densification heterogeneity in western Nunavik include both topographic (type of environment) and historical conditions (1957 shrub cover and time elapsed since the fire). Among these factors, only the 1957 shrub cover had a significant influence on recent densification in all three series of models we ran. Moreover, we found that dwarf birch densification influences the shrub community in terms of abundance and composition.

3.6.1 Local drivers of dwarf birch densification heterogeneity

Given the environmental variables we measured, the 1957 shrub cover appears to be the main driver of dwarf birch densification heterogeneity at the landscape level in western subarctic Québec. Despite the fact that dwarf birch found on terraces and hilltops display the same response to climatic variables over the last decades (Ropars *et al* 2015), densification was greater in sites with a lower shrub cover in 1957 (Figure 3). Although one might argue that this result is merely the consequence of shrub cover saturation, i.e. a shrub cover close to 100%, it is highly unlikely since the shrub cover in 2008 averaged only $48.8\% \pm 7.5$ (mean + SD), suggesting that there is still space for shrub densification in our studied sites.

The time elapsed since the last wildfire was also identified as significant positive influence on dwarf birch densification. Wildfires are a common disturbance in northern regions and they were shown to promote the spread of tall shrubs over the first few decades following

the fire through the increase in nutrient availability and in suitable seedbeds (Zasada *et al* 1983, Bliss and Matveyeva 1992, Landhausser and Wein 1993, Hobbie and Chapin 1998, Racine *et al* 2004, Gough 2006). With an increasing time since the last wildfire, the availability of major soil nutrients is known to decrease in boreal forests (Vitousek 2004), resulting in a decline in vegetation biomass and ecosystem productivity (Walker *et al* 2001, Wardle *et al* 2003) and with a shift from deciduous to evergreen dwarf shrub species (Wardle *et al* 1997). The contradicting effect of the time elapsed since last wildfire on *B. glandulosa* densification we observed could results from its influence on the 1957 shrub cover. In fact, the 1957 shrub cover in our study sites is negatively associated with the time elapsed since the last disturbance (Figure 3), suggesting that older fires have created conditions that had long-lasting effects on shrub abundance. Wildfire severity is also known for its influence on subsequent successional trajectories (Payette 1992) and could have played a role in shrub abundance of our studied sites. However, no information on wildfire severity is currently available for the Boniface River region (S. Payette, personal communication).

The type of environment was the other variable identified as important to explain dwarf birch densification. These findings corroborate the results of Shaver *et al* (1996) that stressed the importance of topography and its impact on micro-climatic conditions for plant establishment and growth in arctic regions. Even though they are both well-drained non-forested sites, terrace and hilltop sites differ in terms of soil texture and occurrence of periglacial processes, which can in turn influence plant performance. Soil properties were indeed pointed out as the main factor explaining the presence of adjacent expanding and stable shrub patches in Alaska (Tape *et al* 2012). According to Payette *et al* (2008), the altitude influences wind velocity, occurrence of freeze-thaw processes and snow cover protection during winter. As a consequence, hilltops, which are located at higher altitude than terraces, should be a more stressful environment limiting plant establishment and growth. However, the effect of the type of environment on shrub densification could only be an indirect effect of the 1957 shrub cover. As shown by Ropars and Boudreau (2012), shrub cover in 1957 was greater on hilltops ($35.3\% \pm 8.5$; mean + SD) than on terraces ($28.6\% \pm 12.1$; mean + SD).

3.6.2 Limits of the model selection approach

Model selection approaches are robust, but they are limited by the factors we measured and the models we built. Other factors, such as soil nutrient availability, soil moisture and browsing pressure could also influence dwarf birch densification in the study region in addition to topographic and historical characteristics. Soil properties such as texture, water holding capacity and cryoturbation are all closely linked to local topography (Shaver *et al* 1996). As we did not measure these variables, we cannot determine their influence on dwarf birch densification in the Boniface River region but further soil analysis should be conducted. Browsing pressure from large herbivores can also modulate shrub expansion (Brathen and Oksanen 2001, Post and Pedersen 2008, Plante *et al* 2014). However, dwarf birch densification has been observed on sites with or without migratory caribou activity evidence, suggesting that the browsing pressure in the region was not sufficiently heavy to inhibit shrub densification. On the other hand, caribou trampling could contribute to dwarf birch densification by exposing mineral soil. Indeed, many *B. glandulosa* seedlings were observed on bare ground in the study region. Because caribou were abundant at the end of the 20th century in the study region (Dufour-Tremblay and Boudreau 2011), the extensive trail network could have allowed better dwarf birch establishment, which could have in turn contributed to its densification.

3.6.3 Consequences on shrub community

Our results suggest that dwarf birch densification negatively influences the cover of the shrub community, but does not have any influence on the species richness (both number of species and the Shannon diversity index). These findings corroborate the results of similar studies that found that the abundance and cover of cryptogam and vascular species were negatively correlated with increasing shrub cover and height (Iason and Hester 1993, Cornelissen *et al* 2001, Wahren *et al* 2005, Walker *et al* 2006, Pajunen *et al* 2011; Pajunen *et al* 2012). At the local scale, erect shrubs can indeed influence other plant species by modulating snow accumulation and duration (Liston *et al* 2002), physical characteristics of snow, litter inputs (Cornelissen *et al* 2007), and nitrogen mineralization rates (Buckeridge



et al 2010). This is particularly true on hilltops that harbor arctic-alpine shrub species. These species, which are stress tolerant but less competitive, can be disadvantaged and be completely displaced in case of the establishment of more competitive species (Maillette *et al* 1988, Wipf *et al* 2009). However, dwarf birch cover in our study sites remains relatively low, allowing less competitive species to remain present in the ecosystem. The absence of negative influence of dwarf birch densification on species richness could therefore be only transitory.

We also found a significant positive relationship between dwarf birch densification and the evenness index (excluding dwarf birch). This surprising trend could be partly explained by the positive association between dwarf birch and 3 other shrub species (*Salix planifolia*, *Salix glauca* and *Alnus crispa*). Indeed, these 3 species become more abundant with increasing dwarf birch cover, suggesting that *S. planifolia*, *S. glauca* and *A. crispa* could benefit from the protective cover dwarf birch can offer. By promoting species that are otherwise completely missing, dwarf birch cover could have a positive influence on shrub community evenness. Another possible explanation could come from the tendency of abundant species to decrease in cover with dwarf birch densification, especially *E. nigrum* which is well known for its allelopathic properties (Mallik 2003, Dufour-Tremblay *et al* 2012). Indeed, *E. nigrum* leachate was found to reduce seed germination (Fisher 1980, Dufour-Tremblay *et al* 2012) and growth (Nilsson *et al* 1993) for different tree species. Even if not significant, the tendency of *E. nigrum* cover to decrease with dwarf birch densification could result in better shrub growth and recruitment on sites where densification is greater. On the other hand, sites harboring large *E. nigrum* patches could have limited all other shrub species performance, including dwarf birch. More even shrub communities could thus be the result of the limited *E. nigrum* performance instead of the recent dwarf birch densification.

3.7 Conclusion

Dwarf birch densification is widespread in Nunavik (McManus *et al* 2012, Ropars and Boudreau 2012, Tremblay *et al* 2012), yet heterogeneous across the landscape. Our results suggest that this heterogeneity is explained by both historical and topographic variables. Among these, the time elapsed since the last wildfire had a significant and positive influence on dwarf birch densification, suggesting that better soil formation is beneficial for its performance. We also found that dwarf birch densification negatively influenced the cover of other shrub species. On the other hand, we did not find any influence on shrub species richness, suggesting that dwarf birch cover is still low enough to allow less competitive shrub species to maintain themselves in the system. In future, detailed pedological investigations would be needed to refine our comprehension of the causes of dwarf birch densification heterogeneity.

3.8 Acknowledgments

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3.9 Tables

Table 3.1 Mean cover ($\pm$ standard deviation) and occurrence of the 13 shrub species encountered in 2009 surveys in the Boniface river region, western Nunavik, Québec. The occurrence of a shrub species is defined as the percentage of sites on which the species was found over the total number of terraces (n = 33) and hilltops (n = 26).

Growth form	Species	Hilltops		Terraces	
		Mean cover $\pm$ SD (%)	Occurrence (%)	Mean cover $\pm$ SD (%)	Occurrence (%)
Deciduous	<i>Alnus crispa</i>	0.0 $\pm$ 0.0	4	0.6 $\pm$ 0.8	42
	<i>Betula glandulosa</i>	32.5 $\pm$ 10.4	100	40.0 $\pm$ 12.5	100
	<i>Rubus chamaemorus</i>	0.1 $\pm$ 0.2	46	0.3 $\pm$ 0.4	82
	<i>Salix glauca</i>	0.1 $\pm$ 0.1	42	0.2 $\pm$ 0.6	27
	<i>Salix planifolia</i>	0.3 $\pm$ 0.4	58	0.7 $\pm$ 1.0	70
	<i>Salix uva-ursi</i>	0.3 $\pm$ 0.4	81	0.1 $\pm$ 0.3	24
	<i>Vaccinium uliginosum</i>	2.5 $\pm$ 2.0	96	2.0 $\pm$ 1.9	94
Evergreen	<i>Arctous alpina</i>	2.0 $\pm$ 2.4	77	0.8 $\pm$ 0.8	58
	<i>Diapensia lapponica</i>	0.0 $\pm$ 0.1	27	0.0 $\pm$ 0.0	6
	<i>Empetrum nigrum</i>	8.7 $\pm$ 9.0	100	6.3 $\pm$ 9.0	97
	<i>Kalmia procumbens</i>	0.6 $\pm$ 0.9	58	0.0 $\pm$ 0.0	3
	<i>Rhododendron groenlandicum</i>	1.7 $\pm$ 2.7	65	4.9 $\pm$ 3.5	100
	<i>Rhododendron tomentosum</i>	10.1 $\pm$ 4.9	100	7.0 $\pm$ 6.2	94

Table 3.2 Akaike's information criterion corrected for small sample size (AICc), differences (Δ AICc), weight (wAICc), cumulative weight (cumul. wAICc) and number of parameters (K) from the linear mixed models explaining the recent densification of *Betula glandulosa* in the Boniface River region, western Nunavik, Québec. The modelisation followed three steps: (a) the first step includes all sites (n = 59) but only 5 variables, (b) the second step includes the 44 sites for which the time elapsed since last fire was known and (c) the third step includes all sites for which all environmental variables were known (n = 27). Height corresponds to the erect shrub height and is used as a proxy for minimal snow depth; the age correspond to the time elapsed since the last wildfire; the geographic position combine the latitude and longitude of one site.

Models	K	AICc	Δ AICc	wAICc	Cumul. wAICc
a) First step with 59 sites					
1957 + Env.	4	402.88	0.00	0.66	0.66
1957 + Env. + Altitude	5	405.05	2.17	0.22	0.88
1957 cover (1957)	3	406.75	3.87	0.10	0.98
1957 + Env. + Altitude + Slope + Aspect	7	409.82	6.94	0.02	1.00
Type of environment (Env.)	3	452.54	49.66	0.00	1.00
Altitude	3	454.98	52.10	0.00	1.00
Slope	3	462.75	59.87	0.00	1.00
Aspect	3	463.41	60.52	0.00	1.00
b) Second step with 44 sites					
1957 + Time fire	4	299.13	0.00	0.46	0.46
1957 + Env. + Time fire	5	299.60	0.47	0.36	0.83
1957 + Env. + Altitude + Time fire	6	301.08	1.95	0.17	1.00
Time elapsed since the last fire (Time fire)	3	338.39	39.26	0.00	1.00
c) Third step with 27 sites					
1957 + Env. + Altitude + Time fire + Org. mat.	7	194.33	0.00	0.46	0.46
1957 + Env. + Altitude + Time fire + Height	7	194.54	0.21	0.41	0.87
1957 + Env. + Altitude + Time fire + Min. soil	7	197.54	3.20	0.09	0.96
1957 + Env. + Altitude + Time fire + Height + Min. soil + Org. Mat.	9	199.38	5.05	0.04	1.00
Organic matter (Org. mat.)	3	214.47	20.14	0.00	1.00
Mineral soil (Min. soil)	3	214.66	20.32	0.00	1.00
Dwarf birch height (Height)	3	215.02	20.68	0.00	1.00

3.10 Figures

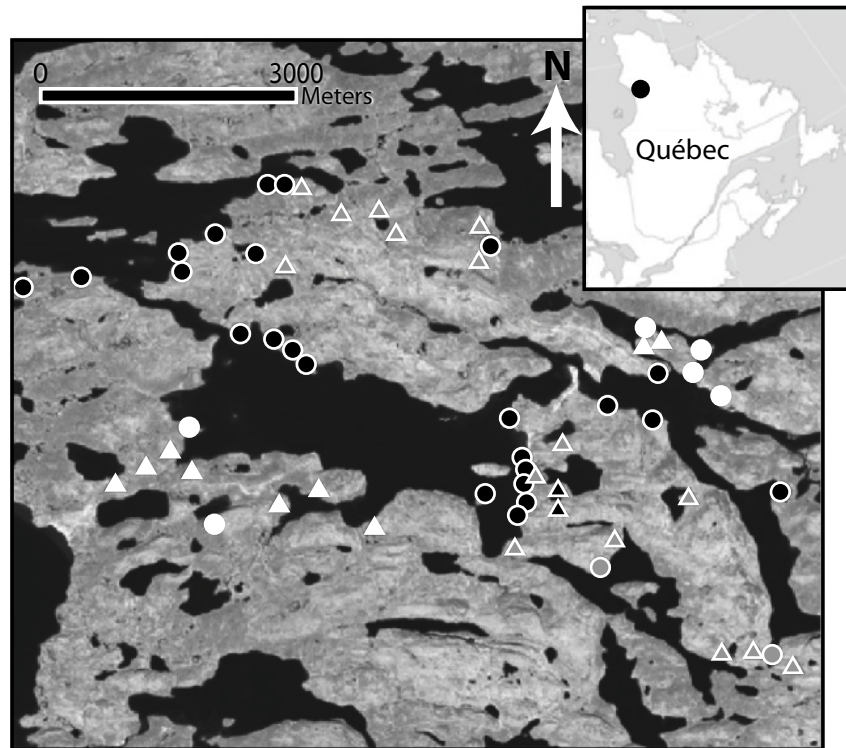


Figure 3.1 WorldView-1 satellite image of the Boniface River region in the Boniface River region, western Nunavik, Québec. Terraces (circles, $n = 33$) and hilltops (triangles, $n = 26$) are identified on the map. White circles ($n = 6$) and triangles ($n = 9$) represent sites for which the time elapsed since the last fire is unknown.

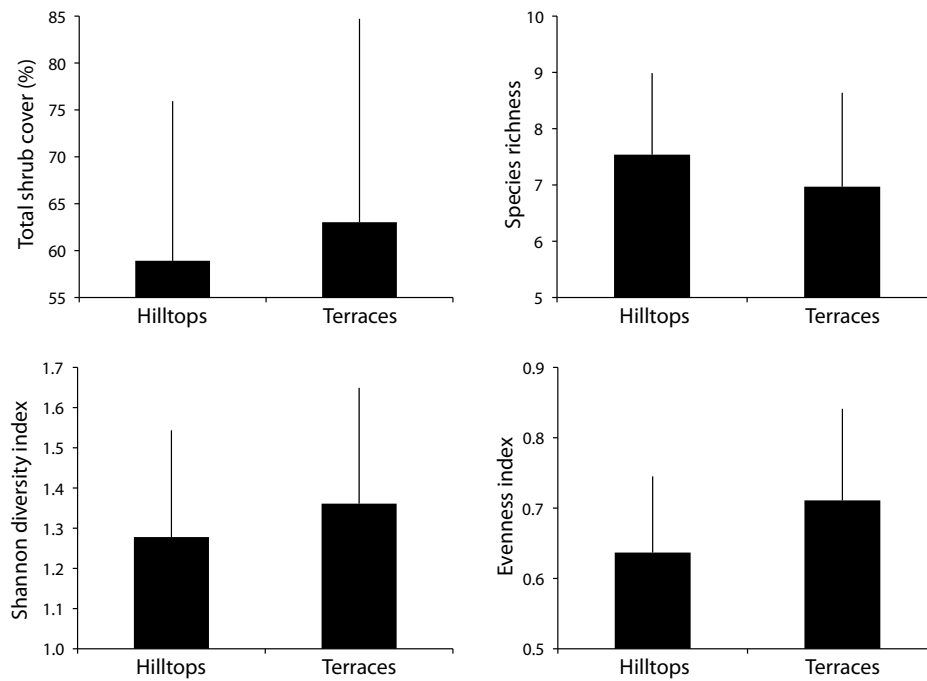


Figure 3.2 Total shrub cover, species richness, Shannon diversity index, and evenness index for terraces (n = 33) and hilltops (n = 26) in the Boniface River region, western Nunavik, Québec. Significant (* $P < 0.01$) differences are indicated above each graph.

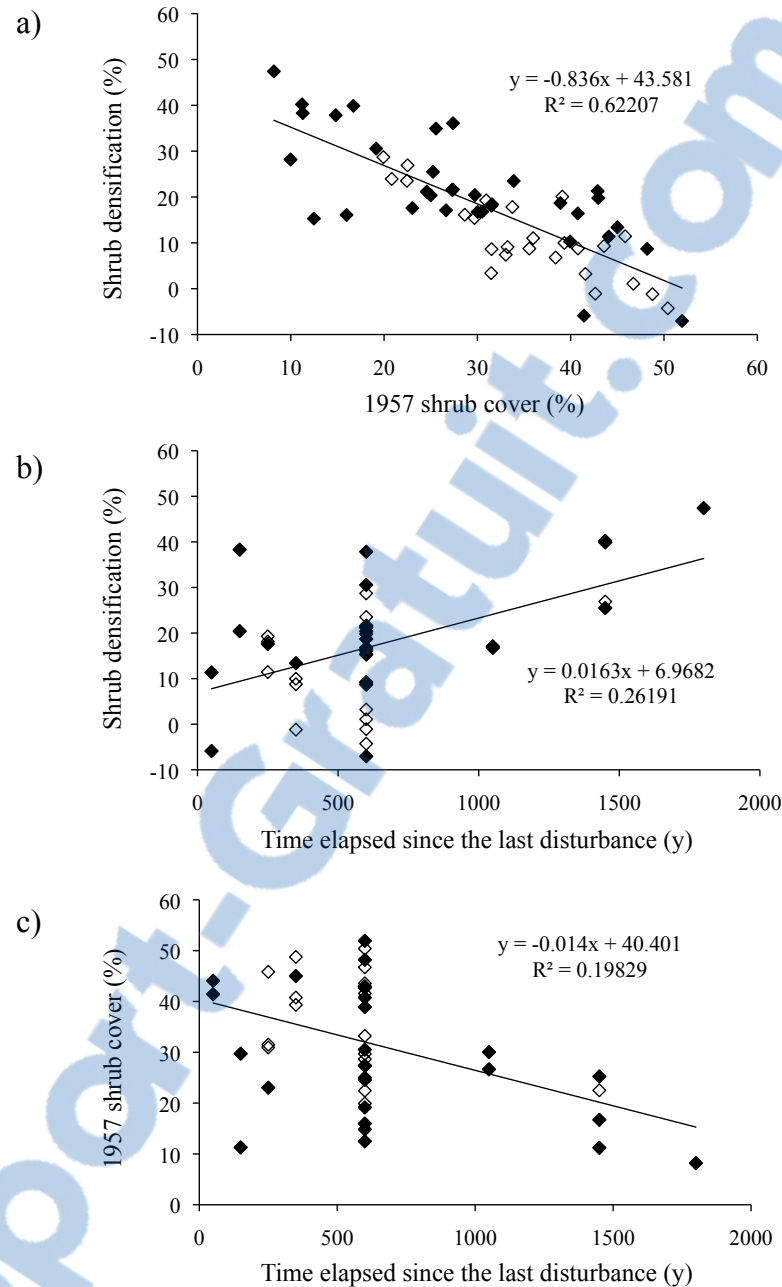


Figure 3.3 (a) Influence of the 1957 shrub cover on the densification of *Betula glandulosa* for 59 sites (terraces: $n = 33$, hilltops: $n = 26$), (b) influence of time elapsed since the last wildfire (i.e. the age of one site) on the densification of *Betula glandulosa* for 44 sites (terraces: $n = 27$, hilltops: $n = 17$) and (c) influence of time elapsed since the last wildfire (i.e. the age of one site) on the 1957 shrub cover for 44 sites (terraces: $n = 27$, hilltops: $n = 17$) in the Boniface River region, western Nunavik, Québec. Terraces and hilltops are represented by black and white diamonds, respectively.

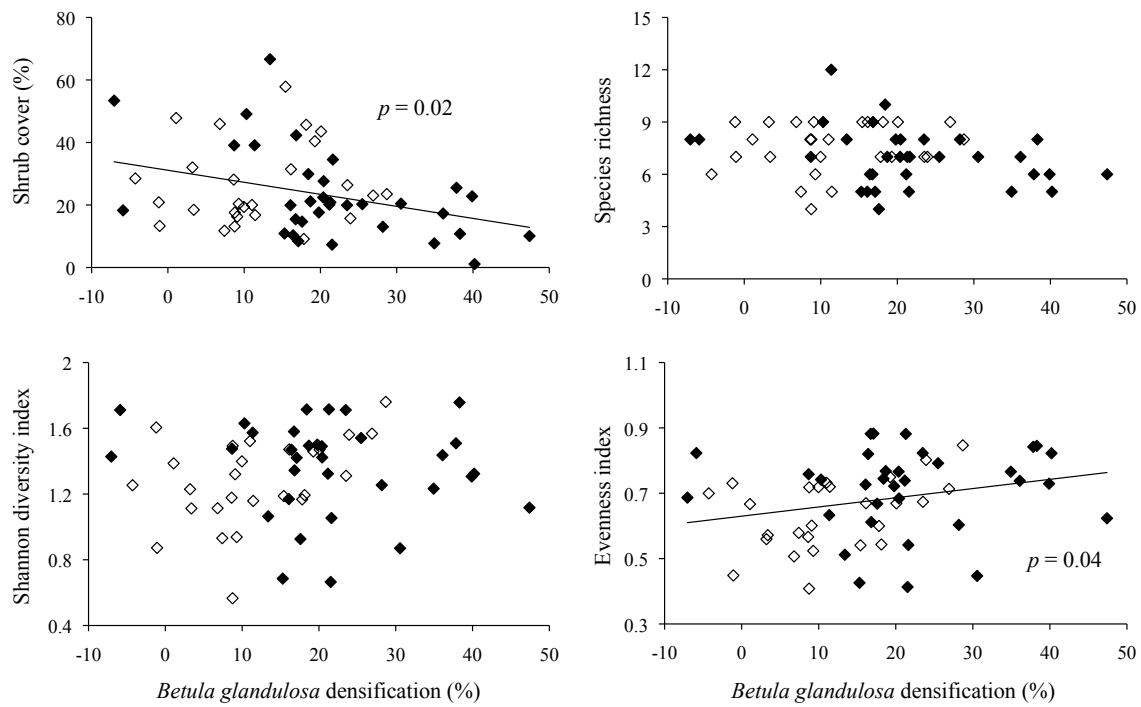


Figure 3.4 Influence of *Betula glandulosa* densification on other shrub species cover, species richness, Shannon diversity index, and evenness index for the 59 sites (terraces: black diamond, $n = 33$ and hilltops: black diamond, $n = 26$) in the Boniface River region, western Nunavik, Québec. *Betula glandulosa* densification had a significant negative and positive influence on other shrub cover and evenness index, respectively.

3.11 Supporting information

Table S3.1 Environmental information, *Betula glandulosa* cover in 1957 and *Betula glandulosa* cover change (densification) between 1957 and 2008 for the 59 sites (terraces n = 33, hilltops n = 26) surveyed in the Boniface River region, western Nunavik, Québec. The age of one site is the time elapsed since the last wildfire whereas the shrub mean height is used as an estimation of the minimum snow depth.

Site	Densification 1957-2008 (%)	1957 cover (%)	Type of environment	Longitude (decimal degree)	Latitude (decimal degree)	Altitude (m a.s.l)	Slope (degree)	Aspect (degree)	Age (years)	Shrub mean height (cm)	Organic layer depth (cm)	Mineral soil cover (%)
1	16.08	15.98	Terrace	-76.232352	57.751142	118.6	3.4	165	600	29.3	2.89	0.5
2	15.29	12.48	Terrace	-76.221663	57.749408	120.2	3.8	239	600	55.7	4.03	0.5
3	28.18	9.98	Terrace	-76.242019	57.741159	119.6	4.6	141				
4	47.41	8.19	Terrace	-76.274814	57.755657	118.9	3.9	314	1800	51.4	13.42	7.5
5	21.17	24.57	Terrace	-76.237444	57.761787	115.1	3.1	318	600	32.5	2.97	0.5
6	38.3	11.28	Terrace	-76.244758	57.759546	113	2.6	266	150	41.8	2.81	0.5
7	20.42	29.73	Terrace	-76.244288	57.757526	115.9	2.3	304	150	36.7	2.33	0.5
8	34.93	25.56	Terrace	-76.144047	57.74763	122	4.0	194				
9	17.1	26.64	Terrace	-76.226261	57.750612	116.1	3.6	213	1050	46.1	3.16	0.5
10	16.75	30.03	Terrace	-76.218748	57.747638	116	3.3	183	1050	57.7	4.84	0.5
11	23.93	20.82	Hilltop	-76.215643	57.734655	125.8	6.3	206				
12	19.79	42.95	Terrace	-76.175582	57.733982	115.8	3.3	300	600	29.3	2.87	0.5
13	16.42	40.76	Terrace	-76.176029	57.735894	114.2	3.0	285	600	43.1	3.21	0.5
14	21.53	27.31	Terrace	-76.168327	57.737531	121	3.1	154	600	35.1	2.74	2.5
15	18.69	38.90	Terrace	-76.176851	57.732223	118.6	5.0	274	600	33.3	2.5	0.5
17	25.49	25.24	Terrace	-76.263426	57.756825	118.4	5.3	18	1450	59.3	5.3	0.5
28	23.53	22.45	Hilltop	-76.18549	57.763413	129.8	2.9	191	600			
29	7.41	33.04	Hilltop	-76.245553	57.738716	135.7	5.0	151				
30	8.75	35.57	Hilltop	-76.240785	57.736284	134.7	4.0	161				
31	11.02	35.98	Hilltop	-76.250335	57.736809	128.7	2.8	139				
32	3.39	31.48	Hilltop	-76.255924	57.734979	139.5	4.8	178				
33	36.09	27.39	Terrace	-76.23663	57.730949	135.6	4.9	283				
34	20.08	39.10	Hilltop	-76.223077	57.733613	123.5	7.8	123				
36	6.8	38.39	Hilltop	-76.205349	57.730917	122.9	4.7	296				
37	-5.88	41.42	Terrace	-76.183396	57.734608	117	3.2	151	50	43.7	10.83	0.5
38	3.22	41.58	Hilltop	-76.177646	57.728971	126.9	7.1	293	600			
41	-7.04	51.94	Terrace	-76.160374	57.726844	132.4	5.4	163	600			
42	-4.27	50.41	Hilltop	-76.157779	57.729992	151.8	11.5	133	600			
43	9.29	43.57	Hilltop	-76.168879	57.735138	131	4.5	179	600	26.9	11.81	0.5
45	11.44	45.83	Hilltop	-76.172676	57.736246	121.8	2.5	264	250			
46	21.3	42.89	Terrace	-76.17535	57.737174	114.1	3.3	241	600	35.9	2.03	2.5
47	30.56	19.15	Terrace	-76.176142	57.738634	115.9	3.2	279	600	28.9	2.36	2.5
48	-1.08	42.64	Hilltop	-76.168492	57.739779	123	2.8	269	600			
49	20.37	25.00	Terrace	-76.178799	57.742812	119.5	5.4	245	600	39.3	1.69	0.5
50	21.63	27.38	Terrace	-76.159537	57.744223	121.9	7.4	218	600	36.5	3.72	0.5
51	8.69	48.20	Terrace	-76.150358	57.74274	122.9	6.9	249	600	45.4	3.18	0.5
52	1.08	46.71	Hilltop	-76.143237	57.734581	140.7	4.3	288	600			
55	-1.19	48.76	Hilltop	-76.130074	57.718226	140	3.5	163	350			
56	8.77	40.78	Hilltop	-76.13558	57.717966	132.5	4.1	199	350			
58	13.39	45.01	Terrace	-76.126501	57.717912	125.2	5.0	192	350			
59	9.97	39.33	Hilltop	-76.121474	57.716824	147.6	4.4	232	350			
86	10.3	39.93	Terrace	-76.137293	57.745226	125.4	6.2	232				
87	11.37	44.08	Terrace	-76.148654	57.747835	118.5	3.5	120	50	36.1	0.92	7.5
88	8.63	31.52	Hilltop	-76.152513	57.750809	120.9	4.4	265				
89	23.49	33.90	Terrace	-76.152291	57.752751	115.7	2.5	320				
90	17.82	33.75	Hilltop	-76.148711	57.751156	129.6	4.8	113				
91	18.41	31.56	Terrace	-76.141196	57.750271	122.2	3.9	245				
94	37.84	14.82	Terrace	-76.228246	57.759953	127.6	2.7	280	600	36	1.97	0.5
95	40.21	11.20	Terrace	-76.226619	57.767046	116	3.8	316	1450	35.4	1.75	0.5
96	39.89	16.71	Terrace	-76.223925	57.767146	120.2	7.8	326	1450	32	5.03	0.5
97	16.13	28.65	Hilltop	-76.211873	57.764117	142.8	5.1	251	600			
98	26.91	22.52	Hilltop	-76.219662	57.766852	137.2	7.7	119	1450			
99	19.27	30.94	Hilltop	-76.204307	57.764393	135.1	3.9	244	250			
100	18.13	31.50	Hilltop	-76.201618	57.762235	142.7	6.4	307	250			
101	16.82	30.52	Terrace	-76.183109	57.761206	122.9	5.3	67	600	22.8	2.14	0.5
102	15.42	29.69	Hilltop	-76.185286	57.759534	142.3	5.2	45	600			
103	28.7	19.93	Hilltop	-76.223191	57.758652	135.8	2.9	188	600			
105	17.59	23.03	Terrace	-76.124809	57.735404	124.7	5.4	228	250	27.7	2.16	2.5
106	9.09	33.23	Hilltop	-76.169043	57.733082	137	4.4	243	600	29.4	17.5	2.5

**CHAPITRE 4 How do climate and topography influence the greening of the forest tundra ecotone in northwestern Québec?
A dendrochronological analysis of *Betula glandulosa***

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4.1 Résumé

Différentes études comparatives d'activité photosynthétique (NDVI) et de photographies aériennes suggèrent une forte densification de la strate arbustive dans les régions subarctiques. Bien que la récente augmentation des températures soit fréquemment invoquée comme principale responsable du phénomène à l'échelle régionale, les facteurs responsables de l'hétérogénéité de la densification de la strate arbustive à l'échelle locale sont méconnus. Les objectifs de cette étude sont d'identifier les facteurs climatiques contrôlant la croissance de *Betula glandulosa* dans trois types d'environnement (terrasse, sommet, combe à neige) ainsi que d'évaluer la relation entre la croissance du bouleau glanduleux et le NDVI enregistré pour la région d'étude. Pour ce faire, nous avons construit une chronologie moyenne de croissance radiale et axiale pour chaque site à l'étude, et utilisé ces dernières pour réaliser des analyses dendroclimatiques de type fonction de réponse. L'influence relative de la croissance de *B. glandulosa* sur le NDVI a été évaluée grâce à des régressions linéaires. Nous avons montré que la croissance radiale de *B. glandulosa* s'est accrue dans les années 1990, pour ensuite enregistrer une forte baisse. Cette tendance à la baisse a été enregistrée pour les sommets et les terrasses, mais pas pour les combes à neige. La croissance de *B. glandulosa* est positivement associée avec les températures estivales sur les terrasses et les sommets, tandis que les précipitations hivernales ont favorisé la croissance dans les combes à neige. L'activité photosynthétique (NDVI) est expliquée en grande partie par la croissance de *B. glandulosa* sur les terrasses et les sommets pour la période 1986-2002 (71 à 80%). En somme, cette étude suggère que la topographie joue un rôle important dans la croissance de *B. glandulosa* et par conséquent, pour la dynamique de la strate arbustive dans la région d'étude. La forte croissance recensée dans les années 1990 suggère que la densification de la strate arbustive est récente dans la région d'étude. Cependant, la chute de croissance observée après 2002 sur les terrasses et les sommets suggère que cette densification pourrait être freinée dans les prochaines années, limitant ainsi la contribution relative de la croissance de *B. glandulosa* au signal photosynthétique de la région.

4.2 Abstract

NDVI analysis and repeated aerial photographs have revealed significant shrub expansion in many subarctic regions. While the recent increase in temperature is usually considered to be the main driver of this phenomenon at regional scales, very little is known about the local heterogeneity of shrub responses across the landscape. In this study, we aim to identify the climatic factors controlling the growth of the largely distributed shrub species *Betula glandulosa* in three types of environments (terrace, hilltop and snowbed). We also aim to evaluate the relationship between *B. glandulosa* growth and the NDVI data for the Boniface River region, in northwestern Québec, where the study took place. In the field, we harvested 180 *B. glandulosa* individuals (20 per site, three sites per type of environment). We constructed specific growth ring width chronologies and mean axial growth rate chronologies for each site, and used them for dendroclimatic analysis (response functions). We also used linear regressions to evaluate the relative influence of dwarf birch growth on the NDVI trend. We found a sharp increase in *B. glandulosa* radial growth in the 1990s followed by a sharp decreasing trend on terraces and hilltops, while growth remained high in snowbeds. *Betula glandulosa* growth was positively correlated with summer temperatures on terraces and hilltops, whereas winter precipitation promoted growth on snowbeds. The NDVI trend was largely correlated to *B. glandulosa* growth on terraces and hilltops for the period between 1986 and 2002 (71 to 80%). Our results suggest that topography plays a major role in *B. glandulosa* growth and therefore, in shrub community dynamics. Because terraces and hilltops represent 70% of the land surface, the sharp *B. glandulosa* growth increase at these sites promoted an important overall expansion of the shrub community in the region. However, the decline in *B. glandulosa* growth observed after 2002 suggests that the expansion could be slowed down in the near future, therefore limiting shrub growth contribution to the regional NDVI signal.

4.3 Introduction

Greening of terrestrial ecosystems has been observed throughout the northern circumpolar region (Myers-Smith *et al* 2011), from North America (Sturm *et al* 2001, Tape *et al* 2006, Olthof and Pouliot 2010, Ropars and Boudreau 2012, Tremblay *et al* 2012, Fraser *et al* 2014) to Eurasia (Forbes *et al* 2010, Hallinger *et al* 2010). Repeated aerial photograph comparisons (Sturm *et al* 2001, Tape *et al* 2006, Beck and Goetz 2011, Ropars and Boudreau 2012, Tremblay *et al* 2012, Fraser *et al* 2014) and Normalized Difference Vegetation Index (NDVI) analyses derived from satellite images (Raynolds *et al* 2006, Forbes *et al* 2010, McManus *et al* 2012, Fraser *et al* 2014) revealed that this greening trend is mainly associated with the rapid expansion of erect shrub species. Resulting from an increase in clonal growth and/or in seedling recruitment, this recent expansion of shrub species occurs either via infilling of pre-existing shrub patches, increases in vertical growth or advancing of the shrubline (Myers-Smith *et al.* 2011).

Encroachment of tall shrub individuals onto previously bare surfaces has profound implications on arctic and subarctic ecosystems. Among them, shrub expansion can decrease albedo (Chapin *et al* 2005), increase evapotranspiration (Swann *et al* 2010), alter surface energy exchange and soil temperatures (Liston *et al* 2002, Pomeroy *et al* 2006, Marsh *et al* 2010), modify biodiversity and ecosystem services (Cornelissen *et al* 2001, Wilson and Nilsson 2009, Pajunen *et al* 2011), and reduce summer permafrost thaw (Blok *et al* 2010). Shrub expansion can also influence animal forage availability, either by decreasing lichen availability in caribou winter ranges (Joly *et al* 2007) or by increasing shrub forage for moose, ptarmigan, and hare (Tape *et al* 2010).

Shrub expansion is commonly attributed to the recent increase in temperatures at high latitudes (Myers-Smith *et al* 2011) through an overall increase in shrub growth. Indeed, dendrochronological studies reveal positive relationships between shrub growth and temperature (Xiao *et al* 2007, Bär *et al* 2008, Liang and Eckstein 2009, Forbes *et al* 2010, Hallinger *et al* 2010, Blok *et al* 2011, Hantemirov *et al* 2011, Boudreau and Villeneuve-Simard 2012), and, to a lesser extent, with winter (Liang and Eckstein 2009, Hallinger *et al* 2010, Schmidt *et al* 2010) and summer (Blok *et al* 2011) precipitation. These results are

corroborated by other studies that have shown an increase in deciduous shrub species abundance when subjected to experimental warming (Hobbie and Chapin 1998b, Jónsdóttir *et al* 2005, Walker *et al* 2006, Elmendorf *et al* 2012b), especially when combined with nutrient addition (Chapin *et al* 1995, Chapin and Shaver 1996, Bret-Harte *et al* 2001, Zamin and Grogan 2012, Paradis *et al* 2014). Vertical growth of deciduous shrubs is also promoted by experimental warming (Chapin and Shaver 1996, Bret-Harte *et al* 2002, Jónsdóttir *et al* 2005, Walker *et al* 2006, Elmendorf *et al* 2012b) as well as by higher snow cover (Wahren *et al* 2005).

Despite the well-known influence of climate on shrub performance, the climatic control on shrub growth is likely heterogeneous at the local scale. Topographic variations can promote large differences in nutrient availability (Tape *et al* 2012) and/or in protecting snow cover (Ropars and Boudreau 2012), which can in turn compromise shrub growth. Large-scale (1-km² to 8-km² pixel size: Jia *et al* 2003, Goetz *et al* 2005, Raynolds *et al* 2006, Olthof and Pouliot 2010) studies of vegetation change such as NDVI analyses might therefore overlook the heterogeneity of shrub expansion across the landscape. On the other hand, site-specific studies using a dendrochronological approach to assess shrub growth might overlook important regional signals.

Even if shrub expansion and its relationship with climate change have been of growing interest in the past decade, very few studies have used a multi-proxy approach to assess this phenomenon (but see Forbes *et al* 2010). Here, we present a regional study integrating dendrochronological analysis and NDVI data to evaluate the long-term growth of *Betula glandulosa* Michx. (hereafter referred to as dwarf birch) and to quantify its contribution to regional greening. Specifically, we aim (1) to identify the climatic factors controlling dwarf birch radial and axial growth, if any, and to evaluate if these factors have a constant effect across the landscape, and (2) to evaluate if the increase in photosynthetic activity in the study area revealed by satellite imagery (NDVI data) can be explained by an increase in dwarf birch growth. We hypothesize that radial and axial growth are respectively driven by summer temperatures and winter precipitation, that the specific drivers of dwarf birch growth vary across the landscape and that NDVI is correlated with dwarf birch growth.

4.4 Methods

4.4.1 Study area

The study site is located at the Boniface River research station of the Centre d'études nordiques (CEN), about 10 km south of the Arctic treeline in subarctic Québec, Canada (57° 45' N, 76° 20' W). The area belongs to the shrub subzone of the forest-tundra ecotone (FTE; Payette 1983) and lies within the discontinuous permafrost zone (Payette 2001). Covering *ca.* 70% of the well-drained sites (Payette *et al* 2008), shrub-lichen tundra communities are found on slopes and low altitude hilltops. Forested stands are currently restricted to well-watered protected sites, but were once part of a more extensive forest cover (Payette and Morneau 1993). Wetlands, which include palsas and snowbeds, cover approximately 7% of the terrestrial surface. At the regional scale, dwarf birch is the most abundant shrub species and is responsible for most of the shrub expansion observed in western (Ropars and Boudreau 2012) as well as in eastern subarctic Québec (Tremblay *et al* 2012) over the last decades.

Fires were frequent in the region during the Holocene period (Arseneault and Payette 1997b, Arseneault and Sirois 2004), but the colder and wetter conditions of the last 1000 years reduced their frequency (Filion 1984). The Rivière-aux-Feuilles migratory caribou (*Rangifer tarandus* L.) herd (RFCH) declined sharply after peaking at $931\,000 \pm 427\,000$ individuals in July 2001 (Couturier *et al* 2004, Aerial migratory caribou count, Québec Government, 2011, data not published). Being at the southern limit of the RFCH summer range, the Boniface River region did not support high densities of caribou. Nevertheless, caribou did expose patches of mineral soils following the destruction of the lichen cover through repeated trampling (Dufour-Tremblay and Boudreau 2011) while evidence of browsing are mostly restricted to *Salix* species.

Inukjuak Meteorological Station (58° 28' N, 78° 05' W; 130 km northwest of the study site) recorded an annual mean temperature of -7 °C for the 1971-2000 period, with the highest and lowest mean monthly temperatures recorded in July (9.4° C) and February (-25.8 °C), respectively (Environment Canada 2013). Annual precipitation averaged 460 mm, of which

42% fell as snow (Environment Canada 2013). Like many regions of northern Québec, Inukjuak has experienced an extensive warming trend since the early 1990's (Chouinard *et al* 2007, Bhiry *et al* 2011). Mean temperatures followed a significant increasing trend between 1990 and 2009 ($+ 0.14^{\circ}\text{C year}^{-1}$, $F_{1,13} = 6.92$, $p = 0.02$) whereas no trend was observed for the previous period (1946 and 1989; $F_{1,40} = 0.11$, $p = 0.74$). Total annual precipitation increased for the 1946-2009 period (3.5 mm year^{-1} , $F_{1,48} = 29.88$, $p < 0.01$), whereas total summer precipitation decreased slightly but not significantly for the same period ($-0.17 \text{ mm year}^{-1}$, $F_{1,51} = 0.26$, $p = 0.61$). Although some climate data are also available for the Boniface River area, we decided to use the Inukjuak climate data for subsequent analyses because (1) the mean monthly temperatures from Inukjuak and Boniface were highly correlated (Pearson correlation coefficients ranging from 0.89 to 0.98, data not shown), (2) the period covered by the available climate data is longer for Inukjuak (1946-2009) than for Boniface (1988-2009) and (3) no precipitation data were available for Boniface.

4.4.2 Site selection and field sampling

In this study, we focused on three different types of environments: sandy terraces (hereafter referred to as terraces), hilltops and snowbeds. Terraces are defined as well-drained low altitude sites (ranging from 110 to 125 m a.s.l) located at the margin of the Boniface River. They are characterized by lichens and graminoids and harbor large patches of shrub species, mainly dwarf birch. Low altitude hilltops (ranging from 120 to 150 m a.s.l) are characterized by the presence of arctic-alpine species and exposed mineral soil. Experiencing harsher winter conditions, shrubs and trees growing at these sites have a limited height. Indeed, drifting ice particles abrade plant stems and meristems at the snow-air interface (Marchand and Chabot 1978), thus limiting erect shrub and tree growth above the protective snow cover (Hadley and Smith 1989). Snowbeds are periglacial environments where snow accumulates preferentially during winter and melts later in the growing season, sometimes as late as in mid-July. Consequently, these environments are characterized by plant species that are well adapted to winter conditions and an excess of moisture (Payette and Lajeunesse 1980, Filion and Payette 1982, Payette *et al* 1985, Morin and Payette 1986). High dwarf birch patches usually surround these environments.

Prior to the field season, we identified 50 terraces, 50 hilltops, and 47 snowbeds on a WorldView-1 Standard Ortho-Ready panchromatic orthorectified satellite image of the study area (resolution 0.5 m) taken on July 15th, 2008. Of these pre-selected sites, we randomly chose three sites for each type of environment (i.e. 3 terraces, 3 hilltops, 3 snowbeds). At each site, we selected 20 dwarf birch individuals that we uprooted in July and August 2009. Relatively isolated large individuals showing a circular form were selected preferentially, as they were thought to be older individuals grown from seed. When they were not available, particular attention was taken to discard individuals that seemed to have grown from vegetative reproduction. The root collar and the two main branches of each dwarf birch individual were collected, carefully cleaned, and left to dry at room temperature for at least 3 months.

4.4.3 Radial growth and climatic data

Growth ring analysis was conducted to evaluate the effect of temperature, precipitation and drought stress on radial growth. To do so, dwarf birch root collars were sliced (*ca.* 25 μ m) using a rotary microtome after being boiled for at least 3 hours. Thin sections were then stained with safranin (1% solution, Safanin O, Fischer Science Education), dried and permanently mounted with a 66% toluene solution (SHUR/mountTM liquid cover glass, Triangle biomedical sciences). Digital photographs of each sample were taken using a binocular-mounted camera (Olympus SZ61 with a SC100 camera). Root collars were discarded if they could not be sliced perpendicularly (branches and roots were too intermingled), or if they were rotten.

Using digital photographs, we aged each sample with the ImageJ freeware (v. 1.40g) while ring widths were measured using the dendrochronological software LignoVision (v. 1.36, Rinntech). When possible, ring widths along two radii were measured for each sample. Growth measurements were visually examined and statistically verified with COFECHA, a widely used statistical crossdating program (Holmes 1983). A horizontal line fitted to the mean was applied to raw chronologies to allow comparison between individuals. This standardization method was used because there was no general age trend among the

different individuals (see Figure S4.1 in Supporting Information), and because we wanted to keep as much variability associated with the climate signal as possible (Weijers *et al* 2010). One growth-ring chronology was produced for each site by averaging the different standardized individual ring width chronologies. The Expressed Population Signal (EPS) was used as an indicator of the reliability of the chronologies (threshold: 0.85; Wigley *et al* 1984).

Response functions were performed with the bootRes package (*dcc* function) of the R software (v. 3.0.2, R Development Core Team) to assess the influence of mean monthly temperatures and total monthly precipitation, as well as drought stress during the growth season on dwarf birch's radial growth. Like the Dendroclim2002 software (Biondi and Waikul 2004), the *dcc* function calculates multivariate estimates from a principal component regression model in which tree-ring values are predicted from monthly climate variables (Zang 2012). The significance of response function coefficients was tested using the 95% percentile range method (Dixon 2001) from 1000 random bootstrapped samples. We used the available mean monthly temperature and precipitation data available from the Inukjuak Meteorological Station (1946 to 2009), but missing values constrained us to discard the years 1952, 1979, 1994, 2001 and 2003 for temperature data and years 1952, 1979, 1994 to 2001, 2003, 2005 and 2007 for precipitation data.

To evaluate the potential effect of drought stress on dwarf birch radial growth during the growth season (May to August), we used the Standardized Precipitation Evapotranspiration Index (SPEI), a drought index commonly used in dendrochronological studies (Kharuk *et al* 2013, Martin-Benito *et al* 2013, Mendivelso *et al* 2014, Vicente-Serrano *et al* 2014; data downloaded from the Global SPEI database: <http://sac.csic.es/spei/database.html>). Based on the climate data of the Climatic Research Unit of the University of East Anglia, the SPEI is calculated as the monthly difference between precipitation and potential evapotranspiration (see Vicente-Serrano *et al* 2010 for more details). Values > 0 indicate months with positive water balance ("wet months") whereas values < 0 indicate months with negative water balance ("dry months"). For the Boniface River area, a slight decreasing trend in the SPEI was observed for the month of July since 1980 (-0.03 year^{-1}). For this period, 20 years (out

of 30) were considered dry, and this trend was even more important when only considering the last decade (7 dry years out of 10; Figure 4.1).

4.4.4 Axial elongation

A stem analysis (see Gamache and Payette 2004) was conducted on the two main branches of the sampled dwarf birch individuals to infer the influence of climate on axial growth. To do so, we sampled each branch at 25 cm intervals. Each section was then boiled, stained and mounted on slides (see previous section) and aged under a dissecting binocular. As no obvious age-growth trend was observed (Figure S4.2), we used raw measurements for further analysis. Axial growth rates were interpolated by dividing the distance between two samples (*i.e.* 25 cm) by the age difference between two consecutive sections. The annual mean axial growth rate for each site was then calculated when at least 5 individual branches were included.

Response functions were performed to evaluate the influence of temperature, precipitation and drought stress on axial growth rate for each site, following the same procedure as the one described in the previous section. However, because axial growth rates were interpolated from the stem analysis, we used a more stringent significance level (0.01).

4.4.5 NDVI data

To determine if the greening observed in the study area is associated with dwarf birch radial growth, we extracted 10-day composite NDVI data from the Canadian long term satellite data record (LTDR) derived from 1-km resolution Advanced Very High Resolution Radiometer (AVHRR) produced by the Canada Center for Remote Sensing (Earth Observation Data Manager processing software; Latifovic *et al* 2005). We chose to use the 21-30 July period since the photosynthetic activity is believed to be at its maximum during this period. We calculated the mean NDVI from the 140 pixels covering the study area, but discarded pixels with values < 0 (water surfaces) and < 0.02 (cloud cover; Latifovic *et al* 2005). The period covered by the available data is 1986 to 2009. The contribution of dwarf birch radial growth to the NDVI signal was evaluated through linear regressions, both for

the 1986-2009 period and for the 1986-2002 period; the latter being tested in order to account for the radial growth decrease observed after 2002 on terraces and hilltops.

4.5 Results

4.5.1 Radial growth and climate

Out of the 20 root collars processed by sites, we constructed dwarf birch ring width chronologies from 13 to 15 individuals (26 to 29 radii) for each of the study sites, except for one hilltop (Figure 4.1). For this particular site, the chronology was built with only 8 individuals (16 radii; Table 4.1) since we had difficulty finding suitable root collars for dendrochronological analysis (either intermingled or rotten). The EPS for all chronologies were > 0.85 threshold considered as acceptable (Wigley *et al* 1984; Table 4.1).

Ring width chronologies were longest on terraces and shortest in snowbeds (Table 4.1). Chronologies from the same environment were highly correlated (Pearson correlation coefficient (PCC) ranging from 0.771 to 0.858 on terraces, from 0.741 to 0.846 on hilltops and from 0.424 to 0.774 in snowbeds; Table S4.1). Visual inspection revealed no age-related trend in the chronologies (Figure S4.1). Dwarf birch ring widths, regardless of the age of the individuals or of the environment type, underwent an abrupt and synchronized increase during the mid-1990s, which is concomitant with an increase in mean annual temperature in the study area (Figure 4.1). However, this trend appeared to be ephemeral on terraces and hilltops as we observed a decrease in dwarf birch radial growth after 2002. In these environments, dwarf birch growth was particularly low in 2004 and 2007, which is concomitant with lower annual and July mean temperatures (Figure 4.1). We did not observe this decreasing trend in snowbeds, although 2004 and 2007 were also characterized by low radial growth.

For terraces, all ring width chronologies were positively associated with July and August mean temperatures (Figure 4.2). Radial growth was also associated with September mean temperature at the end of the previous growing season for two terraces. We obtained comparable results for hilltops although only one site out of three showed a significant association with mean August temperature. We observed no clear pattern for snowbed ring width chronologies, some being associated with previous fall temperatures (1 out of 3 for September, October, November) while others were associated with late spring and summer

temperatures (1 out of 3 for May, June, July). Radial growth was constantly positively associated with March precipitation, regardless of the environment (terraces: 2/3; hilltops: 2/3; snowbeds: 3/3). In some sites, radial growth was also positively associated with April precipitation (H1, SB2, SB3) or negatively associated with July precipitation (T2, T3, H1, SB2). Lastly, radial growth in all terraces and hilltops and in one snowbed was negatively associated with the SPEI in July.

4.5.2 Axial growth and climate

Mean axial growth rate chronologies from the same environment were highly correlated (PCC ranging from 0.870 to 0.969 on terraces, from 0.797 to 0.905 on hilltops and from 0.756 to 0.839 in snowbeds; Table S4.2). Visual inspection revealed no age-related trend in the chronologies (Figure S4.2). Mean axial growth rate from terraces and hilltops followed approximately the same trend, reaching a maximum value of 5 to 6 cm/year in the early 2000s, but declining afterwards (Figure 4.3a). Unlike terraces and hilltops, mean axial growth curves in snowbeds showed more inter-site variation even if they all reached their maximum values around the year 2000. Axial growth in SB1 reached a maximum value of 11.0 ± 6.3 cm/year whereas it reached a maximum value of 6.8 ± 4.9 cm/year in SB2 and 9.5 ± 4.1 cm/year in SB3. As observed for the radial growth, the declining trend detected on terraces and hilltops in axial growth for the 2002-2009 period was not clearly identified in snowbeds. Higher axial growth rates resulted in longer branches in snowbeds (148 to 175 cm compared to 92 to 114 cm on hilltops and 109 to 127 cm on terraces; Figure 4.3b). Even if the SB2 cumulative axial growth chronology was older, its mean cumulative growth in 2009 was comparable to that of the other snowbeds. Terraces and hilltops cumulative axial growth followed the same growth trend.

On terraces and hilltops, all mean axial growth rate chronologies were positively associated with July temperatures, while two terraces were also positively associated with August temperatures (Figure 4.4). Moreover, temperature during the previous month of December also had a positive effect on axial growth in 2 terraces and 1 hilltop (Figure 4.4). Associations between snowbed chronologies and temperatures were scarce and heterogeneous, with only SB2 and SB3 being positively associated with July and previous

December temperatures, respectively. All chronologies (except H2 and T2) were associated with March precipitation, whereas three out of nine chronologies were positively and negatively associated with previous September (SB2, H1, H2) and July precipitation (SB2, H3, T3), respectively. Overall, axial growth was not associated with the SPEI during the growth season except on one hilltop and in one snowbed where it was negatively associated with SPEI in July.

4.5.3 Dwarf birch radial growth and NDVI

NDVI data followed a significant increasing trend of 0.007 year^{-1} for the 1986-2009 period (linear regression, $F_{1,22} = 35.22$, $p < 0.01$). One year had a particularly low value (2004; Figure 4.5a), which is mirrored in the radial growth chronology (Figure 4.1). Regressions between NDVI and dwarf birch radial growth on terraces and hilltops for the 1986-2009 period were all significant (Table 4.2). However, they were stronger when considering only the period 1986-2002, i.e. before the radial growth decrease observed over the last seven years of the chronologies (see R^2 for the two periods in Table 4.2). For snowbeds, all regressions were also significant. Unlike on terraces and hilltops, the association between NDVI and dwarf birch radial growth were generally higher when using the 1986-2009 period (Table 4.2). Only the SB2 regression had a slightly higher regression coefficient when using the 1986-2002 period (Table 4.2).

4.6 Discussion

As high latitude regions are facing rapid environmental change, the need for reliable dendrochronological chronologies becomes necessary to better understand the mechanisms that promote the performance of woody species. In this study, we present a detailed dendroclimatological analysis of *Betula glandulosa*, a widely distributed yet little-studied shrub species. We show that heterogeneity in local topography modulates the response of this species to the regional climate. Moreover, we demonstrate that the greening observed in the Boniface River area is correlated with dwarf birch growth.

4.6.1 Topographic factors influencing dwarf birch growth

Topography, mainly because of its influence on wind exposition and snow accumulation, is one of the most important environmental factors for plant growth in subarctic regions (Payette *et al* 1973). As hypothesized, our results show that the response of dwarf birch to the regional climate is modulated by local topography. Differences in dwarf birch radial and axial growth were mainly observed between terraces/hilltops and snowbeds. Terraces and hilltops are well-drained sites characterized by coarse substrate with low pH, which were previously found to promote dwarf birch growth and distribution (Ducruc and Zarnovican 1976). On the other hand, snowbeds are characterized by important snow accumulation, leading to shorter growing seasons but better frost protection and greater water availability during the growing season.

The increase in radial growth observed on terraces and hilltops, and to a lesser extent in snowbeds (Figure 4.1), corresponds to the significant warming observed in the region in the 1990s (Bhiry *et al* 2011). Warmer temperatures during the short growing season in high-latitude regions are beneficial for both radial and axial growth (see Myers-Smith *et al* 2011), through direct (physiological activity) and indirect (increase soil microbial activity and decomposition rates) effects, as long as other factors do not become limiting. Our results corroborate many studies that have shown that shrub growth is positively correlated with summer temperatures (Bär *et al* 2008, Liang and Eckstein 2009, Forbes *et al* 2010, Hallinger *et al* 2010, Hantemirov *et al* 2011, Boudreau and Villeneuve-Simard 2012) and

temperatures at the end of the previous growing season (Au and Tardif 2007, Liang and Eckstein 2009). The positive association between December temperatures of the previous year and axial growth is likely related to reduced frost damage to exposed branches in a period when dwarf birch is poorly protected by the relatively shallow snow cover (Marchand and Chabot 1978, Sonesson and Callaghan 1991). However, the absence of a consistent association between dwarf birch growth in snowbeds and summer temperatures suggests that other local factors are more limiting in this particular environment. For example, mechanical damage to stems and leaf buds caused by deep snow cover could control dwarf birch radial growth in snowbeds (Payette and Lajeunesse 1980). The heterogeneity in the climate drivers between snowbed sites could also arise from topographic features. For example, SB3 is a large snowbed (*ca.* 25,700 m²) that accumulates important amounts of snow, probably because of its northeast-facing slope (dominant winds in the region come from the west). In this case, warm spring temperatures can promote birch radial growth by accelerating snowmelt and thus extending the growing season.

Dwarf birch radial and axial growth in all environments were also positively associated to March and April precipitation (only snowbed environments for the latter). Other studies have shown such relationships between shrub radial growth and winter precipitation (Zalatan and Gajewski 2006, Liang and Eckstein 2009, Hallinger *et al.* 2010, Franklin 2013). Greater snow accumulation has been associated with better insulation and therefore with higher winter soil temperatures and microbial activity, leading to an increase in nutrient availability at the beginning of the subsequent growing season (Mack *et al* 2004, Chapin *et al* 2005). Higher precipitation in March and April could also reduce the risk of late frost damage following an early spring leaf-out. Axial elongation may not be as strongly influenced by winter precipitation as we hypothesized. Indeed, erect shrub height is closely linked to snow cover (Sturm *et al* 2005, Ropars and Boudreau 2012), but because *B. glandulosa* branches can grow horizontally, axial elongation might be subjected to the same climatic drivers as radial growth. The negative association between radial and axial growth and July precipitations, observed in all environments, is likely the result of the

negative relationship between precipitation and temperature (linear regression; $F_{1,59} = 18.71, p < 0.01$), as a greater cloud cover is likely to reduce the temperatures.

An intriguing result is the decrease in radial growth observed on terraces and hilltops following 2002, a phenomenon not observed in snowbeds. The synchronicity of the growth reduction suggests that it is driven by factors acting at the regional scale. For example, it seems unlikely that nutrient availability, varying from site to site, has been the cause of the growth reduction. Careful examination of the climate data for this period revealed different trends that could explain, at least in part, the decrease in dwarf birch growth recorded after 2002 on terraces and hilltops. First, the growth reduction could be associated with cooler temperatures during the growth season following 2002. For example, the low growth observed in 2004 and 2007 in all environments is likely associated with cooler temperatures during the month of July (9.3°C and 9.5°C respectively, compared to 11.7 ± 1.8 observed for the 1995-2009 period). As dwarf birch growth in snowbeds appears to be less sensitive to summer temperatures, it is possible that individuals from this environment have not responded to cooler temperatures. Another explanation is based on the SPEI data. It is likely that dwarf birch individuals experienced negative water balance in July for seven out of ten years from 2000 to 2009 (Figure 4.1), with two more years showing only a slight positive water balance. Even though this species is known for its tolerance to periodic drought (Andrews *et al* 1980, de Groot *et al.* 1997), such water shortage combined with dwarf birch cover increase (*ca.* 17%) on terraces and hilltops (Ropars and Boudreau 2012), two well-drained environments, could have led to greater drought stress at the site level, resulting in less favorable growth conditions (Rodwell 1991, de Groot *et al* 1997, Myers-Smith *et al* 2011). In fact, several studies using Open-Top Chambers (OTCs) showed that the increase in growth observed for many species was ephemeral as the negative effect of drought stress in OTCs became more important than the positive effect of warmer temperatures (Arft *et al* 1999, Elmendorf *et al* 2012b). Moreover, experimental increase in summer precipitation positively influenced length increment of the related species *Betula nana* (Keuper *et al* 2012). As snowbeds are characterized by greater water availability, the individuals found in this environment would not have experienced the same drought stress intensity as individuals from the two other environments.

4.6.2 Dwarf birch influence on regional greening

Recent greening of terrestrial ecosystems in response to climate change is arguably one of the most important phenomena observed in high-latitude regions. NDVI analyses (Raynolds *et al* 2006), repeated aerial photographs comparisons (Sturm *et al* 2001, Tape *et al* 2006, Ropars and Boudreau 2012, Tremblay *et al* 2012) and field sampling (Ropars and Boudreau 2012, Tremblay *et al* 2012) confirmed that this phenomenon is more important in regions dominated by erect shrub species. However, the relative contribution of erect shrub species versus other functional groups such as graminoids is difficult to quantify. In our study, we demonstrate that dwarf birch radial growth from 1986 to 2002 on terraces and hilltops explained between 71% and 80% of the NDVI data variance. This result suggests that dwarf birch expansion on terraces and hilltops identified through the analysis of two aerial pictures taken in 1957 and 2008 (Ropars and Boudreau 2012) is quite recent. Because *B. glandulosa* is the most abundant shrub species on terraces and hilltops, two environments covering *ca.* 70% of the land surface, it is probable that this species is responsible for most of the greening in the study area. Although one could argue that there is a discrepancy between radial growth and NDVI data after 2002, it is likely that the extended shrub cover resulting from several years of shrub expansion continued to generate high NDVI values, even if individual radial growth decreased following 2002. It is also possible, but less likely, that the increase in dwarf birch growth in other types of environments such as snowbeds (Figure 4.5b), as well as the increase in growth of other functional groups such as graminoids (McManus *et al* 2012), has been sufficient to maintain or increase NDVI value after 2002.



4.7 Conclusion

This research demonstrates the dendrochronological potential of a structural shrub species found in northern regions, *Betula glandulosa*. Our analysis revealed a rapid increase in *B. glandulosa* growth in the second half of the 1990's, especially on well-drained terrain. Differences in topography across the landscape were found to promote differences in *B. glandulosa* radial and axial growth. Our dendrochronological analysis revealed that summer temperature play a major role in the growth of *B. glandulosa* situated on terraces and hilltops whereas, the growth of individuals found in snowbeds is mostly promoted by winter precipitation. Finally, we show that the greening of the region was mainly driven by dwarf birch growth, and that shrub expansion in the region occurred after 1990. Further studies are now needed to determine the drivers responsible for the decrease in *B. glandulosa* radial growth after 2002. Moreover, future studies should aim at quantifying the impact of this reduction in growth on the rate of shrub expansion in the region, as well as characterizing its effects on factors such as thawing of permafrost, biodiversity and ecosystem services.

4.8 Acknowledgments

This research was founded by Natural Sciences and Engineering Research Council of Canada (NSERC), by the Fonds de Recherche Québec - Nature et Technologies (FRQNT), by the Northern Scientific Training Program and by the Northern Research Chair on Disturbance Ecology. The authors are grateful to Sandra Angers-Blondin and Caroline Mercier for their help in the field as well as to Annie Girard, Mélody Dos Santos and Mélissa Paradis for their lab assistance. The authors would also like to thank Steeve Côté and Maël Le Corre for the NDVI data, Ann Delwaide for her valuable help with dendrochronological analysis, Émilie Saulnier-Talbot and Christine Barnard for the linguistic revision and the Centre d'études nordiques for its logistical support.

4.9 Tables

Table 4.1 Description of the nine *Betula glandulosa* ring width chronologies built for the different study sites at Boniface River station, subarctic Québec, Canada.

Chronologies		Number of individuals	Period considered	Chronology length (yr)	EPS
Terraces	T1	14	1931-2009	78	0.924
	T2	15	1936-2009	73	0.957
	T3	14	1928-2009	81	0.863
Hilltops	H1	15	1942-2009	67	0.941
	H2	8	1949-2009	60	0.894
	H3	14	1941-2009	68	0.949
Snowbeds	SB1	13	1949-2009	60	0.967
	SB2	14	1956-2009	53	0.899
	SB3	14	1962-2009	47	0.95

Table 4.2 Relation between Normalized Difference Vegetation Index (NDVI) and *Betula glandulosa* radial growth for the 1986-2009 and 1986-2002 periods at Boniface River station, subarctic Québec, Canada. NDVI data were extracted from the Canadian long term satellite data record (LTDR) derived from 1-km resolution Advanced Very High Resolution Radiometer (AVHRR) produced by the Canada Center for Remote Sensing (Latifovic *et al.* 2005). We used the NDVI data of the 21-30 July period. All regressions were significant at the 0.05 level.

Relation between NDVI and <i>Betula glandulosa</i> radial growth									
Chronologies		Segment 1986-2009				Segment 1986-2002			Adjusted R ²
		Estimate	$F_{1,22}$	p	Adjusted R ²	Estimate	$F_{1,15}$	p	
Terraces	T1	0.06	9.58	0.005	0.30	0.07	61.76	<0.001	0.80
	T2	0.06	12.15	0.002	0.36	0.05	36.17	<0.001	0.71
	T3	0.04	7.22	0.014	0.25	0.05	44.99	<0.001	0.75
Hilltops	H1	0.05	9.39	0.006	0.30	0.06	39.40	<0.001	0.72
	H2	0.04	6.96	0.015	0.24	0.05	48.54	<0.001	0.76
	H3	0.06	14.91	0.001	0.40	0.06	44.57	<0.001	0.75
Snowbeds	SB1	0.06	28.70	<0.001	0.57	0.06	9.67	0.007	0.39
	SB2	0.06	5.60	0.027	0.20	0.06	5.67	0.031	0.27
	SB3	0.08	28.56	<0.001	0.56	0.06	16.99	0.001	0.53

4.10 Figures

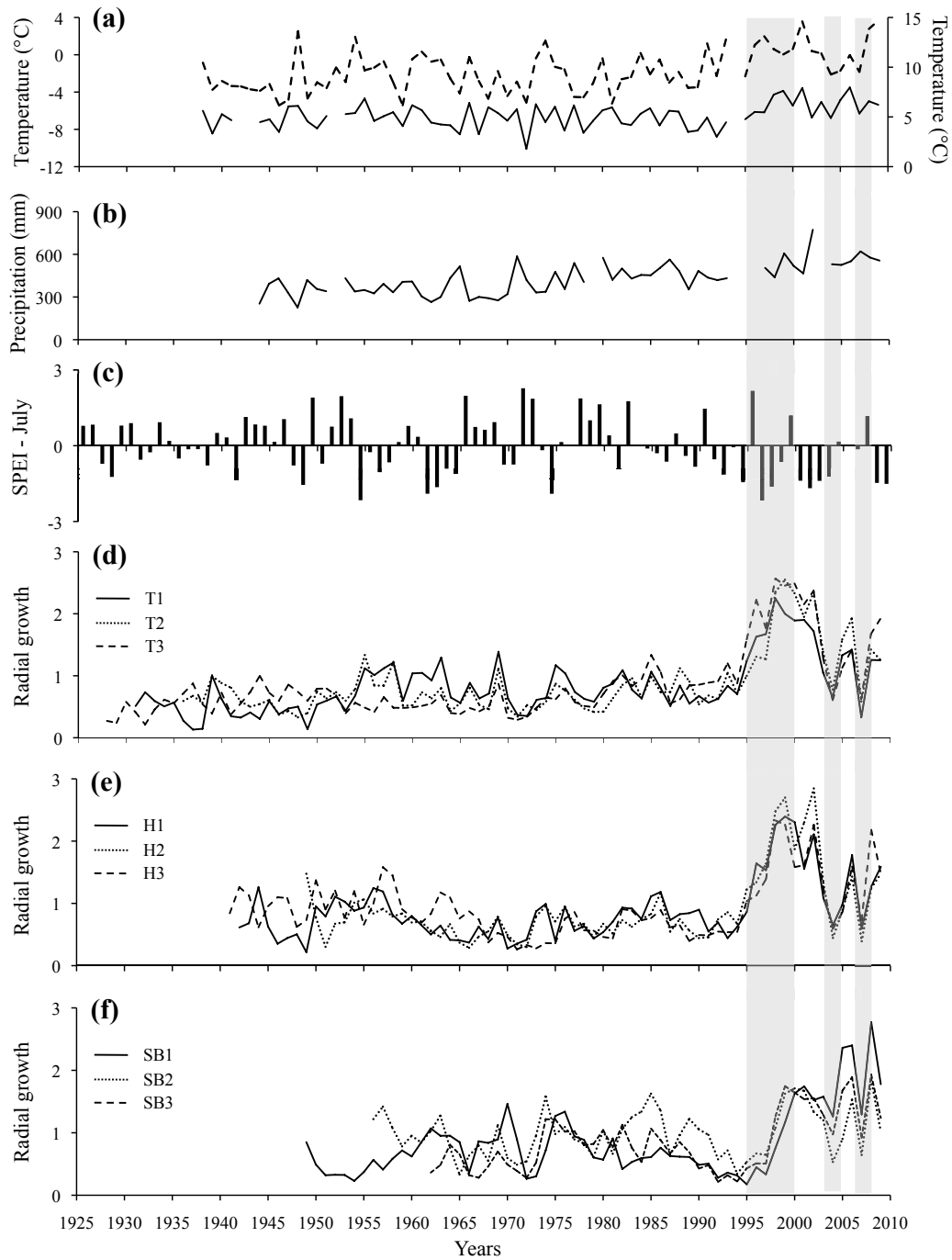


Figure 4.1 (a) Mean annual temperature (black line) and mean July temperature (dotted line), (b) total annual precipitation, (c) July Standardized Precipitation-Evapotranspiration Index (SPEI) and *Betula glandulosa* ring width chronologies for (d) terraces, (e) hilltops and (f) snowbeds. All ring width chronologies were standardized using a horizontal line fitted to the mean. Temperature and

precipitation data were recorded at the nearest weather station, the Inukjuak Meteorological Station (130 km northwest of the study site, subarctic Québec, Canada). SPEI values were extracted for the Boniface River area (0.5 degrees spatial resolution grid) from the Global SPEI database (<http://sac.csic.es/spei/database.html>). Values under 0 indicate negative water balance (drought) whereas values above 0 indicate positive water balance.

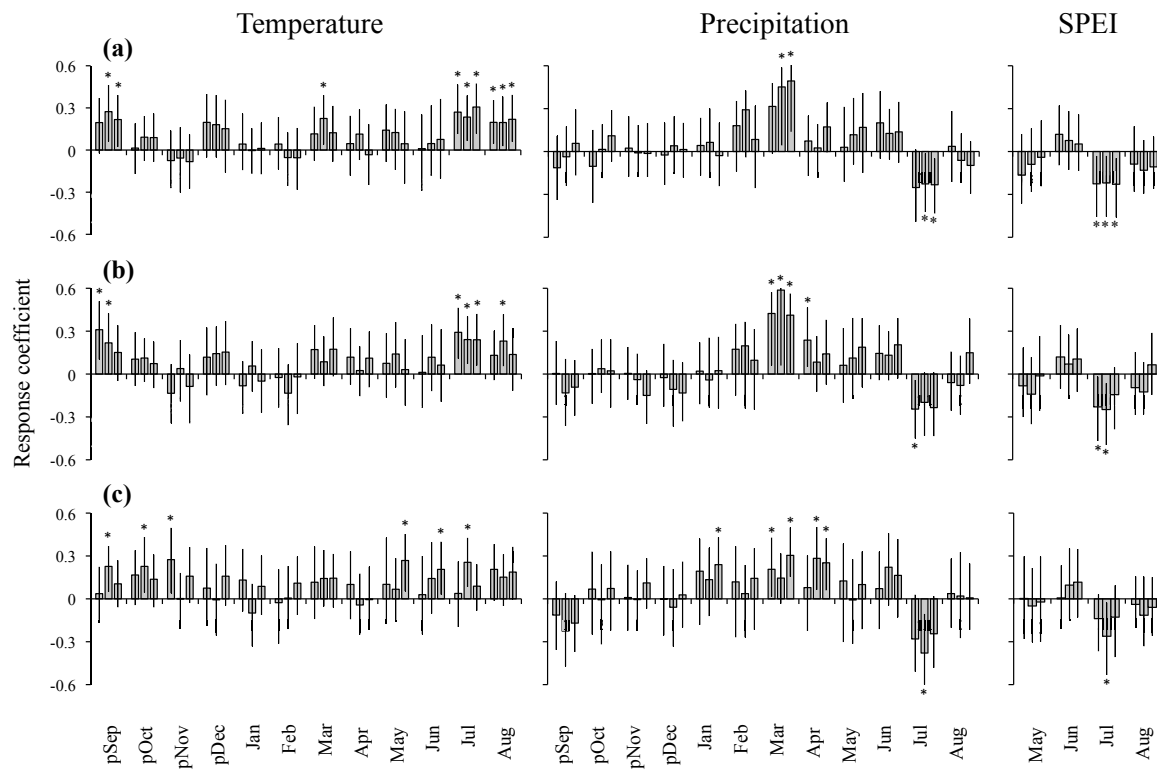


Figure 4.2 Response functions analysis showing the relationship between the different *Betula glandulosa* ring width chronologies on (a) terraces, (b) hilltops and (c) snowbeds and the monthly mean temperature (1946-2009 except 1952, 1979, 1994, 2001 and 2003), the monthly total precipitation (1946-2009 except 1952, 1979, 1994-2001, 2003, 2005 and 2007) and the SPEI for the growing season (1946-2009). Temperature and precipitation data were recorded at the Inukjuak Meteorological Station (130 km northwest of the study site, subarctic Québec, Canada). SPEI values were extracted for the Boniface River station (0.5 degrees spatial resolution grid) from the Global SPEI database (<http://sac.csic.es/spei/database.html>). The three chronologies of a same type of environment are presented in a unique graph. A *p* preceding a month stands for previous year. All significant coefficients (0.05) are indicated by an asterisk.

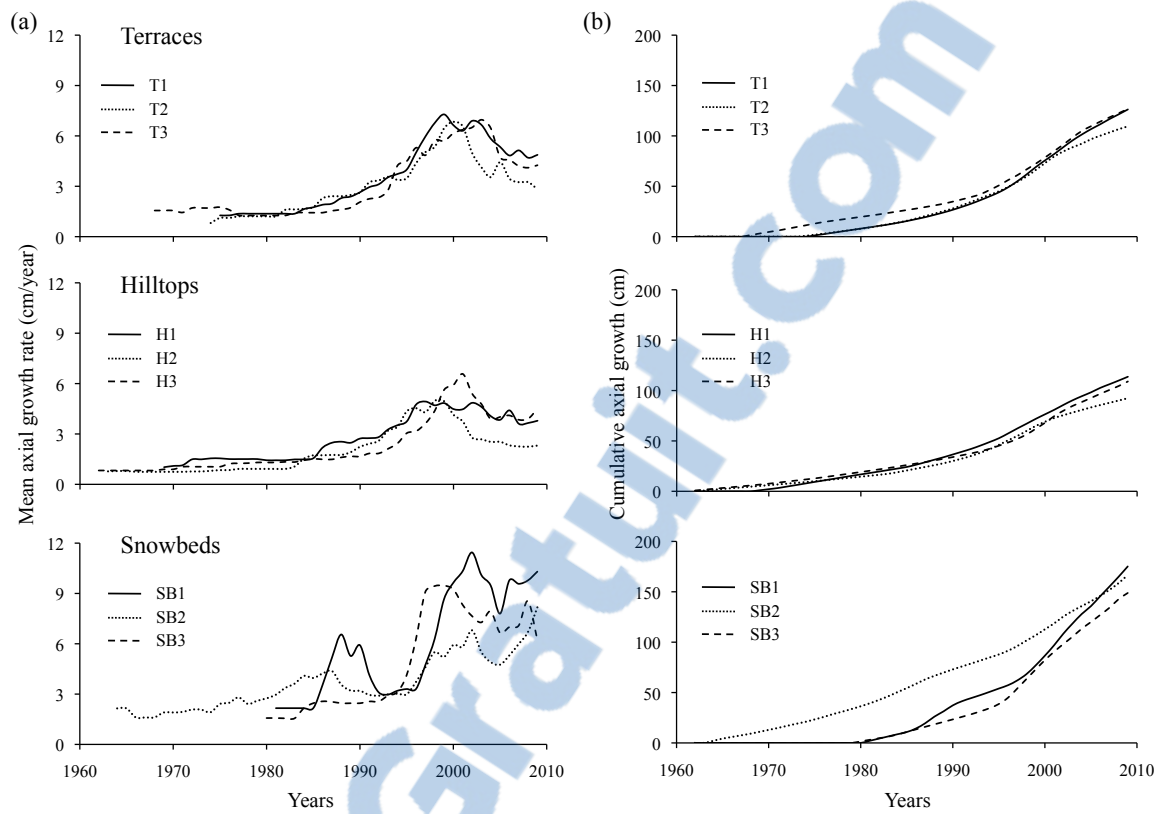


Figure 4.3 (a) Mean axial growth rates and (b) cumulative axial growth for each of the 9 sites studied at Boniface River region, subarctic Québec, Canada. Axial growth rates were inferred from the stem analysis for each branch. The annual mean axial growth rate was calculated when at least five individual branches were included.

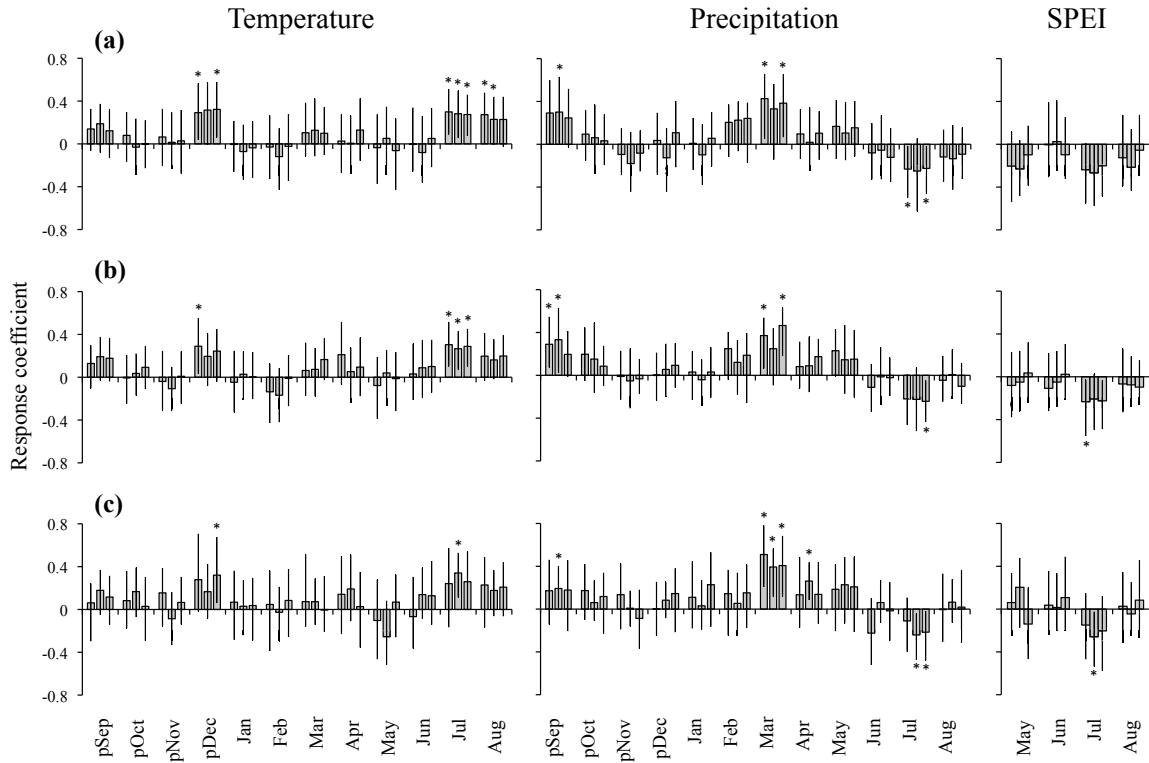


Figure 4.4 Response functions analysis showing the relationship between *Betula glandulosa* mean axial growth rate on (a) terraces, (b) hilltops and (c) snowbeds and the monthly mean temperatures (1946-2009 except 1952, 1979, 1994, 2001 and 2003), the monthly total precipitation (1946-2009 except 1952, 1979, 1994-2001, 2003, 2005 and 2007) and the SPEI for the growing season (1946-2009). Temperature and precipitation data were recorded at the Inukjuak Meteorological Station (130 km northwest of the study site, subarctic Québec, Canada). SPEI values were extracted for the Boniface River station (0.5 degrees spatial resolution grid) from the Global SPEI database (<http://sac.csic.es/spei/database.html>). The three chronologies of a same type of environment are presented in a single graph. A *p* preceding a month stands for previous year. All significant coefficients (0.01) are indicated by an asterisk.

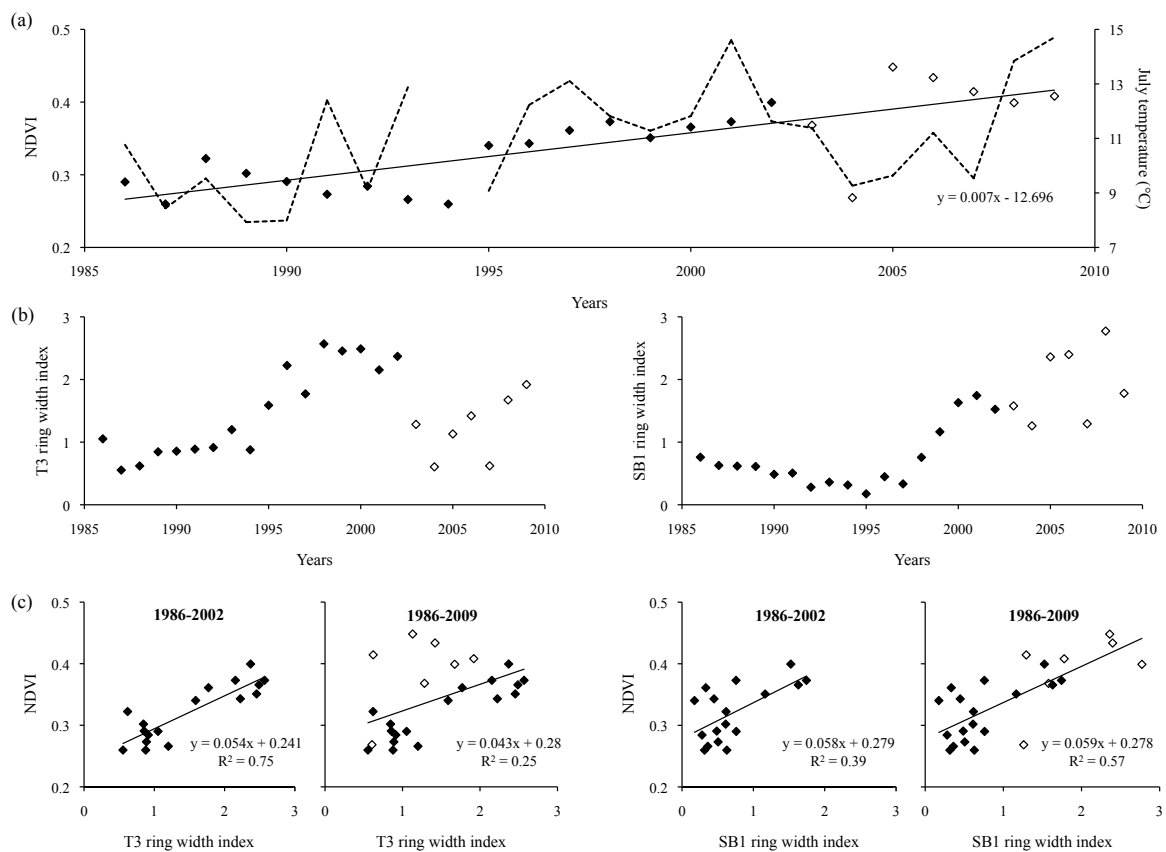


Figure 4.5 (a) Normalized difference vegetation index (NDVI) trend and July mean temperature (dotted line), (b) *Betula glandulosa* ring width chronologies (left: terrace, right: snowbed) and (c) regressions between NDVI and ring width chronologies for both the 1986-2002 and 1986-2009 periods. Dark dots represent the values for the 1986-2002 period, whereas the white ones represent the values for the remaining years (2003-2009).

4.11 Supporting information

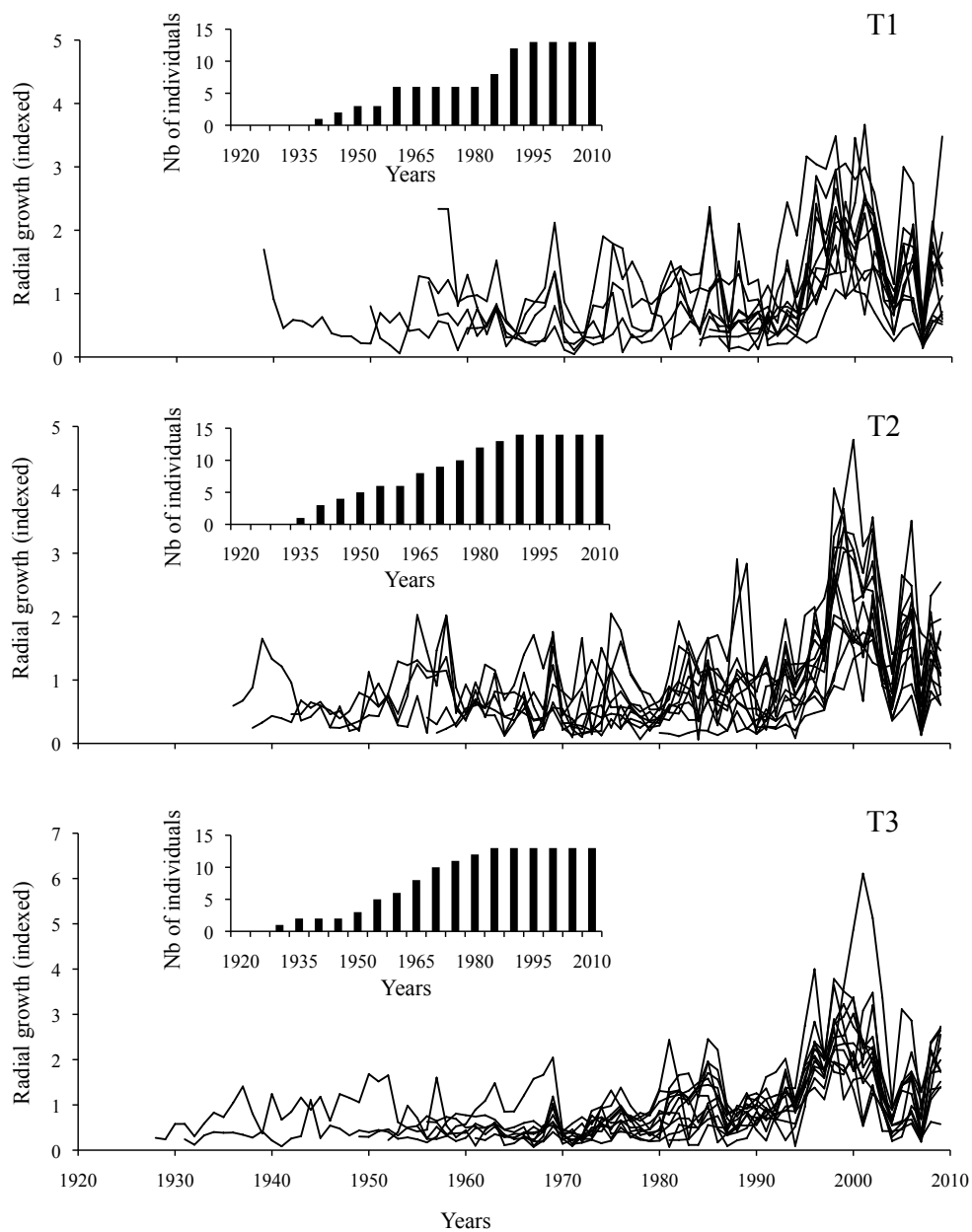
Table S4.1 Pearson correlation coefficients amongst the nine *Betula glandulosa* ring width chronologies from Boniface River station, subarctic Québec, Canada.

	T1	T2	T3	H1	H2	H3	SB1	SB2	SB3
T1	1	0.8576	0.771	0.7811	0.7768	0.6547	0.3715	0.5068	0.5855
T2		1	0.8361	0.8632	0.8546	0.7408	0.4668	0.5504	0.7041
T3			1	0.8527	0.8568	0.699	0.3641	0.4672	0.5643
H1				1	0.8463	0.7414	0.3155	0.6149	0.6587
H2					1	0.7829	0.3542	0.5247	0.6329
H3						1	0.4008	0.542	0.6552
SB1							1	0.4243	0.7736
SB2								1	0.6988
SB3									1

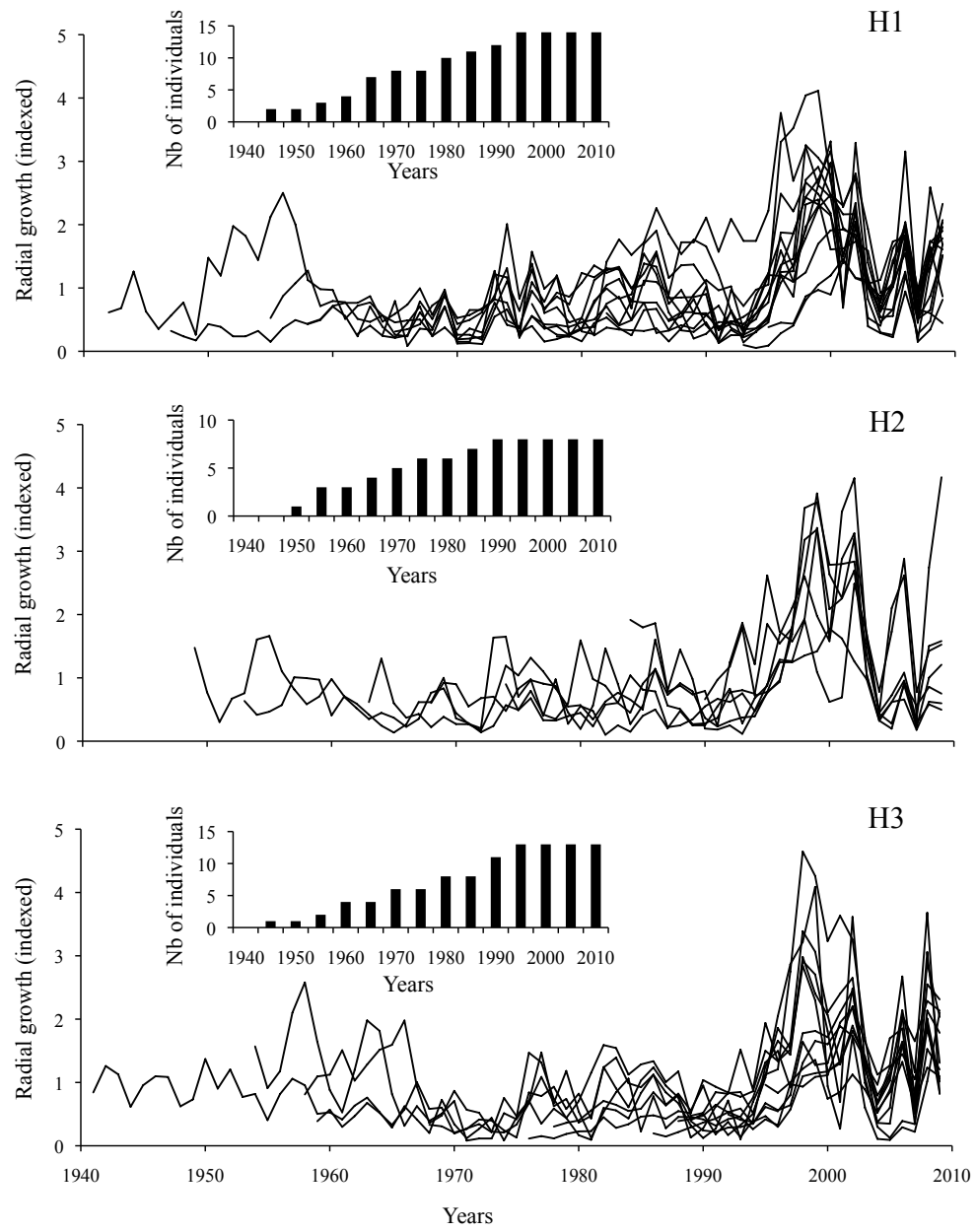
Table S4.2 Pearson correlation coefficients amongst the nine *Betula glandulosa* axial growth chronologies from Boniface River station, subarctic Québec, Canada.

	T1	T2	T3	H1	H2	H3	SB1	SB2	SB3
T1	1	0.9228	0.9689	0.9667	0.8238	0.9502	0.7622	0.7453	0.9514
T2		1	0.8695	0.9111	0.8964	0.9004	0.582	0.6223	0.8434
T3			1	0.9362	0.806	0.9388	0.7294	0.731	0.9032
H1				1	0.8958	0.905	0.6885	0.751	0.8989
H2					1	0.7965	0.2524	0.6016	0.7031
H3						1	0.8315	0.8603	0.9217
SB1							1	0.8391	0.7675
SB2								1	0.756
SB3									1

(a)



(b)



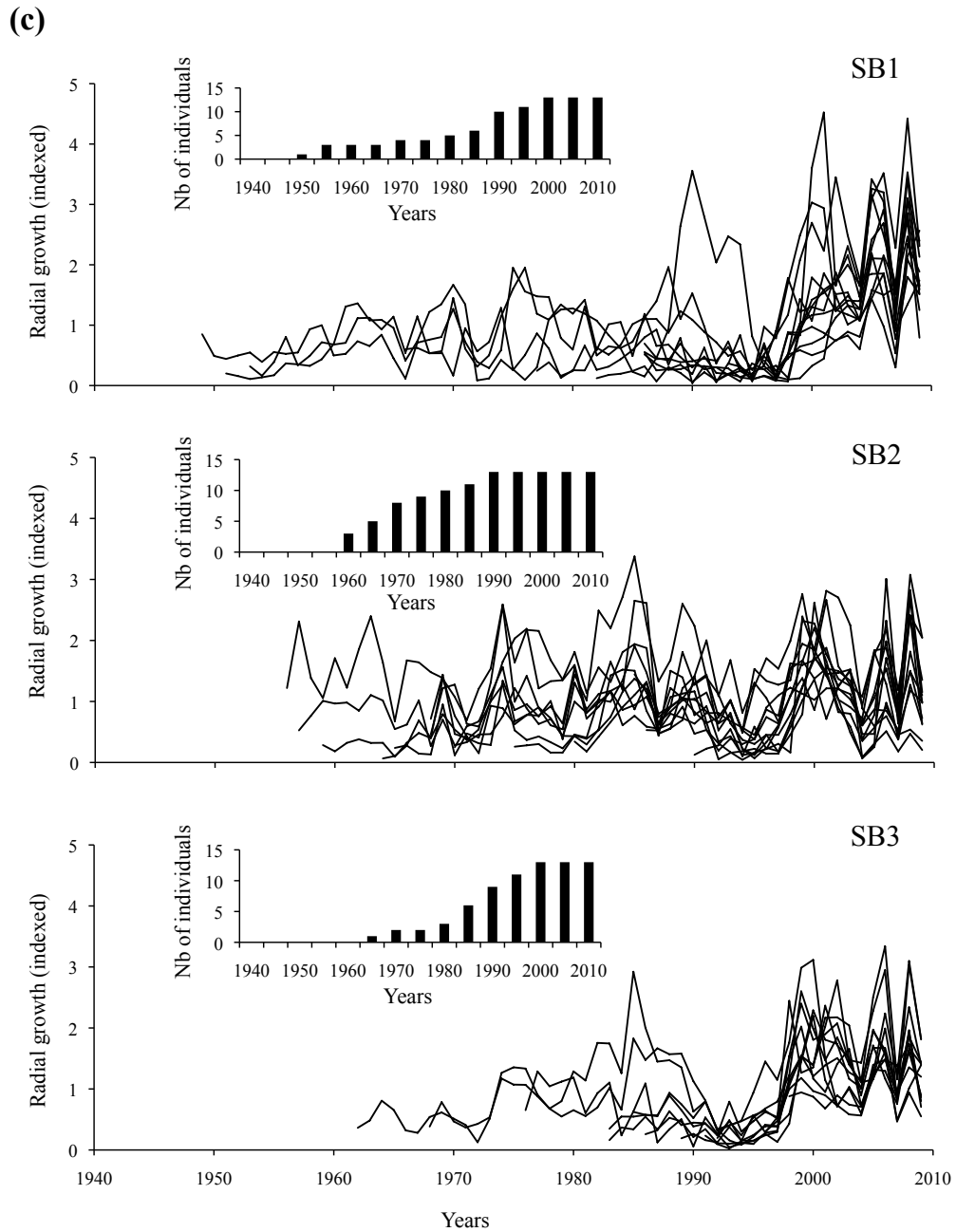
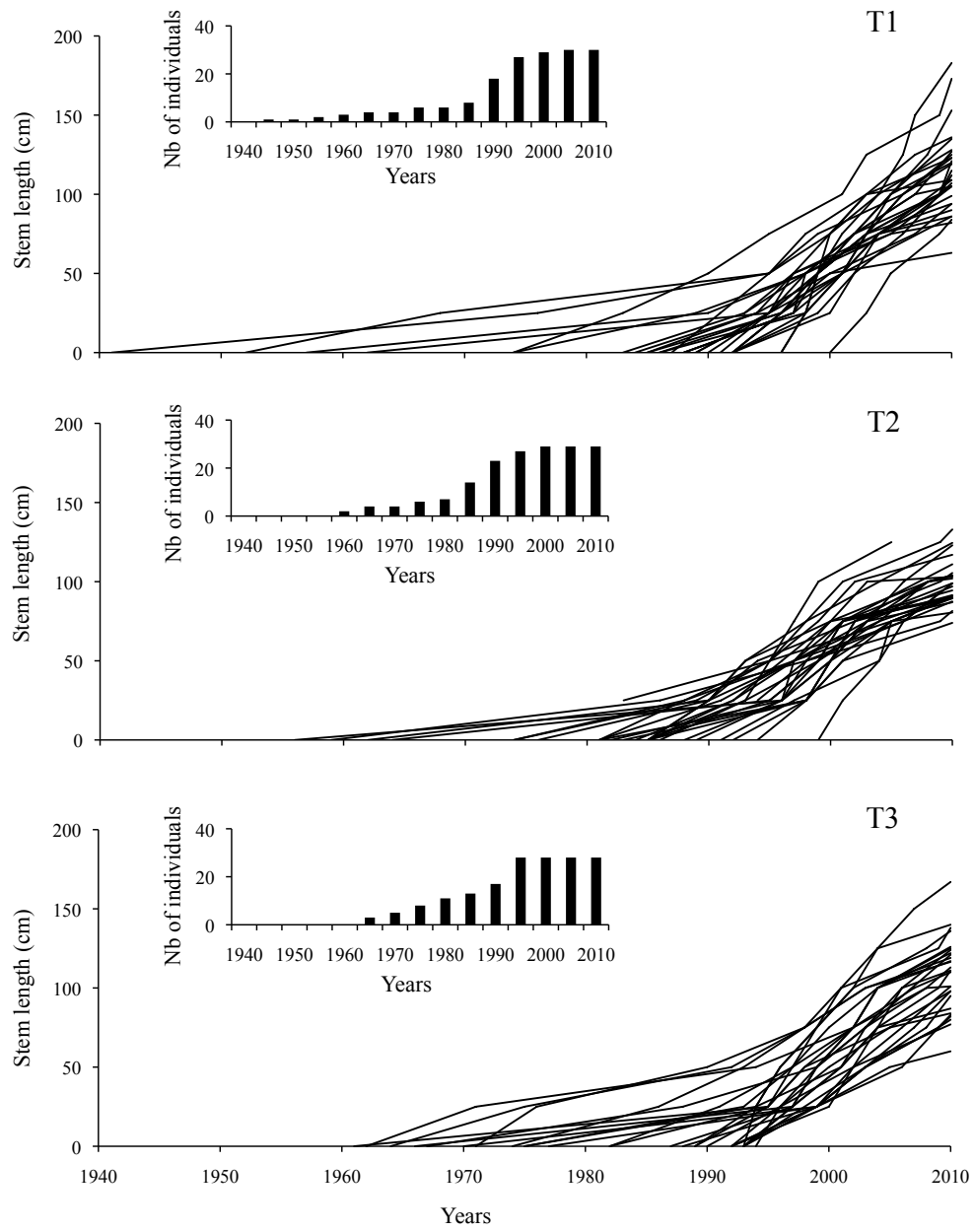
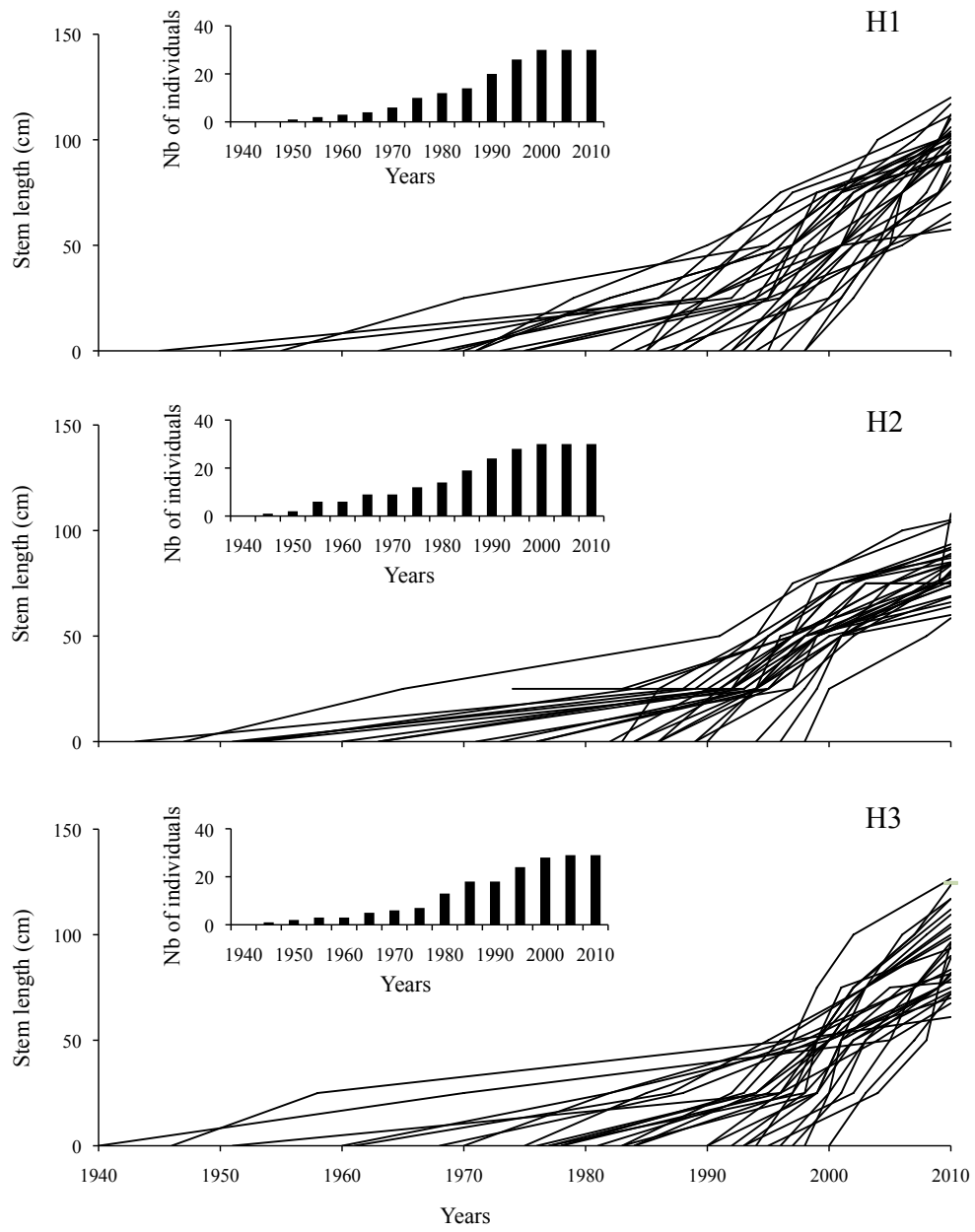


Figure S4.1 Age-growth relationships for each individual ring width chronologies per sites for (a) terraces, (b) hilltops and (c) snowbeds studied in the Boniface River region, northern Québec, Canada. Inset figures represent the age distribution of individual root collars included in the mean chronology.

(a)



(b)



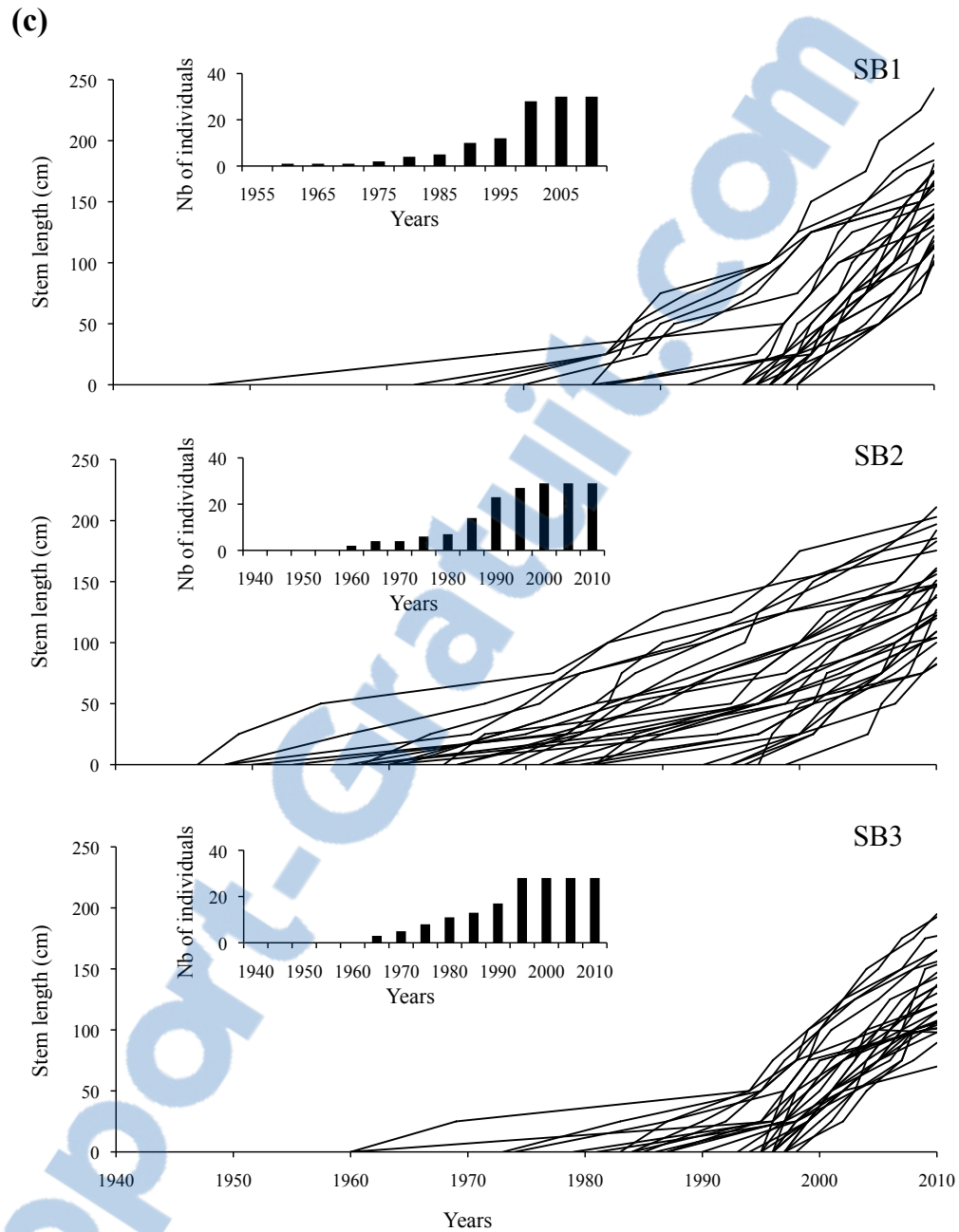


Figure S4.2 Age-growth relationships for each individual stem per sites for (a) terraces, (b) hilltops and (c) snowbeds studied in the Boniface River region, northern Québec, Canada. Inset figures represent the age distribution of individual stem used to calculate the mean axial growth rate.

CHAPITRE 5 Conclusions générales

Les changements climatiques récents et leurs effets déjà observables à l'échelle planétaire entraînent leur lot d'interrogations au sein de la communauté scientifique et de la population en général. Les régions nordiques, où les conséquences de ces changements sont parmi les plus importantes, sont au cœur des préoccupations environnementales. Dans ce contexte, des efforts considérables ont été mis en branle pour mieux comprendre la dynamique de ces environnements afin de mieux en prévoir les conséquences. Parmi les grands changements en cours dans ces régions, la densification de la strate arbustive est certainement l'un des plus importants.

Mon projet de thèse s'intègre dans cet effort de recherche en proposant une étude détaillée de la dynamique récente de la strate arbustive dans une région où celle-ci était peu connue, l'écotone forêt boréale-toundra du nord-ouest du Québec. De plus, mon projet s'intéresse particulièrement à *Betula glandulosa*, une espèce arbustive largement répandue en Amérique du Nord et qui a subi, au cours des dernières décennies, des changements dramatiques. Dans cette conclusion générale, je détaillerai les principaux résultats obtenus dans l'ensemble de mes travaux doctoraux, étayerai du même fait les principales contributions de ma thèse et exposerai les différentes perspectives qui en découlent.

5.1 Retour sur les résultats, contributions et limites

5.1.1 Étendue de la densification de la strate arbustive à l'écotone forêt boréale-toundra

Le chapitre 2 m'a permis de confirmer que la région de la rivière Boniface a connu une densification de sa strate arbustive au cours des dernières décennies. Cette densification a été enregistrée dans la très grande majorité des sites étudiés (54 sur 59) et ce, indépendamment du type d'environnement considéré. Bien qu'en moyenne la densification de la strate arbustive soit de 17 %, l'étendue de celle-ci varie grandement d'un site à l'autre (de -7,0 % à +47,4 % entre 1957 et 2008). Ces résultats suggèrent que la strate arbustive réagit à un signal régional important, mais que cette réponse est modulée par des facteurs

locaux propres aux sites où croissent les espèces impliquées dans ce phénomène. Dans le chapitre 2, j'ai également montré que *B. glandulosa* était la principale espèce responsable de la densification de la strate arbustive dans la région d'étude. Connue pour sa grande plasticité morphologique, cette espèce est aussi largement responsable de la densification de la strate arbustive dans deux autres portions de l'écotone forêt boréale-toundra au Québec subarctique (sud-est, région d'Umiujaq : Provencher-Nolet 2014 ; nord-est, région de Kangiqsualujjuaq : Tremblay *et al* 2012).

L'un des points forts de l'analyse réalisée dans ce chapitre est la résolution spatiale avec laquelle la densification de la strate arbustive a été quantifiée (mailles de 4 m x 4 m). En plus de permettre une évaluation fine de ce phénomène, l'analyse utilisée nous suggère que la densification de la strate arbustive dans la région d'étude avait un patron de répartition fortement agrégée, ce qui laisse penser que la densification s'est principalement effectuée grâce à une croissance clonale accrue. Sur le terrain cependant, plusieurs plantules de *B. glandulosa* ont été observées, en particulier sur le sol minéral mis à nu par le passage répété des caribous. Ceci suggère que le recrutement de nouveaux individus établis par graines pourrait lui aussi avoir joué un rôle dans la densification de la strate arbustive ou qu'il y jouera un rôle dans les décennies à venir. De plus, la présence importante de plantules de *B. glandulosa* dans les milieux piétinés par le caribou porte à croire qu'une perturbation préalable du milieu, que ce soit par les caribous ou par d'autres mécanismes (feu : Racine *et al* 2004, Lantz *et al* 2010, inondations : Tape *et al* 2006, 2012), peut favoriser une réponse positive des espèces arbustives face à l'adoucissement des températures de l'air.

Une autre force de l'analyse réalisée dans ce chapitre est la conjugaison de l'analyse de photographies aériennes à une validation exhaustive sur le terrain. Dans ce type d'analyse, une bonne connaissance du milieu ainsi qu'une validation sur le terrain sont nécessaires afin de confirmer les résultats obtenus. D'aussi bonnes qualités soient elles, les photographies utilisées lors de ce type d'analyse ne demeurent qu'un reflet de la réalité et peuvent donc être trompeuses. Dans cette étude, l'important couvert du bouleau glanduleux révélé par les relevés de végétation effectués sur le terrain suggérait déjà que cette espèce était responsable de la densification de la strate arbustive. Mais c'est grâce à la

géolocalisation des transects le long desquels ces relevés ont été réalisés que nous avons pu montrer hors de tout doute que le bouleau glanduleux en était bel et bien le principal responsable. En effet, le pourcentage de recouvrement du bouleau glanduleux évalué sur le terrain et celui évalué le long des mêmes transects sur l'image satellitaire de 2008 étaient très similaires, confirmant ainsi que ce que j'identifiais comme des arbustes dans mon analyse de photographies aériennes étaient bel et bien du bouleau glanduleux.

Il va sans dire cependant que l'analyse de photographies aériennes comporte certaines limitations et que celles-ci doivent être connues afin d'apprécier à leur juste valeur les résultats obtenus grâce à cette analyse. Premièrement, j'ai limité mon analyse de photographies aériennes aux types d'environnements où la strate arbustive est facilement distinguable des autres types de végétation. J'ai donc dû exclure les milieux humides ainsi que les peuplements forestiers, car les arbustes pouvaient être confondus avec le couvert muscinal ou arborescent. Bien que les milieux non forestiers et bien drainés représentent une forte proportion du paysage dans la région d'étude (près de 70 % du milieu terrestre), il n'en demeure pas moins que l'analyse réalisée ne donne aucune information sur la dynamique récente de la strate arbustive dans les milieux exclus de l'analyse. De plus, ce type d'analyse ne donne aucune information sur le moment où la densification de la strate arbustive s'est produite, ni même sur ses causes. Grâce à différentes analyses réalisées dans le cadre des deux autres chapitres, j'ai cependant réussi à répondre partiellement à ces questions.

5.1.2 Causes et conséquences de la densification de la strate arbustive

Comme mentionné précédemment, l'étendue de la densification de la strate arbustive montre une certaine hétérogénéité à l'échelle du paysage, et ce même à l'intérieur d'un même type d'environnement. Bien que l'importance de la densification enregistrée dans la région suggère un signal régional, cette hétérogénéité montre l'importance des caractéristiques locales contrôlant la croissance des espèces en place.

Dans le chapitre 3, j'ai montré que les facteurs qui expliquent le plus vraisemblablement l'hétérogénéité de la densification de la strate arbustive sont le temps écoulé depuis le dernier feu (facteur historique), le type d'environnement, l'altitude et l'épaisseur du couvert nival (facteurs topographiques). Parmi ces facteurs, le temps écoulé depuis le dernier feu semble être le plus important. Plus celui-ci est long, plus la densification de la strate arbustive est importante. Ceci suggère entre autres que des facteurs pédologiques reliés au temps depuis la dernière grande perturbation pourraient être importants pour expliquer la performance du bouleau glanduleux. Dans les milieux arctiques et subarctiques où tous les processus biologiques sont ralentis par les conditions climatiques difficiles, une longue période sans perturbation pourrait avoir favorisé un meilleur développement du sol, permettant ainsi l'accumulation d'une plus grande quantité de nutriments. De ce fait, le bouleau glanduleux aurait pu profiter de meilleures conditions de croissance sur les sites les plus âgés lorsque les températures se sont réchauffées dans les années 1990. Le type d'environnement, l'altitude ainsi que l'épaisseur du couvert nival pourraient eux aussi avoir une influence sur les caractéristiques pédologiques d'un site, notamment en ce qui a trait à la récurrence de phénomènes périglaciaires, à l'activité microbienne et à la rétention de l'eau et des nutriments.

L'approche par sélection de modèles avec le critère d'information d'Akaike utilisée pour déterminer les facteurs responsables de l'hétérogénéité de la densification de la strate arbustive est une approche robuste permettant de comparer plusieurs hypothèses (modèles) et d'en faire ressortir le ou les plus plausibles (c'est-à-dire ceux pour lesquels la perte d'information est la moins grande). Il faut cependant garder en tête que cette approche nous permet seulement de comparer les modèles que nous avons préalablement identifiés comme étant écologiquement valables, considérant les variables que nous avons mesurées sur le terrain. Dans mon analyse, le modèle le plus plausible pour expliquer l'hétérogénéité de la densification de la strate arbustive (temps écoulé depuis le dernier feu + type d'environnement + altitude + épaisseur du couvert nival) suggère que des facteurs reliés aux conditions pédologiques du site pourraient être importants pour expliquer le phénomène. Or, très peu de variables pédologiques ont été mesurées sur le terrain au moment de la récolte des données, limitant ainsi notre compréhension du phénomène et

l'interprétation que l'on peut en faire. Afin de peaufiner cette analyse, il serait donc pertinent d'inclure certaines variables reliées aux caractéristiques pédologiques déjà identifiées comme influençant la réponse de certaines espèces impliquées dans la densification arbustive (texture, humidité, densité, pH; Tape *et al* 2012).

Dans le chapitre 3, je me suis également intéressée aux conséquences de la densification du bouleau glanduleux sur les autres espèces de la strate arbustive. À l'instar de plusieurs autres études (Pajunen *et al* 2012), j'ai découvert qu'une augmentation du couvert de bouleau glanduleux avait un effet négatif sur le couvert des autres taxons. Cependant, aucune relation n'a été décelée entre la densification du bouleau glanduleux et différents indicateurs de la richesse spécifique (nombre d'espèces et indice de diversité de Shannon). Ce dernier résultat pourrait néanmoins qu'être simplement provisoire. En effet, le couvert relativement faible de bouleau glanduleux (< 60 % sur les sites les plus densément peuplés) pourrait ne pas être suffisant pour exclure complètement certaines espèces plus vulnérables à une forte compétition interspécifique telles que les espèces arctiques alpines. Dans l'éventualité où la densification de la strate arbustive se poursuivrait dans les prochaines années, il est donc probable que les espèces arbustives les plus vulnérables puissent être évincées de certains sites. Cependant, la diminution de croissance observée dans les dernières années sur les terrasses et les sommets nous laisse croire que la densification pourrait ne pas se poursuivre de façon aussi importante, à moins d'un fort recrutement ou d'un autre changement dans la dynamique de ces écosystèmes.

5.1.3 La relation entre le climat et la croissance de *Betula glandulosa*

L'analyse de photographies aériennes réalisées dans le cadre du chapitre 2 nous a révélé que la région de la rivière Boniface avait bel et bien connu une densification de sa strate arbustive au cours des cinq dernières décennies. Bien que cette densification soit généralement attribuée à l'augmentation récente des températures, cette analyse ne nous permettait pas de vérifier cette relation causale. De surcroît, nous ne pouvions non plus statuer sur la façon dont ce phénomène a évolué au cours des cinq décennies qui séparaient les deux séries de photographies aériennes ; la strate arbustive s'était-elle densifiée peu à

peu ou avait-elle au contraire connu une augmentation importante durant une courte période? L'analyse dendrochronologique exhaustive que j'ai réalisée dans le cadre du quatrième chapitre m'a permis d'apporter des éléments de réponses à ces interrogations.

Dans un premier temps, j'ai pu constater une forte augmentation de la croissance radiale et axiale du bouleau glanduleux entre les années 1990 et 2002, en particulier chez ceux trouvés sur les milieux bien drainés (terrasses et sommets). Parce que ces derniers représentent 70 % de la surface terrestre de la région à l'étude, ce résultat nous suggère que la densification de la strate arbustive enregistrée entre 1957 et 2008 (analyse de photographies aériennes) s'est produite en grande partie au cours des deux dernières décennies. De plus, la baisse importante de croissance enregistrée après 2002 pourrait signifier qu'un ralentissement dans la densification de la strate arbustive est en cours. Parmi les facteurs potentiellement responsables de cette baisse, notons par exemple les températures particulièrement froides du mois de juillet enregistrées en 2004 et 2007. De plus, la récurrence des années pour lesquelles le mois de juillet a enregistré un déficit d'humidité dans la dernière décennie (7 sur 10) pourrait expliquer le phénomène. La densification récente du bouleau glanduleux combinée à ce manque à gagner en eau dans des sites déjà bien drainés pourrait en effet entraîner une forte compétition intraspécifique et ainsi limiter la croissance de chaque individu en place. Ceci expliquerait également pourquoi la baisse de croissance chez le bouleau glanduleux n'est pas observée chez les individus croissant dans les milieux humides (combes à neige).

Deuxièmement, j'ai déterminé que la croissance radiale et axiale des bouleaux glanduleux présents dans les milieux bien drainés (terrasses et sommets) est fortement et positivement associée aux températures estivales. Ce résultat suggère que la densification de la strate arbustive observée dans la région d'étude est bel et bien associée au réchauffement climatique récent, comme c'est le cas pour plusieurs autres espèces arbustives dans différentes régions nordiques (voir Myers-Smith *et al* 2012 ainsi que les références qui y sont citées). Cependant, il est important de mentionner que cette relation croissance-climat n'est pas la même à l'échelle du paysage. En effet, la croissance radiale et axiale des individus présents dans les combes à neige est plutôt associée aux précipitations hivernales,

suggérant ainsi que les températures durant la saison de croissance peuvent ne pas être le facteur le plus limitant pour la croissance du bouleau glanduleux dans certains types d'environnement.

Pour terminer, j'ai pu montrer que l'augmentation de l'activité photosynthétique (NDVI) enregistrée dans la région de la rivière Boniface était fortement associée à la croissance du bouleau glanduleux, et ce particulièrement pour la période 1986-2002. Ceci suggère que cette espèce est la principale responsable de l'augmentation du NDVI dans la région, et constitue de ce fait un des points forts de mon analyse. En effet, il est souvent difficile d'estimer la contribution relative de chacun des groupes taxonomiques aux fluctuations du NDVI. En comparant directement la croissance radiale du bouleau glanduleux aux valeurs de NDVI, j'ai pu montrer que celle-ci expliquait jusqu'à 80 % de la variance de cet indice d'activité photosynthétique. Cependant, il est également possible que chacun des groupes taxonomiques répondent de la même façon à la hausse des températures. Bien que ceci se traduirait par une relation positive entre la croissance et le NDVI dans tous les cas, il est peu probable qu'un autre groupe taxonomique ait contribué autant que le bouleau glanduleux à l'augmentation du NDVI dans la région d'étude. En effet, cette espèce est de loin la plus abondante dans bon nombre de types d'environnement. Dans un autre ordre d'idées, la chute de croissance observée chez le bouleau glanduleux après 2002 ne semble pas s'être traduite pour une chute du NDVI ; cette apparente contradiction pourrait être expliquée par le fait que l'imposant appareil photosynthétique mis en place lors de la densification du bouleau glanduleux pourrait continuer à produire des valeurs élevées de NDVI, et ce malgré une chute de croissance individuelle.

Un autre point fort de l'analyse effectuée dans ce chapitre vient de l'imposant dispositif mis en place. En effet, la croissance radiale et axiale ont toutes deux été évaluées, et ce dans différents types d'environnement. Ceci m'a donc permis de tirer des conclusions sur l'ensemble de la croissance du bouleau glanduleux, en plus d'en apprécier les différences à l'échelle du paysage. Il va sans dire que dans le contexte actuel, il devient primordial d'avoir une bonne connaissance de la dynamique d'un acteur aussi important que la strate arbustive dans son ensemble et du bouleau glanduleux en particulier dans le Québec

nordique. Comprendre cette dynamique implique à la fois de connaître les patrons généraux, mais aussi d'en faire ressortir les différences locales. En évaluant la croissance du bouleau glanduleux dans trois types d'environnement différents, j'ai donc pu contribuer à peaufiner notre compréhension des patrons locaux de la strate arbustive.

Il demeure toutefois certains milieux où l'échantillonnage est difficile et donc pour lesquels nous n'avons aucune information concernant la dynamique de la strate arbustive. Bien que le bouleau glanduleux puisse y être présent en forte densité, les peuplements forestiers demeurent des milieux pour lesquels il est souvent ardu de trouver le collet de l'arbuste, c'est-à-dire sa partie la plus vieille. Dans certains cas, la base des plus grosses branches peut être récoltée afin d'effectuer des analyses dendrochronologiques, mais de plus en plus d'indices me portent à croire que ce type d'échantillonnage ne permet pas d'obtenir des résultats qui reflètent la réponse de l'ensemble de l'individu.

5.2 Perspectives

L'intérêt pour la strate arbustive dans le contexte des changements climatiques récents est grandissant depuis le début des années 2000 et souligne l'importance de celle-ci dans la dynamique des écosystèmes nordiques. J'ai, à travers cette thèse, mis l'épaule à la roue afin de peaufiner notre compréhension de la strate arbustive, en particulier celle d'une espèce largement répandue en Amérique du Nord mais encore peu étudiée, *Betula glandulosa*. Alors que ma thèse a permis, entre autres, de quantifier la densification de la strate arbustive dans la région de la rivière Boniface ainsi que d'en identifier certaines causes et conséquences, plusieurs questions restent en suspens ou ont émergé des résultats que j'ai obtenus. J'étayerai donc dans cette dernière section les différentes avenues possibles dans la poursuite de notre connaissance de la dynamique récente de la strate arbustive.

Comme je l'ai mentionné plus haut, l'analyse de photographies aériennes réalisée dans le cadre du deuxième chapitre m'a permis de quantifier la densification du couvert arbustif, mais également de constater que celle-ci s'était faite de façon agrégée. Ce résultat suggérait

que la densification s'était en grande partie effectuée grâce à une croissance clonale accrue, mais en aucun cas ne le confirmait. La contribution relative de la croissance clonale et du recrutement de nouveaux individus n'est donc pas connue pour la région à l'étude. Afin de mieux prédire les changements auxquels fera face la région de la rivière Boniface, il serait pertinent de connaître l'apport relatif de ces deux modes de recrutement. Des études génétiques de peuplements arbustifs en expansion pourraient entre autres être menées pour répondre à ces interrogations (voir Douhovnikoff *et al* 2010). De surcroît, nous connaissons mal la biologie de la reproduction du bouleau glanduleux (mais voir Weis et Hermanutz 1988) ; la germination des graines est-elle limitée par la température ? Quelles conditions édaphiques favorisent la production, la viabilité et la germination des graines de cette espèce ? Peaufiner nos connaissances sur cette sphère de la dynamique du bouleau glanduleux contribuerait à notre compréhension globale du phénomène.

Dans cette thèse, je me suis aussi intéressée à l'influence qu'un couvert plus important de bouleau glanduleux pouvait avoir sur les espèces arbustives non impliquées dans la densification récemment observée dans la région de la rivière Boniface. Bien que j'aie pu constater l'influence négative du bouleau glanduleux sur le couvert occupé par les autres espèces arbustives, il n'en demeure pas moins que nous avons peu d'information sur l'influence de la densification de la strate arbustive sur les autres strates présentes dans la région. Parmi ces dernières, notons par exemple la strate arborescente qui pourrait être particulièrement affectée par ce phénomène. En effet, la limite des arbres dans la région ne s'est pas déplacée vers le nord en réponse à l'adoucissement récent des températures. Cette absence de réponse est souvent attribuée au temps nécessaire à la production de graines viables de la principale espèce arborescente de la région (*Picea mariana* ; Lescop-Sinclair et Payette 1995, MacDonald *et al* 1998), mais pourrait également être reliée à la diminution du nombre et de l'étendue de sites propices à la germination des graines de cette espèce (sol minéral ; Dufour-Tremblay et Boudreau 2011). En formant un couvert dense où une grande quantité de litière s'accumule année après année, le bouleau glanduleux pourrait en effet limiter le recrutement nécessaire à une avancée nordique de la limite des arbres, mais également favoriser une plus grande récurrence des feux de forêts. Des études

expérimentales de germination sous différentes densités de bouleau glanduleux pourraient entre autres nous éclairer sur le rôle potentiel du bouleau glanduleux sur la strate arborescente et ainsi nous permettre de mieux prédire les changements à venir à l'écotone forêt boréale-toundra.

Il va sans dire que la densification de la strate arbustive entraîne son lot de conséquences dans les milieux où elle se produit, tant sur les conditions biotiques qu'abiotiques. Une plus grande densité d'arbustes érigés peut modifier les propriétés physiques de la neige (Liston *et al* 2002, Pomeroy *et al* 2006, Marsh *et al* 2010) et de ce fait favoriser une plus grande activité microbienne (Sturm *et al* 2005) ; elle peut également réduire la profondeur de dégel du pergélisol en diminuant la quantité d'intrants solaires atteignant le sol en été (Blok *et al* 2011). Par contre, ces conséquences sur l'environnement biotique et abiotique pourraient être modulées par l'architecture de croissance des espèces arbustives impliquées dans le phénomène de densification. Plusieurs espèces arbustives préalablement identifiées comme responsables étant à l'origine d'une densification récente de la strate arbustive à l'échelle circumpolaire, dont le bouleau glanduleux, sont connues pour leur grande plasticité morphologique (Bret-Harte *et al* 2001). Or, une croissance accrue en hauteur de ces espèces n'aura pas les mêmes conséquences qu'une croissance plutôt horizontale, notamment sur l'accumulation de neige. Une compréhension plus fine des stratégies de croissances adoptées par les arbustes ainsi que les conditions (édaphiques, topographies) expliquant l'adoption de l'une ou l'autre de ces stratégies me semblent essentielles afin de mieux prédire les conséquences d'une densification de la strate arbustive dans les régions nordiques.

Pour conclure, l'apport de ma thèse dans la compréhension de la dynamique de la strate arbustive est considérable, mais reste somme toute localisé à la région de la rivière Boniface. Il serait intéressant et primordial pour notre compréhension globale d'étendre cette étude à l'ensemble du Québec nordique dans un premier temps. Une étude récente de McManus et collaborateurs (2012) a révélé que l'activité photosynthétique (NDVI) avait

augmenté de façon particulièrement importante à l'écotone forêt boréale-toundra par rapport aux autres régions du Québec et que cette augmentation était hétérogène. Ce résultat soulève plusieurs questionnements, notamment en ce qui a trait à l'uniformité des causes de la densification de la strate arbustive. Nous savons déjà que le bouleau glanduleux est le principal responsable de ce phénomène dans différentes portions de l'écotone forêt boréale-toundra (Tremblay *et al* 2012, Provencher-Nolet 2014), mais est-il contrôlé par les mêmes facteurs climatiques qu'il l'est dans la région de la rivière Boniface ? De plus, l'augmentation moins importante de l'activité photosynthétique dans les autres régions est-elle expliquée par le fait que d'autres facteurs sont plus limitants que la température pour la croissance du bouleau glanduleux ou est-ce simplement le résultat d'un très faible couvert de la strate arbustive ? Un portrait général de la dynamique de la strate arbustive du Québec nordique pourrait de ce fait nous permettre de mieux comprendre l'influence d'un gradient latitudinal sur la croissance du bouleau glanduleux.

Je ne peux terminer cette thèse autrement qu'en spécifiant que la beauté de la recherche et ce qui la rend si intéressante réside dans le fait qu'elle soulève souvent plus de questionnements qu'elle n'y répond.

Bibliographie

- ACIA (2005) *Arctic climate impact assessment*. Cambridge University Press, Cambridge, UK. p. 1042.
- Allard M, Séguin MK (1987) Le pergélisol au Québec nordique : bilan et perspectives. *Géographie physique et Quaternaire* **41**: 141-152.
- Anderson PM, Brubaker LB (1994) Vegetation history of northcentral Alaska: a mapped summary of late-quaternary pollen data. *Quaternary Science Reviews* **20**: 194-214.
- Andrews JT, Mode WN, Webber PJ, Miller GH, Jacobs JD (1980) Report on the distribution of dwarf birches and present pollen rain, Baffin Island, N.W.T., Canada. *Arctic* **33**: 50-58.
- Anschlag K, Broll G, Holtmeier FK (2008) Mountain birch seedlings in the treeline ecotone, subarctic Finland: variation in above- and below-ground growth depending on microtopography. *Arctic, Antarctic and Alpine Research* **40**: 609-616.
- Anthelme F, Villaret JC, Brun JJ (2007) Shrub encroachment in the Alps gives rise to the convergence of subalpine communities on a regional scale. *Journal of Vegetation Science* **18**: 355-362.
- Arft AM, Walker MD, Gurevitch J, Alatalo JM, Bret-Harte MS, Dale M, Diemer M, Gugerli F, Henry GHR, Jones MH, Hollister RD, Jónsdóttir IS, Laine K, Lévesque E, Marion GM, Molau U, Molgaard P, Nordenhäll U, Raszhivin V, Robinson CH, Starr G, Stenström A, Totland O, Turner PL, Walker LJ, Webber PJ, Welker JM, Wookey PA (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* **69**: 491-511.
- Arseneault D, Payette S (1992) A postfire shift from lichen spruce to lichen tundra vegetation at tree line. *Ecology* **73**: 1067-1081.
- Arseneault D, Payette S (1997a) Landscape change following deforestation at the Arctic tree line in Quebec, Canada. *Ecology* **78**: 693-706.
- Arseneault D, Payette S (1997b) Reconstruction of millennial forest dynamics from tree remains in a subarctic tree line peatland. *Ecology* **78**: 1873-1883.
- Arseneault D, Sirois L (2004) The millennial dynamics of a boreal forest stand from buried trees. *Journal of Ecology* **92**: 490-504.

- Au R, Tardif JC (2007) Allometric relationship and dendroecology of the dwarf shrub *Dryas integrifolia* near Churchill, subarctic Manitoba. *Canadian Journal of Botany* **85**: 585-597.
- Baez S, Collins SL (2008) Shrub invasion decreases diversity and alters community stability in northern Chihuahuan Desert plant communities. *Plos One* **3**: e2332.
- Bär A, Pape R, Brauning A, Löffler J (2008) Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences *Journal of Biogeography* **35**: 625-636.
- Beck PSA, Goetz SJ (2011) Satellite observations of high northern latitude vegetation productivity changes between 1982 and 2008: ecological variability and regional differences. *Environmental Research Letters* **6**: 045501.
- Berg EE, McDonnell-Hillman K, Dial R, Deruwe A (2009) Recent woody invasion of wetlands on the Kenai Peninsula Lowlands, south-central Alaska: a major regime shift after 18 000 years of wet *Sphagnum*-sedge peat recruitment. *Canadian Journal of Forestry Research* **39**: 2033-2046.
- Bhiry N, Delwaide A, Allard M, Bégin Y, Filion L, Lavoie M, Nozais C, Payette S, Pienitz R, Saulnier-Talbot E, Vincent W (2011) Environmental change in the Great Whale River region: five decades of multidisciplinary research by Centre d'études nordiques (CEN). *Ecoscience* **18**: 182-203.
- Biondi F, Waikul K (2004) DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences* **30**: 303-311.
- Bliss LC, Matveyeva NV (1992) *Circumpolar Arctic vegetation*. Pages 59-89 in FS Chapin III (ed). *Arctic ecosystems in a changing climate: an ecophysiological perspective*. Academic Press, San Diego, CA, USA.
- Blok D, Heijmans MMPD, Schaepman-Strub G, Kononov AV, Maximov TC, Berendse F (2010) Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Global Change Biology* **16**: 1296-1305.
- Blok D, Sass-Klaassen U, Schaepman-Strub G, Heijmans MMPD, Sauren P, Berendse F (2011) What are the main climate drivers for shrub growth in Northeastern Siberian tundra? *Biogeosciences* **8**: 1169–1179.
- Bonan GB, Pollard D, Thompson SL (1992) Effects of boreal forest vegetation on global

- climate. *Nature* **359**: 716-718.
- Boudreau S, Payette S (2004) Caribou-induced changes in species dominance of lichen woodlands: an analysis of plant remains. *American Journal of Botany* **91**: 422-429.
- Boudreau S, Villeneuve-Simard MP (2012) Dendrochronological evidence of shrub growth suppression by trees in a subarctic lichen woodland. *Botany* **90**: 151–156.
- Boulanger-Lapointe N, Lévesque E, Boudreau S, Henre GHR, Schmidt NM (2014) Population structure and dynamics of Arctic willow (*Salix arctica*) in the High Arctic. *Journal of Biogeography* **41**: 1967-1978.
- Brathen KA, Oksanen J (2001) Reindeer reduce biomass of preferred plant species. *Journal of Vegetation Science* **12**: 473-480.
- Bret-Harte MS, Shaver GR, Zoerner JP, Johnstone JF, Wagner JL, Chavez AS, Gunkelman RF, Lippert SC, Laundre JA (2001) Developmental plasticity allows *Betula nana* to dominate tundra subjected to an altered environment. *Ecology* **82**: 18-32.
- Bret-Harte MS, Shaver GR, Chapin III FS (2002) Primary and secondary stem growth in arctic shrubs: implications for community response to environmental change. *Journal of Ecology* **90**: 251-267.
- Buckeridge KM, Zufelt E, Chu HY, Grogan P (2010) Soil nitrogen cycling rates in low arctic shrub tundra are enhanced by litter feedbacks. *Plant and Soil* **330**: 407-21.
- Burnham KP, Anderson DR (2002) *Model selection and multimodel inference: a practical information-theoretic approach, 2nd edition*. Springer, New York, USA.
- Callaghan TV (1973) A comparison of the growth of tundra plant species at several widely spaced sites. *Institute of Terrestrial Ecology, Merlewood Research and Development Paper*, No. 53.
- Camill P, Clark JS (1998) Long-term perspectives on lagged ecosystem responses to climate change: permafrost in boreal peatlands and the grassland/woodland boundary. *Ecosystems* **3**: 534-544.
- Cannone N, Sgorbati S, Guglielmin M (2007) Unexpected impacts of climate change on alpine vegetation. *Frontiers in Ecology and the Environment* **5**: 360-364.
- Chapin FS III, Shaver GR (1985) Individualistic growth response of tundra plant species to environmental manipulations in the field. *Ecology* **66**: 564-576.
- Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of

- arctic tundra to experimental and observed changes in climate. *Ecology* **76**: 694–711.
- Chapin FS III, Shaver GR (1996) Physiological and growth responses of arctic plants to a field experiment simulating climatic change. *Ecology* **77**: 822-840.
- Chapin FS III, Starfield AM (1997) Time lags and novel ecosystems in response to transient climatic change in arctic Alaska. *Climatic Change* **35**: 449-461.
- Chapin FS III, McGuire AD, Randerson J, Pielke R, Baldocchi D, Hobbie SE, Roulet N, Eugster W, Kasischke E, Rastetter EB, Zimov SA, Running SW (2000) Arctic and boreal ecosystems of western North America as components of the climate system. *Global Change Biology* **6**: 211-223.
- Chapin FS III, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd AH, McGuire AD, Rupp TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman LD, Jia G, Ping CL, Tape KD, Thompson CDC, Walker DA, Welker JM (2005) Role of land-surface changes in Arctic summer warming. *Science* **310**: 657-660.
- Chouinard C, Fortier R, Mareschal JC (2007) Recent climate variations in the subarctic inferred from three borehole temperature profiles in northern Québec, Canada. *Earth and Planetary Science Letters* **263**: 355-369.
- Couturier S, Jean D, Otto R, Rivard S (2004) Démographie des troupeaux de caribous migrants-toundriques (*Rangifer tarandus*) au Nord-du-Québec et au Labrador. Ministère des Ressources naturelles, de la Faune et des Parcs, Direction de l'aménagement de la faune du Nord-du-Québec, Direction de la recherche sur la faune, Québec, Canada.
- Cornelissen JHC, Callaghan TV, Alatalo JM, Michelsen A, Graglia E, Hartley AE, Hik DS, Hobbie SE, Press MC, Robinson CH, Henry GHR, Shaver GR, Phoenix GK, Jones DG, Jonasson S, Chapin III FS, Molau U, Neill C, Lee JA, Melillo JM, Sveinbjornsson B, Aerts R (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology* **89**: 984-994.
- Cornelissen JHC, van Bodegom PM, Aerts R, Callaghan TV, van Logtestijn RSP, Alatalo J, Chapin III FS, Gerdol R, Gudmundsson J, Gwynn-Jones D, Hartley AE, Hik DS, Hofgaard A, Jónsdóttir IS, Karlsson S, Klein JA, Laundre J, Magnusson B, Michelsen

- A, Molau U, Onipchenko VG, Quested HM, Sandvik SM, Schmidt IK, Shaver GR, Solheim B, Soudzilovskaia NA, Stenstrom A, Tolvanen A, Totland O, Wada N, Welker JM, Zhao XQ (2007) Global negative vegetation feedback to climate warming responses of leaf litter decomposition rates in cold biomes. *Ecology Letters* **10**: 619-627.
- Cranston BH, Hermanutz L (2013) Seed-seedling in conifers as a result of plant-plant interactions at the forest-tundra ecotone. *Plant Ecology & Diversity* **6**: 319-327.
- Crête M, Huot J, Gauthier L (1990) Food selection during early lactation by caribou calving on the tundra in Québec. *Arctic* **43**: 60-65.
- Daniëls FJA, de Molenaar JG, Chytry M, Tichy L (2011) Vegetation change in Southeast Greenland? Tasiilaq revisited after 40 years. *Applied Vegetation Science* **14**: 230-241.
- de Groot WJ, Thomas PA, Wein RW (1997) *Betula nana* L. and *Betula glandulosa* Michx. *Journal of Ecology* **85**: 241-264.
- DeLuca TH, Nilsson MC, Zackrisson O (2002) Nitrogen mineralization and phenol accumulation along a fire chronosequence in northern Sweden. *Oecologia* **133**: 206-214.
- Dial RJ, Berg EE, Timm K, McMahon A, Geck J. 2007. Changes in the alpine forest-tundra ecotone commensurate with recent warming in southcentral Alaska: evidence from orthophotos and field plots. *Journal of Geophysical Research* **112**: G04015.
- Dixon PM (2001) *Bootstrap resampling* in AH El-Shaarawi & WW Piegorsch (eds). The Encyclopedia of Environmetrics. Wiley, New York, USA.
- Dolezal J, Ishii H, Kyncl T, Takahashi K, Vetrova VP, Homma K, Sumida A, Hara T (2010) Climatic factors affecting radial growth of *Betula ermanii platyphylla* in Kamchatka. *Canadian Journal of Forest Research* **40**: 273-285.
- Dormann CF, Woodin SJ (2002) Climate change in the Arctic: using plant functional types in a meta-analysis of field experiments. *Functional Ecology* **16**: 4-17.
- Douhovnikoff V, Goldsmith GR, Tape KD, Huang C, Sur N, Bret-Harte MS (2010) Clonal diversity in an expanding community of arctic *Salix* spp. and a model for recruitment modes of arctic plants. *Arctic, Antarctic, and Alpine Research* **42**: 406-411.
- Ducruc JP, Zarnovican R (1976) Notes sur l'écologie de trois espèces ligneuses à la bordure méridionale de la baie d'Ungava, Nouveau-Québec: *Betula glandulosa*, *Larix*

laricina, *Picea mariana*. *Canadian Journal of Botany* **54**: 1775-1783.

- Dufour-Tremblay G, Boudreau S (2011) Black spruce regeneration at the treeline ecotone: synergistic impacts of climate change and caribou activity. *Canadian Journal of Forestry Research* **41**: 460-68.
- Dufour-Tremblay G, De Vriendt L, Lévesque E, Boudreau S (2012) The importance of ecological constraints on the control of multi-species treeline dynamics in eastern Nunavik, Québec. *American Journal of Botany* **99**: 1638-1646.
- Dullinger S, Dirnbock T, Grabherr G (2003) Patterns of shrub invasion into high mountain grasslands of the Northern Calcareous Alps, Austria. *Arctic, Antarctic, and Alpine Research* **35**: 434-441.
- Dullinger S, Dirnbock T, Kock R, Hochbichler E, Englisch T, Sauberer N, Grabherr G (2005) Interactions among tree-line conifers: differential effects of pine on spruce and larch. *Journal of Ecology* **93**: 948-957.
- Elmendorf SC, Henry GHR, Hollister RD, Bjork RG, Boulanger-Lapointe N, Cooper EJ, Cornelissen JHC, Day TA, Dorrepaal E, Elumeeva TG, Gill M, Gould WA, Harte J, Hik DS, Hofgaard A, Johnson DR, Johnstone JF, Jonsdottir IS, Jorgensen JC, Klanderud K, Klein JA, Koh S, Kudo G, Lara M, Levesque E, Magnusson B, May JL, Mercado-Diaz JA, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Onipchenko VG, Rixen C, Schmidt NM, Shaver GR, Spasojevic MJ, Porhallsdottir PE, Tolvanen A, Troxler T, Tweedie CE, Villareal S, Wahren CH, Walker X, Webber PJ, Welker JM, Wipf S (2012a) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change* **2**: 453-457.
- Elmendorf SC, Henry GHR, Hollister RD, Bjork RG, Bjorkman AD, Callaghan TV, Collier LS, Cooper EJ, Cornelissen JHC, Day TA, Fosaa AM, Gould WA, Gretarsdottir J, Harte J, Hermanutz L, Hik DS, Hofgaard A, Jarrad F, Jónsdóttir IS, Keuper F, Klanderud K, Klein JA, Koh S, Kudo G, Lang SI, Lowen V, May JL, Mercado J, Michelsen A, Molau U, Myers-Smith IH, Oberbauer SF, Pieper S, Post E, Rixen C, Robinson CH, Schmidt NM, Shaver GR, Stenstrom A, Tolvanen A, Totland O, Troxler T, Wahren CH, Webber PJ, Welker JM, Wookey PA (2012b) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters* **15**: 164-175.

- Environment Canada (2010) *Canadian climate normals or averages 1971-2000* URL http://www.climate.weatheroffice.ec.gc.ca/climate_normals.
- Environment Canada (2013) *Canadian climate normals or averages 1971-2000*. URL http://www.climate.weatheroffice.ec.gc.ca/climate_normals.
- Epstein HE, Calef MP, Walker MD, Chapin III FS, Starfield AM (2004a) Detecting changes in arctic tundra plant communities in response to warming over decadal time scales. *Global Change Biology* **10**: 1325-1334.
- Epstein HE, Beringer J, Gould WA, Lloyd AH, Thompson CD, Chapin III FS, Michaelson GJ, Ping CL, Rupp TS, Walker DA (2004b) The nature of spatial transitions in the Arctic. *Journal of Biogeography* **31**: 1917-1933.
- Eskelinen A, Oksanen J (2006) Changes in the abundance, composition and species richness of mountain vegetation in relation to summer grazing by reindeer. *Journal of Vegetation Science* **17**: 245-254.
- Filion L, Payette S (1982) Régime nival et végétation chionophile à Poste-de-la-Baleine, Nouveau-Québec. *Naturaliste Canadien* **109**: 557-571.
- Filion L (1984) A relationship between dunes, fire and climate recorded in the Holocene deposits of Québec. *Nature* **309**: 543-546.
- Fisher RF (1980) Allelopathy: a potential cause of regeneration failure. *Journal of Forestry* **78**: 346-350.
- Forbes BC, Ebersole JJ, Strandberg B (2001) Anthropogenic disturbance and patch dynamics in circumpolar arctic ecosystems. *Conservation Biology* **15**: 954-969.
- Forbes BC, Stammer F, Kumpula T, Meschytyb N, Pajunen A, Kaarlejarvia E (2009) High resilience in the Yamal-Nenets social-ecological system, West Siberian Arctic, Russia. *Proceedings of the National Academy of Sciences of the United States* **106**: 22041-22048.
- Forbes BC, Fauria MM, Zetterberg P (2010) Russian Arctic warming and “greening” are closely tracked by tundra shrub willows. *Global Change Biology* **16**: 1542-1554.
- Forest L, Padilla F, Martinez S, Demongeot J, San Martin J (2006) Modelling of auxin transport affected by gravity and differential radial growth. *Journal of Theoretical Biology* **241**: 241-251.
- Franklin RS (2013) Growth response of the alpine shrub, *Linanthus pungens*, to snowpack

- and temperature at a rock glacier site in the eastern Sierra Nevada of California, USA. *Quaternary International* **310**: 20-33.
- Fraser RH, Lantz TC, Olthof I, Kokelj SV, Sims RA (2014) Warming-induced shrub expansion and lichen decline in the western Canadian arctic. *Ecosystems*, doi: 10.1007/s10021-014-9783-3.
- Frost GV, Epstein HE, Walker DA, Matyshak G, Ermokhina K (2012) Linkages between patterned ground, alder shrubland development, and active layer temperature in Northwest Siberian Low Arctic. *Proceedings of the Tenth International Conference on Permafrost* **1**: 119-124.
- Frost GV, Epstein HE (2014) Tall shrub and tree expansion in Siberian tundra ecotones since the 1960s. *Global Change Biology* **20**: 1264-1277.
- Gamache I, Payette S (2004) Height growth response of tree line black spruce to recent climate warming across the forest-tundra of eastern Canada. *Journal of Ecology* **92**: 835-845.
- Gajewski K, Payette S, Ritchie JC (1993) Holocene vegetation history at the boreal-forest-shrub-tundra transition in north-western Québec. *Journal of Ecology* **81**: 433-443.
- Goetz SJ, Bunn AG, Fiske GJ, Houghton RA (2005) Satellite-observed photosynthetic trends across boreal North America associated with climate and fire disturbance. *Proceedings of the National Academy of Science* **102**: 13521-13525.
- Gordon C, Wynn JM, Woodin SJ (2001) Impacts of increased nitrogen supply on high Arctic heath: the importance of bryophytes and phosphorus availability. *New Phytologist* **149**: 461-471.
- Gough L (2006) Neighbor effects on germination, survival, and growth in two Arctic tundra plant communities. *Ecography* **29**: 44-56.
- Graae BJ, Alsos IG, Ejrnaes R. (2008) The impact of temperature regimes on development, dormancy breaking and germination of dwarf shrub seeds from arctic, alpine and boreal sites. *Plant Ecology* **198**: 275-284.
- Greene DF, Noel J, Bergeron Y, Rousseau M, Gauthier S (2004) Recruitment of *Picea mariana*, *Pinus banksiana*, and *Populus tremuloides* across a burn severity gradient following wildfire in the southern boreal forest of Québec. *Canadian Journal of Forest Research* **34**: 1845-1857.

- Grogan P, Chapin III FS (2000) Initial effects of experimental warming on above and belowground components of net ecosystem CO² exchange in arctic tundra. *Oecologia* **125**: 512-520.
- Hadley JL, Smith WK (1989) Wind erosion of leaf surface wax in alpine timberline conifers. *Arctic and Alpine Research* **21**: 392-398.
- Hallinger M, Manthey M, Wilmking M (2010) Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia. *New Phytologist* **186**: 890-899.
- Hantemirov R, Shiyatov S, Gorlanova L (2011) Dendroclimatic study of Siberian juniper. *Dendrochronologia* **29**: 119-122.
- Harsch MA, Hulme PE, McGlone MS, Duncan RP (2009) Are treelines advancing? A global meta-analysis of treeline response to climate warming. *Ecology Letters* **12**: 1040-1049.
- Hill GB, Henry GHR (2011) Responses of High Arctic wet sedge tundra to climate warming since 1980. *Global Change Biology* **17**: 276-287.
- Hobbie SE (1996) Temperature and plant species control over litter decomposition in Alaskan tundra. *Ecological Monographs* **66**: 503-522.
- Hobbie SE, Chapin III FS (1998a) An experimental test of limits to tree establishment in Arctic tundra. *Journal of Ecology* **86**: 449-461.
- Hobbie SE, Chapin III FS (1998b) Response of tundra plant biomass, aboveground production, nitrogen, and CO₂ flux to experimental warming. *Ecology* **79**: 1526-1544.
- Holmes RL (1983) Computer assisted quality control in tree ring dating and measurement. *Tree-Ring Bulletin* **43**: 69-78.
- Hudson JMG, Henry GHR (2009) Increased plant biomass in a high arctic heath community from 1981 to 2008. *Ecology* **90**: 2657-2663.
- Iason GR, Hester AJ (1993) The response of heather (*Calluna vulgaris*) to shade and nutrients - predictions of the carbon-nutrient balance hypothesis. *Journal of Ecology* **81**: 75-80.
- IPCC (2007a) *Climate Change 2007: The physical science basis*. Cambridge University Press, Cambridge, UK.

- IPCC (2007b) *Climate Change 2007: Impacts, adaptation and vulnerability*. Cambridge University Press, Cambridge, UK.
- IPCC (2013) *Climate Change 2013: The physical science basis*. Cambridge University Press, Cambridge, UK.
- Jia GSJ, Epstein HE, Walker DA (2003) Greening of the arctic Alaska, 1981-2001. *Geophysical Research Letters* **30**: 2067.
- Johnson JB, Omland KS (2004) Model selection in ecology and evolution. *Trends in Ecology and Evolution* **19**: 101-108.
- Joly K, Jandt RR, Meyers CR, Cole MJ (2007) Changes in vegetation cover on Western Arctic Herd winter range from 1981 to 2005; potential effects of grazing and climate change. *Rangifer* **17**: 199-206.
- Jonasson S, Michelsen A, Schmidt IK, Nielsen EV (1999) Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. *Ecology* **80**: 1828-1843.
- Jónsdóttir IS, Magnusson B, Gudmundsson J, Elmarsdóttir A, Hjartarson H (2005) Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology* **11**: 553-563.
- Jorgenson MT, Racine CH, Walters JC, Osterkamp TE (2001) Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change* **48**: 551-579.
- Jorgensen RH, Hallinger M, Ahlgrimm S, Friemel J, Kollmann J, Meilby (2015) Growth response to climatic change over 120 years for *Alnus viridis* and *Salix glauca* in West Greenland. *Journal of Vegetation Science* **26**: 155-165.
- Kemper JT, Macdonald SE (2009) Directional change in upland tundra plant communities 20-30 years after seismic exploration in the Canadian low-arctic. *Journal of Vegetation Science* **20**: 557-567.
- Klein JA, Harte J, Zhao XQ (2004) Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters* **7**: 1170-1179.
- Koerner C (2000) Biosphere responses to CO₂ enrichment. *Ecological Applications* **10**: 1590-1619.

- Kullman L (1995) Holocene tree-limit and climate history from the Scandes Mountains, Sweden. *Ecology* **76**: 2490-2502.
- Krause HH (1986) Ericaceous vegetation as a site factor in jack pine growth of New Brunswick plantation. Proceedings of IUFRO Workshop, Canadian Forest Service, Fredericton. 182 p.
- Landhausser SM, Wein RW (1993) Postfire vegetation recovery and tree establishment at the arctic treeline: climate-change vegetation-response hypotheses. *Journal of Ecology* **81**: 665–672.
- Lantz TC, Kokelj SV, Gergel SE, Henry GHR (2009) Relative impacts of disturbance and temperature: persistent changes in microenvironment and vegetation in retrogressive thaw slumps. *Global Change Biology* **15**: 1664-1675.
- Lantz TC, Gergel SE, Henry GHR (2010) Response of green alder (*Alnus viridis* subsp. *fruticosa*) patch dynamics and plant community composition to fire and regional temperature in north-western Canada. *Journal of Biogeography* **37**: 1597-1610.
- Larsen JA (1980) *The boreal ecosystem*. Academic Press, New York, USA.
- Latifovic R, Trishchenko PA, Chen J, Park MW, Khlopenkov VK, Fernandes AR, Pouliot D, Ungureanu C, Luo Y, Wang S, Davidson A, Cihlar J (2005) Generating historical AVHRR 1-km baseline satellite data records over Canada suitable for climate change studies. *Canadian Journal of Remote Sensing* **31**: 324-346.
- Lavallée C (2013) Impact de l'augmentation du couvert ligneux érigé et d'un réchauffement expérimental sur la productivité d'*Empetrum nigrum* L., *Vaccinium uliginosum* L. et *V. vitis-idaea* L. à Kangiqsujuaq et Kangiqsualujjuaq (Nunavik). Mémoire de maîtrise, Université du Québec à Trois-Rivières, Trois-Rivières, Québec.
- Lescop-Sinclair K, Payette S (1995) Recent advance of the arctic treeline along the eastern coast of Hudson Bay. *Journal of Ecology* **83**: 929-936.
- Liang EY, Eckstein D (2009) Dendrochronological potential of the alpine shrub *Rhododendron nivale* on the south-eastern Tibetan Plateau. *Annals of Botany* **104**: 665-670.
- Liston GE, McFadden JP, Sturm M, Pielke RA (2002) Modeled changes in arctic tundra snow, energy and moisture fluxes due to increased shrubs. *Global Change Biology* **8**: 17-32.

- Lloyd AH, Rupp TS, Fastie CL, Starfield A (2002) Patterns and dynamics of treeline advance on the Seward Peninsula, Alaska. *Journal of Geophysical Research-Atmospheres* **107** (D2): 8161.
- Lloyd AH, Fastie CL (2003) Recent changes in treeline forest distribution and structure in interior Alaska. *Ecoscience* **10**: 176-185.
- Lloyd AH, Yoshikawa K, Fastie CL, Hinzman L, Fraver M (2003) Effects of permafrost degradation on woody vegetation at Arctic treeline on the Seward Peninsula, Alaska. *Permafrost and Periglacial Processes* **14**: 93-101.
- Loranty MM, Goetz SJ, Beck PSA (2011) Tundra vegetation effects on pan-arctic albedo. *Environmental Research Letters* **6**: 024014.
- MacDonald GM, Edwards TWD, Moser KA, Pienitz R, Smol JP (1993) Rapid response of treeline vegetation and lakes to past climate change. *Nature* **361**: 243-246.
- MacDonald GM, Case RA, Szeicz JM (1998) A 538-year record of climate and treeline dynamics from the lower Lena River region of northern Siberia, Russia. *Arctic and Alpine Research* **30**: 334-339.
- MacDonald SE, Yin FY (1999) Factors influencing size inequality in peatland black spruce and tamarack: evidence from post-drainage release growth. *Journal of Ecology* **87**: 404-412.
- Mack M, Schuur EA, Bret-Harte MS, Shaver GR, Chapin FS III (2004) Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* **431**: 440-443.
- Mackay JR, Burn CR (2011) A century (1910-2008) of change in a collapsing pingo, Parry Peninsula, Western Arctic Coast, Canada. *Permafrost and Periglacial Processes* **22**: 266-272.
- Maillette L, Bélisle L, Séguin MK (1988) Decrease in competitive ability through adaptation to the physical environment, exemplified by *Salix uva-ursi* in the tundra of northern Québec. *Canadian Journal of Botany* **66**: 1532-1538.
- Mallik AU (1994) Autecological response of *Kalmia angustifolia* to forest types and disturbance regime. *Forest Ecology Management* **65**: 231-249.
- Mallik AU (1995) Conversion of temperate forests into heaths: role of ecosystem disturbance and ericaceous plants. *Environmental Management* **19**: 675-684.

- Mallik AU (2003) Conifer regeneration problems in boreal and temperate forests with ericaceous understory: role of disturbance, seedbed limitation, and keystone species change. *Critical Reviews in Plant Science* **22**: 341-366.
- Manseau M, Huot J, Crête M (1996) Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. *Journal of Ecology* **84**: 503-513.
- Marchand PJ, Chabot BF (1978) Winter water relations of tree-line plant species on Mt. Washington, New Hampshire. *Arctic and Alpine Research* **10**: 105-116.
- Marsh P, Russel M, Pohl S, Haywood H, Onclin C (2009) Changes in thaw lake drainage in the Western Canadian Arctic from 1950 to 2000. *Hydrological Processes* **23**: 145-158.
- Marsh P, Bartlett P, MacKay M, Pohl S, Lantz T (2010) Snowmelt energetics at a shrub tundra site in the western Canadian Arctic. *Hydrological Processes* **24**: 3603–3620.
- Mazerolle MJ (2006) Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia* **27**: 169-180.
- Mazerolle MJ (2014) Package 'AICcmodavg'. <http://cran.r-project.org/web/packages/AICcmodavg/AICcmodavg.pdf>
- McManus KM, Morton DC, Masek JG, Wang DD, Sexton JO, Nagol JR, Ropars P, Boudreau S (2012) Satellite-based evidence for shrub and graminoid tundra expansion in northern Quebec from 1986 to 2010. *Global Change Biology* **18**: 2313-2323.
- Morin H, Payette S (1986) The vegetation of snow patches from the Richmond Gulf, northern Québec. *Canadian Journal of Botany* **64**: 1515-1524.
- Mueller-Dombois D, Ellenberg H (1974) *Aims and methods of vegetation ecology*. Wiley, New York, USA.
- Myers-Smith IH (2011) Shrub encroachment in arctic and alpine tundra: mechanisms of expansion and ecosystem impacts. PhD thesis, University of Alberta, Edmonton, Canada.
- Myers-Smith IH, Forbes BC, Wilmsking M, Hallinger M, Lantz T, Blok D, Tape KD, Marcias-Fauria M, Sass-Klaassen U, Lévesque E, Boudreau S, Ropars P, Hermanutz

- L, Trant A, Collier LS, Weijers S, Rozema J, Rayback SA, Schmidt NM, Schaepman-Strub G, Wipf S, Rixen C, Menard CB, Venn S, Goetz S, Andreu-Hayles L, Elmendorf S, Ravolainen V, Welker J, Grogan P, Epstein HE, Hik DS (2011a) Shrub expansion in tundra ecosystems: dynamics, impacts and research priorities. *Environmental Research Letters* **6**: 045509.
- Myers-Smith IH, Hik DS, Kennedy C, Cooley D, Johnstone JF, Kenney A, Krebs CJ (2011b) Expansion of canopy-forming willows over the twentieth century on Herschel Island, Yukon Territory, Canada. *Ambio* **40**: 610-623.
- Myers-Smith IH, Hik DS (2013) Shrub canopies influence soil temperatures but not nutrient dynamics: an experimental test of tundra snow-shrub interactions. *Ecology and Evolution* **3**: 3683-3700.
- Myers-Smith IH, Elmendorf SC, Beck PSA, Wilmking M, Hallinger M, Blok D, Tape KD, Rayback SA, Macias-Fauria M, Forbes BC, Speed JDM, Boulanger-Lapointe N, Rixen C, Lévesque E, Schmidt NM, Baittinger C, Trant AJ, Hermanutz L, Collier LS, Dawes MA, Lantz TC, Weijers S, Jorgensen RH, Buchwal A, Buras A, Naito AT, Ravolainen V, Schaepman-Strub G, Wheeler JA, Wipf S, Guay KC, Hik DS, Vellend M (2015) Climate sensitivity of shrub growth across the tundra biome. *Nature Climate Change*, DOI: 10.1038/NCLIMATE2697.
- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increased plant growth in the northern latitudes from 1981 to 1991. *Nature* **386**: 698-702.
- Myneni RB, Tucker CJ, Asrar G, Keeling CD (1998) Interannual variations in satellite-sensed vegetation index data from 1981 to 1991. *Journal of Geophysical Research-Atmospheres* **103**: 19839.
- Naito AT, Cairns DM (2011) Patterns and processes of global shrub expansion. *Progress in Physical Geography* **35**: 423-442.
- Nilsson MC, Hogberg P, Zackrisson O, Wang FY (1993) Allelopathic effects by *Empetrum hermaphroditum* on development and nitrogen uptake by roots and mycorrhizae of *Pinus sylvestris*. *Canadian Journal of Botany* **71**: 620-628.
- Nilsson MC, Zackrisson O, Sterner O, Wallsted A (2000) Characterization of the differential interference effects of two boreal dwarf shrub species. *Oecologia* **123**: 122-128.

- Nilsson MC, Wardle DA (2005) Understory vegetation as a forest ecosystem driver: evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment* **3**: 421-428
- Oksanen L, Virtanen R (1997) *Adaptation to disturbance as a part of the strategy of arctic and alpine plants. Perspectives for management and restoration*. Pages 91-113 in RMM Crawford (ed). Disturbance and recovery in arctic lands. Kluwer, Belgium.
- Olofsson J, Oksanen L, Callaghan T, Hulme PE, Oksanen T, Suominen O (2009) Herbivores inhibit climate-driven shrub expansion on the tundra. *Global Change Biology* **15**: 2681-2693.
- Olthof I, Pouliot D (2010) Treeline vegetation composition and change in Canada's western subarctic from AVHRR and canopy reflectance modeling. *Remote Sensing of Environment* **114**: 805-815.
- Pajunen A, Oksanen J, Virtanen R (2011) Impact of shrub canopies on understory vegetation in western Eurasian tundra. *Journal of Vegetation Science* **22**: 837-846.
- Pajunen A, Virtanen R, Roininen H (2012) Browsing-mediated shrub canopy changes drive composition and species richness in forest-tundra ecosystems. *Oikos* **121**: 1544-1552.
- Parnesan C (2006) Ecological and evolutionary responses to recent climate change. *Annual Review of Ecology, Evolution, and Systematics* **37**: 637-669.
- Parnikoza I, Convey P, Dykyyz I, Trokhymets V, Milinevsky G, Tyschenko O, Inozemtseva D, Kozeretska I (2009) Current status of the Antarctic tundra formation in the Central Argentine Islands. *Global Change Biology* **15**: 1685-1693.
- Payette S, Filion L, Ouzilleau J (1973) Snow vegetation relationships in the forest tundra of New-Québec Hudson Bay. *Naturaliste Canadien* **100**: 493-508.
- Payette S, Lajeunesse R (1980) Les combes à neige de la Rivière aux Feuilles (Nouveau-Québec) : indicateurs paléoclimatiques holocènes. *Géographie physique et Quaternaire* **34**: 209-220.
- Payette S (1983) The forest tundra and present tree-lines of the northern Québec-Labrador peninsula. *Tree-line Ecology, Proceedings of the Northern Québec Tree-line Conference* (Québec: Nordica) p. 3-23
- Payette S, Boudreau F, Gagnon R (1985) Gélifluxion néoglaciale dans une combe à neige à la limite des arbres (Québec Nordique). *Géographie physique et Quaternaire* **39**:

91-97.

- Payette S, Gagnon R (1985) Late Holocene deforestation and tree regeneration in the forest-tundra of Québec. *Nature* **313**: 570-572.
- Payette S (1992) *Fire as a controlling process in the North American boreal forest*. Pages 144-169 in HH Shugart, R Leemans & GB Bonan (eds). A systems analysis of the global boreal forest. Cambridge University Press, Cambridge.
- Payette S, Morneau C (1993) Holocene relict woodlands at the eastern Canadian tree line *Quaternary Research* **39**: 84-89.
- Payette S (2001) *Les processus et les formes périglaciaires*. Pages 199-239 in S Payette & L Rochefort (eds). Écologie des tourbières du Québec-Labrador. Presses de l'Université Laval, Québec, Canada.
- Payette S, Fortin MJ, Gamache I (2001) The subarctic forest-tundra: the structure of a biome in a changing climate. *BioScience* **51**: 709-718.
- Payette S, Filion L, Delwaide A (2008) Spatially explicit fire-climate history of the boreal forest-tundra (eastern Canada) over the last 2000 years. *Philosophical Transactions of the Royal Society B: Biological Sciences* **363**: 2301-2316.
- Pérez-Devesa M, Cortina J, Vilagrosa A, Vallejo R (2008) Shrubland management to promote *Quercus suber* L. establishment. *Forest Ecology and Management* **255**: 374-382.
- Plante S, Champagne E, Ropars P, Boudreau S, Lévesque E, Tremblay B, Tremblay JP (2014) Shrub cover in northern Nunavik: can herbivores limit shrub expansion? *Polar Biology* **37**: 611-619.
- Pomeroy JW, Bewley DS, Essery RLH, Hedstrom NR, Link T, Granger RJ, Sicart JE, Ellis CR, Janowicz JR (2006) Shrub tundra snowmelt. *Hydrological Processes* **20**: 923-941.
- Poore RE, Lamanna CA, Ebersole JJ, Enquist BJ (2009) Controls on radial growth of Mountain Big Sagebrush and implications for climate change. *Western North American Naturalist* **69**: 556-562.
- Porsild AE, Cody WJ (1980) *Vascular plants of continental Northwest Territories, Canada*. National Museum of Natural Sciences, Natural Museums of Canada. Ottawa, Canada.
- Post E, Pedersen C (2008) Opposing plant community responses to warming with and

- without herbivores. *Proceedings of the Natural Academy of Sciences* **105**: 12353-12358.
- Provencher-Nolet L (2014) Détection de changement à court terme de la toundra arbustive à partir de photographies aériennes, région d'Umiujaq, Nunavik (Québec, Canada). Mémoire de maîtrise, Institut national de la recherche scientifique, Québec.
- Racine C, Jandt R, Meyers C, Dennis J (2004) Tundra fire and vegetation change along a hillslope on the Seward Peninsula, Alaska, USA. *Arctic, Antarctic and Alpine Research* **36**: 1-10.
- Raynolds MK, Walker DA, Maier HA (2006) NDVI patterns and phytomass distribution in the circumpolar Arctic. *Remote Sensing of Environment* **102**: 271-281.
- Rinnan R, Stark S, Tolvanen A (2009) Responses of vegetation and soil microbial communities to warming and simulated herbivory in a subarctic heath. *Journal of Ecology* **97**: 788-800.
- Rodwell JS (1991) *British plant communities*, vol 2. *Mires and heaths*. Cambridge University Press, Cambridge, UK.
- Romanovsky VE, Osterkamp TE (1995) Interannual variations of the thermal regime of the active layer and near-surface permafrost in northern Alaska. *Permafrost and Periglacial Processes* **6**: 313-315.
- Ropars P, Boudreau S (2012) Shrub expansion at the forest tundra ecotone: spatial heterogeneity linked to local topography. *Environmental Research Letters* **7**: 015501.
- Ropars P, Lévesque E, Boudreau S (2015) How do climate and topography influence the greening of the forest-tundra ecotone in northern Quebec? A dendrochronological analysis of *Betula glandulosa*. *Journal of Ecology* **103**: 679-690.
- Schimel JP, Gullledge JM, Clein-Curley JS, Lindstrom JE, Braddock JF (1999) Moisture effects on microbial activity and community structure in decomposing birch litter in the Alaskan taiga. *Soil Biology and Biochemistry* **31**: 831-838.
- Schmitz OJ, Post E, Burns CE, Johnstone KM (2003) Ecosystem responses to climate change: moving beyond color mapping. *Bioscience* **53**: 1199-1205.
- Schmidt NM, Baittinger C, Kollman J, Forchhammer MC (2010) Consistent dendrochronological response of the dioecious *Salix arctica* to variation in local snow precipitations across gender and vegetation types. *Arctic Antarctic and Alpine*

Research **42**: 471-475.

- Schuur EAG, Crummer KG, Vogel JG, Mack MC (2007) Plant species composition and productivity following permafrost thaw and thermokarst in Alaskan tundra. *Ecosystems* **10**: 280-292.
- Senfeldr M, Treml V, Madera P, Volarik D (2014) Effects of prostrate dwarf pine on Norway spruce clonal groups in the treeline ecotone of the Hruby Jeseník mountains, Czech Republic. *Arctic, Antarctic, and Alpine Research* **46**: 430-440.
- Serreze MC, Walsh JE, Chapin III FS, Osterkamp T, Dyurgerov M, Romanovsky V, Oechel WC, Morison J, Zhang T, Barry RG (2000) Observational evidence of recent change in the northern high-latitude environment. *Climatic Change* **46**: 159-207.
- Shaver GR, Cutler JC (1979) The vertical distribution of live vascular phytomass in cottongrass tussock tundra. *Arctic and Alpine Research* **11**: 335-342.
- Shaver GR, Laundre JA, Giblin AE, Nadelhoffer KJ (1996) Changes in live plant biomass, primary production and species composition along a riverside toposequence in Arctic Alaska, USA. *Arctic and Alpine Research* **28b**: 363-379.
- Shuman B, Newby P, Huang YS, Webb T (2004) Evidence for the close climatic control of New England vegetation history. *Ecology* **85**: 1297-1310.
- Silapaswan CS, Verbyla DL, McGuire AD (2001) Land cover change on the Seward Peninsula: the use of remote sensing to evaluate the potential influences of climate warming on historical vegetation dynamics. *Canadian Journal of Remote Sensing* **27**: 542-554.
- Sonesson M, Callaghan TV (1991) Strategies of survival in plants of the Fennoscandian tundra. *Arctic* **44**: 95-105.
- Soukupova L, Frantik T, Jenik J (2001) Grasslands versus krummholz in arctic-alpine tundra of the Giant Mountains. *Opera Corcontica* **38**: 63-76.
- Speed JDM, Austrheim G, Hester AJ, Mysterud A (2010) Experimental evidence for herbivore limitation of the treeline. *Ecology* **91**: 3414-3420.
- Spiech C (2014) Spatial distribution, abundance and productivity of berry producing shrubs in the vicinity of Baker Lake, Nunavut: a baseline study linking science with local knowledge. Mémoire de maîtrise, Université du Québec à Trois-Rivières, Trois-Rivières, Québec.

- Stow DA, Hope A, McGuire D, Verbyla D, Gamon J, Huemmrich F, Houston S, Racine, C, Sturm M, Tape K, Hinzman L, Yoshikawa K, Tweedie C, Noyle B, Silapaswan C, Douglas D, Griffith B, Jia G, Epstein H, Walker D, Daeschner S, Petersen A, Zhou L, Myneni R (2004) Remote sensing of vegetation and land-cover change in Arctic tundra ecosystems. *Remote sensing of Environment* **89**: 281-308.
- Sturm M, Racine C, Tape K (2001a) Increasing shrub abundance in the Arctic. *Nature* **411**: 546-547.
- Sturm M, McFadden JP, Liston GE, Chapin FS III, Racine CH, Holmgren J (2001b) Snow-shrub interactions in Arctic tundra: A hypothesis with climatic implications. *Journal of Climate* **14**: 336-344.
- Sturm M, Schimel J, Michaelson G, Welker JM, Oberbauer SF, Liston GE, Fahnestock J, Romanovsky VE (2005) Winter biological processes could help convert arctic tundra to shrubland. *Bioscience* **55**: 17-26.
- Sugiura N (1978) Further analysis of the data by Akaike's information criterion and the finite corrections. *Communications in Statistics - Theory and Methods* **A7**: 13-26.
- Sveinbjörnsson B (2000) North American and European treelines: external forces and internal processes controlling position. *Ambio* **29**: 388-395.
- Sveinbjörnsson B, Hofgaard A, Lloyd AH (2002) Natural causes of the tundra-taiga boundary. *Ambio*, Special Report **12**: 23-29.
- Swann AL, Fung IY, Levis S, Bonan GB, Doney SC (2010) Changes in Arctic vegetation amplify high-latitude warming through the greenhouse effect. *Proceeding of the National Academy of Science of the United States of America* **107**: 1295-1300.
- Schweingruber FH (2007) *Wood structure and environment*. Springer-Verlag, Berlin, Allemagne. 279 p.
- Tape KD, Sturm M, Racine C (2006) The evidence for shrub expansion in northern Alaska and the pan-Arctic. *Global Change Biology* **12**: 686-702.
- Tape KD, Lord R, Marshall HP, Ruess RW (2010) Snow-mediated ptarmigan browsing and shrub expansion in Arctic Alaska. *Ecoscience* **17**: 186-193.
- Tape KD, Hallinger M, Welker JM, Ruess RW (2012) Landscape heterogeneity of shrub expansion in arctic Alaska. *Ecosystems* **15**: 711-724.
- Thorpe N, Eyegetok S, Hakongak N, Elders K (2002) *Nowadays it is not the same : Inuit*

- Quajimajatuqangit, climate caribou in the Kitikmeot région of Nunavut, Canada.* Pages 198-239 in I Krupnik & D Jolly (eds). *The Earth is faster: Indigenous observations of Arctic environmental change.* Arctic Research Consortium of the United States and the Smithsonian Institution, Fairbanks, Alaska, USA.
- Tinner W, Lotter AF (2001) Central European vegetation response to abrupt climate change at 8.2 ka. *Geology* **29**: 551-554.
- Tremblay B, Lévesque E, Boudreau S (2012) Recent expansion of erect shrubs in the Low Arctic: evidence from eastern Nunavik. *Environmental Research Letters* **7**: 035501.
- Vaartaja O (1959) Photoperiodic response in germination of four species of *Betula*. *Bi-monthly Progress Report, Forest Biology Division, Department of Agriculture, Canada* **15**: 2.
- Verbyla D (2008) The greening and browning of Alaska based on 1982-2003 satellite data. *Global Ecology and Biogeography* **17**: 547-555.
- Vicente-Serrano SM, Begueria S, Lopez-Moreno JI (2010) A multiscalar drought index sensitive to global warming: the standardized precipitation evapotranspiration index. *Journal of Climate* **23**: 1696-1718.
- Vistness II, Nellesmann C (2008) Reindeer winter grazing in alpine tundra: impacts on ridge community composition in Norway. *Arctic, Antarctic, and Alpine Research* **40**: 215-224.
- Vitousek PM (2004) *Nutrient cycling and limitation. Hawaii as a model system.* Princeton University Press, New Jersey, USA.
- Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan arctic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology* **11**: 537-552.
- Walker J, Thompson CH, Reddell P, Rapport DJ (2001) The importance of landscape age in influencing landscape health. *Ecosystem Health* **7**: 7-14.
- Walker DA, Epstein HE, Jia GJ, Balser A, Copass C, Edwards EJ, Gould WA, Hollingsworth J, Knudson J, Maier HA, Moody A, Raynolds MK (2003) Phytomass, LAI, and NDVI in northern Alaska: Relationships to summer warmth, soil pH, plant functional types, and extrapolation to the circumpolar Arctic. *Journal of Geophysical Research: Atmosphere* **108**: 8169.

- Walker MD, Wahren CH, Hollister RD, Henry GHR, Ahlquist LE, Alatalo JM, Bret-Harte MS, Calef MP, Callaghan TV, Carrol AB, Epstein HE, Jónsdóttir IS, Klein JA, Magnusson B, Molau U, Oberbauer SF, Rewa SP, Robinson CH, Shaver GR, Suding KN, Thompson CC, Tolvanen A, Totland O, Turner PL, Tweedie CE, Webber PJ, Wookey PA (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the Natural Academy of Sciences* **103**: 1342-1346.
- Wardle DA, Zackrisson O, Hornberg G, Gallet C (1997) Influence of island area on ecosystem properties. *Science* **277**: 1296-1299.
- Wardle DA, Hörnberg G, Zackrisson O, Kalela-Brundin M, Coomes DA (2003) Long-term effects of wildfire on ecosystem properties across an island area gradient. *Science* **300**: 972-975.
- Weijers S, Broekman R, Rozema J (2010). Dendrochronology in the High Arctic: July air temperatures reconstructed from annual shoot length growth of the circumarctic dwarf shrub *Cassiope tetragona*. *Quaternary Science Reviews* **29**: 3831-3842.
- Weis IM, Hermanutz LA (1988) The population biology of the arctic dwarf birch *Betula glandulosa*: seed rain and germinable seed bank. *Canadian Journal of Botany* **66**: 2055-2061.
- Wigley TML, Briffa KR, Jones PD (1984) On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *Journal of Climate and Applied Meteorology* **23**: 201-213.
- Wilson SD, Nilsson C (2009) Arctic alpine vegetation change over 20 years. *Global Change Biology* **15** : 1676–1684.
- Wipf S, Stoeckli V, Bebi P (2009) Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing. *Climate Change* **94**: 105-121.
- Xiao SC, Xiao HL, Kobayashi O, Liu PX (2007) Dendrochronological investigations of sea buckthorn (*Hippophae rhamnoides*) and reconstruction of the equilibrium line altitude of the July first glacier in the Western Qilian Mountains, northwestern China. *Tree-Ring Research* **63**: 15-26.
- Zalatan R, Gajewski K (2006) Dendrochronological potential of *Salix alaxensis* from the Kuujju River area, Western Canadian Arctic. *Tree-ring Research* **62**: 75-82.
- Zamin TJ, Grogan P (2012) Birch shrub growth in the low Arctic: the relative importance

of experimental warming, enhanced nutrient availability, snow depth and caribou exclusion. *Environmental Research Letters* **7**: 034027.

Zang C (2012) The bootRes package for bootstrapped response and correlation functions. <http://cran.rproject.org/web/packages/bootRes/index.html> [Consulted in june 2013].

Zasada JC, Norum RA, Vanveldhuizen RM, Teutsch CE (1983) Artificial regeneration of trees and tall shrubs in experimentally burned upland black spruce feather moss stands in Alaska. *Canadian Journal of Forestry Research* **13**: 903-913.