Étude de l'impact des changements climatiques sur les écosystèmes terrestres nordiques à l'aide de la dendrochronologie

Mémoire

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Résumé

Les changements climatiques ont entraîné une augmentation de la productivité végétale à l'échelle des régions circumpolaires. Ce phénomène, appelé verdissement, est documenté par des données de télédétection démontrant une augmentation de l'indice de végétation par différence normalisée (NDVI) et est principalement attribuable au phénomène d'arbustation. Le verdissement et l'arbustation suscitent un intérêt grandissant pour l'étude de la réponse des espèces arbustives aux changements climatiques et des facteurs responsables de l'hétérogénéité du verdissement. L'étude de la réponse des espèces arbustives nécessite toutefois des méthodes dendrochronologiques adaptées à leur forme de croissance particulière. De plus, peu d'études se sont concentrées sur la réponse différentielle des espèces arborescentes et arbustives aux changements climatiques. Les deux objectifs principaux de ce projet de recherche étaient donc (1) de déterminer si la conversion des largeurs de cernes en surface peut être utilisée comme méthode de standardisation en dendrochronologie des arbustes et (2) de déterminer si une réponse différentielle des espèces arbustives et arborescentes aux changements climatiques pourrait être à l'origine de l'hétérogénéité du verdissement des régions nordiques. L'utilisation des surfaces de cernes au lieu des largeurs standardisées de façon conventionnelle nous a permis d'obtenir des résultats de sensibilité climatique plus robustes et constants et de diminuer l'écart de sensibilité entre les branches et les collets. Nos résultats démontrent aussi que les arbres et les arbustes présentent des différences de réactivité aux changements climatiques et que la contribution aux augmentations de NDVI d'une espèce peut varier spatialement. Ce projet représente une contribution majeure au domaine de l'écologie nordique en adaptant les méthodes en dendrochronologie des arbustes et en améliorant notre compréhension du verdissement des régions circumpolaires.

Abstract

Climate change has triggered an increase in plant productivity across circumpolar regions that can be seen on satellite images through increases in the Normalized Difference Vegetation Index (NDVI). This Arctic greening, mainly linked to shrub expansion, has triggered a growing interest in studying the response of shrub species to global warming as well as the factors responsible for the Arctic greening heterogeneity. To study the response of shrubs, dendrochronological methods need to be adapted to the particular growth form of shrub species. Moreover, very few studies have focused on the differential response of trees and shrubs species to climate change. Therefore, the two main objectives of this project were (1) to determine if the conversion of ring width into ring area is an appropriate detrending method when shrub stems are used in dendrochronological studies and (2) to determine whether differential responses of shrub and tree species to climate change could partially explain the greening heterogeneity of the Arctic and subarctic regions. We obtained more robust and consistent climate sensitivity results and a reduced sensitivity gap between stems and root collars of shrubs when using ring areas instead of conventionally standardized ring widths. Our results also showed that trees and shrubs differ in their response to climate change and that the contribution of a given species to the NDVI may vary spatially. This project represents a major contribution to the field of northern ecology by adapting methods in shrub dendrochronology and by improving our understanding of the greening of circumpolar regions.

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« Si vos rêves ne vous font pas peur, c'est qu'ils ne sont
pas assez grands »

\- Ellen Johnson Sirleaf

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Avant-propos

Ce projet de recherche visait à déterminer si une réponse différentielle des arbres et des arbustes pourrait être à l'origine de l'hétérogénéité du verdissement des régions circumpolaires. Puisque nos analyses seraient basées sur des séries dendrochronologiques, nous souhaitions premièrement améliorer les méthodes en dendrochronologie des arbustes. Plus précisément, nous souhaitions apporter une alternative aux méthodes de standardisation conventionnelles inappropriées pour les courtes chronologies construites à partir de branches d'arbustes. Ensuite, nous avons utilisé cette méthode pour comparer la sensibilité climatique au niveau de la croissance radiale du bouleau glanduleux (arbuste) et de l'épinette noire (arbre) à la limite des arbres au Nunavik, et évaluer leur contribution respective aux augmentations de NDVI. Ce mémoire est divisé entre quatre sections. La première section correspond à une introduction générale, présentant le cadre théorique de l'étude et la problématique. S'en suivent deux chapitres sous forme d'articles scientifiques rédigés en anglais, présentant les résultats liés aux deux objectifs principaux de l'étude. La dernière section est une conclusion générale qui fait un retour sur les principaux résultats et ouvre sur des perspectives d'études.

Le chapitre 1 du mémoire est présenté sous la forme d'un article scientifique intitulé *The use of basal area increment to preserve the multi-decadal climatic signal in shrub growth ring chronologies : a case study of Betula glandulosa in subarctic Québec* dont une version révisée a été soumise le 17 août 2022 à la revue *Antarctic, Arctic and Alpine Research*. Les auteurs de ce manuscrit sont, dans l'ordre, Julie-Pascale Labrecque-Foy, Sandra Angers-Blondin, Pascale Ropars, Martin Simard et Stéphane Boudreau. Le chapitre 2 du mémoire est présenté sous la forme d'un article scientifique intitulé *Radial growth of subarctic tree and shrub species: relationship with climate and contribution to the greening of the forest-tundra ecotone* dont une version révisée a été soumise le 26 septembre 2022 à la revue *Arctic Science*. Les auteurs de ce manuscrit sont, dans l'ordre, Julie-Pascale Labrecque-Foy, Anna Gaspard, Martin Simard et Stéphane Boudreau.

Je figure en tant que première auteure sur ces deux articles puisque, pour l'article 1, j'ai réalisé les étapes suivantes: conception, mesures et estimation des surface de cernes, analyse des données, réalisation des figures et rédaction de l'article. Pour l'article 2, j'ai participé à la conception et à l'échantillonnage, mesuré les cernes de croissance d'épinette noire, analysé les données, réalisé les figures et rédigé l'article.

Introduction

Les facteurs climatiques limitant la productivité végétale en régions nordiques

Les environnements arctiques et subarctiques sont soumis à des conditions climatiques rigoureuses qui limitent la productivité des espèces végétales qui s'y trouvent (Jia et al., 2009). Bien que la température soit le principal facteur limitant la productivité végétale dans les régions de haute latitude (Jia et al., 2009; Menzel et al., 2003), d'autres facteurs tels que la durée de la saison de croissance (Chapin, 1983; Vicente-Serrano et al., 2020), les précipitations (Kaufmann et al., 2004; Ols et al., 2019) et la disponibilité des nutriments (Aerts et al., 2006; Chapin, 1983) peuvent potentiellement limiter la productivité primaire dans ces régions.

Les basses températures observées en milieux nordiques influencent négativement la physiologie et la phénologie des espèces végétales. Au niveau physiologique, la température a une influence directe sur le taux de photosynthèse des plantes, lequel est diminué quand les températures sont sous-optimales (Taiz et al., 2015). Au niveau phénologique, les faibles températures peuvent retarder divers processus tels que la formation des graines (Meunier et al., 2007; Sirois et al., 1999), le débourrement des bourgeons et la floraison (Aerts et al., 2006). De plus, la saison de croissance, qui délimite la période durant laquelle les plantes sont physiologiquement actives, est typiquement courte dans les régions nordiques (Chapin, 1983; Vicente-Serrano et al., 2020). Puisqu'elle correspond en général au nombre de jours qui séparent le dernier gel au printemps du premier gel à l'automne, la durée de la saison de croissance est influencée par les températures atmosphériques (Menzel et al., 2003).

Les précipitations peuvent aussi être limitantes pour les végétaux dans les milieux nordiques (Boulanger-Lapointe et al., 2014; Kaufmann et al., 2004) et leur influence varie en fonction de la saison. Durant la saison de croissance, elles sont nécessaires au processus de photosynthèse (Larcher, 2003). En effet, une bonne disponibilité de l'eau est essentielle pour absorber les minéraux du sol et pour maintenir l'équilibre hydrique des plantes, en compensant pour les pertes d'eau lors de l'absorption du dioxyde de carbone par les stomates des feuilles (Taiz et al., 2015). En automne et en hiver, les précipitations sous forme solide contribuent à la formation d'un couvert nival qui protège les tissus aériens et souterrains de la dessication hivernale et des dommages causés par les températures très froides des environnements nordiques (Frost &

Epstein, 2014; Hallinger et al., 2010). De plus, le couvert nival peut contribuer à maintenir le sol à une température plus élevée (Ols et al., 2019), ce qui peut avoir un effet positif sur la respiration microbienne des sols et, par conséquent, sur la disponibilité des nutriments. Également, la fonte du couvert nival au printemps résulte en une disponibilité d'eau accrue, ce qui favorise la reprise de la croissance végétale (Owczarek et al., 2021).

Finalement, le climat plutôt froid et sec des régions nordiques limite l'activité microbienne des sols (Chapin, 1983). Ainsi, bien que les sols des régions arctiques et subarctiques puissent contenir une grande quantité de matière organique, la dégradation de cette dernière y est très lente (Aerts et al., 2006). Conséquemment, peu de nutriments sont disponibles pour les espèces végétales (Chapin, 1983), ce qui limite la croissance et la formation de nouveaux tissus (Larcher, 2003).

Les changements climatiques et la modification des conditions de croissance

Le réchauffement climatique observé depuis les années 1950 est l'un des plus importants depuis des millénaires (IPCC, 2014). Au courant du 20e siècle, les températures atmosphériques se sont réchauffées en moyenne de 0,65 à 1,06°C à l'échelle du globe (Bush & Lemmen, 2019). De plus, cette tendance semble se poursuivre puisque les températures enregistrées entre 1983 et 2012 sont les plus chaudes que la Terre ait connu en 1400 ans (IPCC, 2014).

Le réchauffement climatique est toutefois hétérogène à l'échelle du globe, étant plus important dans les régions de haute latitude de l'hémisphère nord (Bush & Lemmen, 2019). Entre les années 2009 et 2019 uniquement, les températures des régions arctiques ont augmenté de 0,75°C en moyenne (Post et al., 2019). Au Canada, les températures se sont réchauffées près de deux fois plus rapidement que la moyenne planétaire, et si l'on considère uniquement l'Arctique canadien, le réchauffement y est près de trois fois plus important (Bush & Lemmen, 2019). Cette amplification du réchauffement climatique dans les régions de haute latitude est en grande partie attribuable à la diminution du couvert de glace sur l'océan Arctique et à la fonte précoce de la neige au printemps, deux phénomènes qui contribuent à diminuer l'albédo de ces régions (Serreze & Barry, 2011). Cette amplification du réchauffement dans les régions nordiques devrait même s'intensifier au cours des prochaines décennies (Serreze & Barry, 2011). Les différents scénarios d'émission de CO_2 prédisent une augmentation supplémentaire de la température variant entre 1,8 et 6,0°C d'ici la fin du siècle dans ces régions (Bush & Lemmen, 2019). Au

Nunavik, dans le nord du Québec, cette augmentation pourrait même atteindre 10°C (Charron, 2015).

Avec ces augmentations rapides, la température devrait être moins limitante pour la productivité primaire dans les régions nordiques. Notamment, des températures plus chaudes contribuent à l'allongement de la saison de croissance en favorisant la fonte précoce de la neige et un dégel hâtif du sol au printemps, ce qui a pour effet de devancer le début de la saison de croissance. Les températures plus élevées ont également un effet positif à la fin de la saison de croissance puisqu'elles retardent la sénescence des feuilles et l'arrivée de la neige (Zeng et al., 2011). Toutefois, puisque la fin de la saison de croissance dépend également de la photopériode et de divers déterminants génétiques (Aerts et al., 2006), l'impact des températures plus clémentes est plus important au début de la saison de croissance. Somme toute, les augmentations de température atmosphérique du dernier siècle ont permis d'allonger la saison de croissance d'environ une semaine (Menzel et al., 2003), et on prévoit un allongement supplémentaire de 20 jours d'ici 2070 pour le nord du Québec (Charron, 2015).

Les changements climatiques ne se limitent toutefois pas aux augmentations de température, le régime de précipitations étant aussi sujet à changer. D'ailleurs, des tendances à la hausse ont été observées au niveau des précipitations dans l'hémisphère nord depuis 1901 (IPCC, 2014). Cependant, le peu de données de précipitations entraîne une plus grande variabilité dans les modèles prédictifs. Ainsi, les précipitations annuelles pourraient augmenter de 7 à 24% d'ici la fin du siècle au Canada, et encore davantage dans les régions de haute latitude selon les différents scénarios d'émission de CO_2 (Bush & Lemmen, 2019). Or, en raison de l'augmentation des températures atmosphériques, il est attendu que la proportion des précipitations tombant sous forme de neige diminue au Canada, principalement au printemps et à l'automne, mais également pendant l'hiver (Krasting et al., 2013).

Finalement, le climat plus chaud et humide associé aux changements climatiques devrait aussi stimuler l'activité microbienne des sols, ce qui résultera en une disponibilité accrue des nutriments qui sont souvent limitants en régions arctiques et subarctiques (Aerts et al., 2006; Chapin, 1983). Par exemple, des expériences de réchauffement du sol à court (2 ans; Biasi et al., 2008) et à long (9 ans; Chapin et al., 1995) termes ont permis de mettre en évidence que le réchauffement du sol stimule la minéralisation et augmente la disponibilité de nutriments essentiels tels que l'azote et le phosphore. La dégradation du pergélisol, qui rend la couche active du sol de plus en plus profonde, devrait également accentuer ce phénomène (Salmon et al., 2016). En effet, après un dégel expérimental du pergélisol pendant 5 ans, Salmon et al. (2016) ont observé une augmentation de la disponibilité en azote de 136% en saison estivale et de 86% en saison hivernale.

Le verdissement des régions arctiques et subarctiques

L'amélioration des conditions de croissance pour les végétaux a contribué à l'augmentation de la productivité des communautés végétales arctiques et subarctiques (Beck et al., 2011; Beck & Goetz, 2011). Quasi-généralisé à l'échelle de la région circumpolaire (Tape et al., 2006), ce phénomène peut être quantifié par imagerie satellitaire à l'aide de l'indice de végétation par différence normalisée (NDVI; Myneni et al., 1997). Cet indice est calculé à l'aide de l'équation suivante :

$$NDVI = \frac{PIR - R}{PIR + R}$$

qui met en relation les rayonnements proche infrarouge (PIR) et rouge (R) reflétés par la végétation. Cet indice de productivité est utilisé en tant que proxy de la productivité primaire des végétaux et de leur biomasse foliaire (Epstein et al., 2012; Goetz et al., 2005; Vicente-Serrano et al., 2020; Walker et al., 2012).

Des augmentations de NDVI ont été observées au cours des dernières décennies dans plusieurs régions de l'hémisphère nord (Bunn et al., 2007; Bunn & Goetz, 2006; Jia et al., 2009; Ju & Masek, 2016; McManus et al., 2012). Ce phénomène, plus communément appelé « verdissement », a d'ailleurs été qualifié de phénomène pan-Arctique (Tape et al., 2006). Les augmentations de NDVI, étroitement liées aux augmentations de températures dans les régions nordiques, sont le résultat de la transformation du couvert végétal (Jia et al., 2009; Jia et al., 2003). Entre autres, le verdissement des régions circumpolaires serait attribuable au phénomène d'arbustation, soit à la colonisation de nouveaux milieux par les espèces arbustives (Lantz et al., 2013; Provencher-Nolet et al., 2014; Sturm et al., 2001), à la densification de peuplement végétaux existants (Lantz et al., 2013; Ropars & Boudreau, 2012) de même qu'à l'augmentation de la croissance des espèces végétales (Myers-Smith et al., 2011; Wang & Friedl, 2019). Bien que moins fréquemment rapporté, ce phénomène est également observable au niveau des peuplements forestiers (Frost & Epstein, 2014; Tremblay et al., 2012).

Les conséquences du verdissement

L'augmentation de la productivité végétale dans les régions arctiques et subarctiques entraîne des conséquences importantes sur la composition et la dynamique des communautés végétales. La principale modification du couvert végétal observée dans les régions arctiques et subarctiques du globe est l'augmentation de la présence d'espèces arbustives. Ce phénomène a d'ailleurs été documenté dans plusieurs régions circumpolaires telles que la Sibérie (Frost & Epstein, 2014), le Québec subarctique (Provencher-Nolet et al., 2014; Ropars & Boudreau, 2012; Tremblay et al., 2012), le nord canadien (Lantz et al., 2013) et l'Alaska (Sturm et al., 2001; Tape et al., 2006) grâce à l'analyse de photographies aériennes. L'augmentation du couvert arbustif s'est principalement effectué au détriment des zones dominées par le couvert lichénique (Provencher-Nolet et al., 2014). Par exemple, en comparant des photographies aériennes prises en 1980 et 2013 au nord-ouest du Canada, Fraser et al. (2014) ont constaté qu'une augmentation de 40% du couvert arbustif était accompagnée d'une diminution d'environ 67% du couvert lichénique. De plus, Chagnon et Boudreau (2019) ont démontré qu'en plus d'entraîner une diminution du couvert lichénique, l'augmentation de couvert arbustif entraîne une diminution de la richesse spécifiques des lichens. En plus de l'augmentation de la présence d'arbuste et la diminution du couvert lichénique, des changements au niveau de la limite nordique des arbres ont été observés (Dufour-Tremblay et al., 2012). Deux études portant chacune sur plus de 150 sites situés à la limites de la distribution des espèces arborescentes ont permis de démontrer qu'environ la moitié des peuplements forestiers étudiés avaient avancé vers de plus hautes latitudes (Harsch et al., 2009; Rees et al., 2020).

Ces changements ont des impacts important sur la mégafaune, notamment pour le caribou, pour lequel la présence accrue d'arbustes constitue une augmentation de la quantité de nourriture disponible durant la saison estivale (Lemay et al., 2021). Toutefois, puisque son régime alimentaire hivernal est principalement composé de lichens, la diminution du couvert lichénique pourrait avoir des répercussions importantes sur sa survie l'hiver (Chagnon & Boudreau, 2019).

De plus, la transformation des communautés végétales nordiques est susceptible d'amplifier le réchauffement climatique, en diminuant l'albedo terrestre et en augmentant la vapeur d'eau atmosphérique (Swann et al., 2010). Premièrement, l'augmentation du couvert arbustif au détriment du lichen entraine la diminution de l'albédo des surfaces terrestres (Myers-Smith et al., 2011; Swann et al., 2010). En effet, Aartsma et al. (2020) ont démontré que les peuplements arbustifs peuvent avoir des valeurs d'albédo jusqu'à 50% inférieures aux peuplements dominés par le lichen. Ainsi, dans plusieurs régions de l'hémisphère nord, l'augmentation de la présence d'arbustes entre 1980 et 2006 a entraîné des diminutions d'albédo de près de 10% (Miller & Smith, 2012). Aussi, l'augmentation de l'évapotranspiration, associée à l'augmentation de la présence de plantes vasculaires, entraîne une augmentation des vapeurs d'eau atmosphériques (Bonfils et al., 2012; Swann et al., 2010). Ces deux facteurs contribuent à augmenter l'absorption des radiations solaires à la surface du sol et à diminuer la proportion de rayons qui seraient normalement réfléchis vers l'espace (Myers-Smith et al., 2011; Swann et al., 2010).

Également, l'augmentation du couvert arbustif contribuerait à accélérer la dégradation du pergélisol (Bonfils et al., 2012). En effet, l'augmentation de la croissance en hauteur des arbustes permet une plus grande accumulation de neige en hiver, ce qui isole davantage le sol et lui permet de conserver une température plus élevée (Paradis et al., 2016). Par exemple, Myers-Smith et Hik (2013) ont observé que la température du sol en janvier était de 4 à 5 °C plus chaude dans les sites avec un couvert d'arbustes érigés par rapport à ceux qui en étaient dépourvus. L'accumulation préférentielle de la neige et la meilleure isolation du sol résultent en une couche active plus profonde dans le sol et en une dégradation accélérée du pergélisol (Bonfils et al., 2012). Cela devrait entrainer l'émission d'importantes quantités de gaz à effet de serre vers l'atmosphère (Turetsky et al., 2019).

L'hétérogénéité du verdissement

Les tendances NDVI dans les régions nordiques sont hétérogènes, peu importe l'échelle spatiale considérée (Epstein et al., 2012). À l'échelle circumpolaire, le nord de l'Amérique du Nord et la Sibérie semblent être les deux régions présentant les plus importantes augmentations de NDVI entre 1982 et 2003 (Bunn & Goetz, 2006). À l'échelle continentale, Ju et Masek (2016) ont montré que le Nunavik (Québec subarctique) et le Labrador ont connu un verdissement plus important que l'Alaska et le reste du Canada entre 1984 et 2012.

Quelques études ont tenté d'identifier les facteurs pouvant être à l'origine d'une telle hétérogénéité du verdissement. Cette hétérogénéité pourrait notamment être attribuable à la topographie (Chen et al., 2021), aux propriétés des sols (Campbell et al., 2021), de même qu'à l'herbivorie (Lindén et al., 2021). En effet, les sites de plus haute altitude et orientés vers le nord seraient plus propices au verdissement (Berner et al., 2020; Choler et al., 2021). Le verdissement se produirait également préférentiellement dans les sites les moins exposés au vent (Lemay et al., 2018), tels que les vallées (Tape et al., 2006) ou les terrasses de sable (Ropars & Boudreau, 2012), et dans les environnements où la température et l'humidité du sol sont plus élevées (Berner et al., 2020; Tape et al., 2012).

L'herbivorie pourrait également être responsable de l'hétérogénéité du verdissement. En effet, la présence de grands herbivores tels que le caribou ou le bœuf musqué limiterait l'établissement d'espèces arbustives (Post, 2013). De plus, les valeurs de NDVI seraient diminuées par le broutage intense effectué notamment par le caribou ou le bœuf musqué, mais également par d'autres plus petits herbivores tels que le lièvre ou le lemming (Blanco et al., 2008; Lindén et al., 2021; Te Beest et al., 2016). Également, Andruko et al. (2020) ont démontré que le déclin démographique important d'un troupeau de caribous des Territoires du Nord-Ouest a entraîné une augmentation de l'abondance et de la taille des espèces arbustives, ce qui démontre l'influence qu'ont les herbivores sur le phénomène d'arbustation dans les régions subarctiques.

Peu d'études ont tenté de déterminer si l'hétérogénéité du verdissement pouvait résulter en partie de la réponse différentielle des espèces végétales aux changements climatiques. Pourtant, on observe déjà une différence au niveau de l'expansion de deux importants groupes fonctionnels : les espèces arbustives et les espèces arborescentes. En effet, alors qu'une augmentation quasi-généralisée de la présence d'arbustes a été observée à l'échelle circumpolaire (Myers-Smith et al., 2011; Tape et al., 2006), seulement environ la moitié des peuplements forestiers semblent profiter des changements climatiques pour étendre leur répartition vers le nord (Harsch et al., 2009; Rees et al., 2020).

Est-ce que la réponse différentielle des divers groupes fonctionnels aux changements climatiques pourrait être un déterminant significatif de l'hétérogénéité du verdissement ?

La dendrochronologie

Une méthode efficace pour quantifier la réponse des espèces arborescentes et arbustives aux variations climatiques est la dendrochronologie. Dans les régions présentant une forte saisonnalité, l'alternance entre des conditions climatiques favorables à la croissance des végétaux et des saisons de dormance entraîne la formation de cernes annuels de croissance radiale chez les espèces ligneuses (Deslauriers et al., 2010). La dendrochronologie est l'étude de ces cernes de croissance et a comme objectif de reconstituer ou d'identifier des conditions environnementales ou des événements écologiques qui ont pu influencer la croissance d'individus ligneux (Payette, 2010). En coupant de façon transversale les tiges des espèces ligneuses, il est possible de dater et de mesurer les cernes de croissance pour construire des chronologies de croissance radiale (Delwaide & Filion, 2010). Les chronologies de croissance des espèces ligneuses peuvent contenir différents signaux. En effet, les tendances observées dans les chronologies de croissance radiale peuvent résulter de variations climatiques, mais peuvent également contenir différents signaux écologiques associés à la démographie de la population, à la dynamique des peuplements, ou à des perturbations diverses. Par exemple, dans une série dendrochronologique, l'effet de la taille ou de l'âge d'un individu se traduit généralement par une diminution progressive de la largeur des cernes du centre de la tige vers l'écorce. Cette tendance, qui est principalement causée par le périmètre croissant de la tige, doit être supprimée à l'aide d'une variété d'approches de standardisation puisqu'elle risque de masquer le signal climatique (Briffa & Melvin, 2011; Dietrich & Anand, 2019; Peters et al., 2015). La standardisation par lissage à l'aide d'une spline cubique est la méthode de standardisation la plus largement utilisée, bien que des études ont parfois recours à d'autres méthodes telles que l'ajustement à l'aide de fonctions exponentielles négatives ou de modèles polynomiaux (Nicault et al., 2010). La standardisation permet de supprimer les signaux indésirables des séries dendrochronologiques afin d'isoler et d'amplifier des signaux d'intérêt tels que les signaux climatiques (Cook et al., 1990). Il est donc nécessaire de standardiser les séries dendrochronologiques avant de mette en relation la croissance radiale des individus et différentes variables environnementales (Nicault et al., 2010).

Une fois la standardisation effectuée, les séries dendrochronologiques peuvent être mises en relation avec des données climatiques dans le but d'identifier les déterminants climatiques de la croissance des individus, i.e. les facteurs climatiques qui semblent avoir le plus influencé les variations de croissance radiale annuelle (Bär et al., 2008; Dorado-Liñán et al., 2020; Hoffmann et al., 2020). Il est ensuite possible de calculer un indice de sensibilité climatique (Myers-Smith, Elmendorf, et al., 2015; Myers-Smith & Hik, 2018; Owczarek et al., 2021) et de comparer cette sensibilité entre espèces (Hoffmann et al., 2020), entre formations végétales ou entre régions

(Myers-Smith, Elmendorf, et al., 2015). La dendrochronologie peut donc être utilisée pour comparer la réponse de différentes espèces végétales aux variations climatiques, permettant ainsi de déterminer si la croissance d'une espèce est plus susceptible d'être influencée par les changements climatiques que celle d'une autre espèce.

Le domaine de la dendrochronologie avec les espèces arbustives

La dendrochronologie est largement utilisée pour étudier la croissance radiale des espèces arborescentes (Baral et al., 2019; Gamache & Payette, 2005; Huang et al., 2010; Mamet & Kershaw, 2013). Récemment, l'application de la dendrochronologie aux espèces arbustives a gagné en popularité, en raison du nombre grandissant d'études portant sur la réponse des espèces arbustives aux changements climatiques en régions nordiques (Hollesen et al., 2015; Myers-Smith et al., 2011; Owczarek et al., 2021; Ropars et al., 2015). Or, les méthodes développées pour les espèces arborescentes ne sont pas nécessairement adaptées pour les espèces arbustives, et plusieurs problèmes demeurent (Myers-Smith, Hallinger, et al., 2015).

Une des principales questions en dendrochronologie des espèces arbustives concerne la nature des échantillons à utiliser pour construire les chronologies de croissance radiale. En effet, la forme de croissance des espèces arbustives diffère substantiellement de celle des arbres, ce qui représente un défi important en dendrochronologie. Chez les individus arbustifs issus de la reproduction sexuée, la structure aérienne est constituée de plusieurs branches qui se développent à partir d'un seul collet, soit l'interface entre le système racinaire et la biomasse aérienne (Myers-Smith, Hallinger, et al., 2015). Ce collet, qui est généralement plus vieux que les branches qui sont souvent remplacées (Ropars et al., 2017), est l'équivalent anatomique de la base du tronc chez les individus arborescents (Figure 1). Il est généralement comprimé et enfoui dans le sol, ce qui complique sa récolte sur le terrain. En effet, la récolte des collets nécessite bien souvent de déterrer les individus au complet, une approche fastidieuse et destructrice qui représente une contrainte logistique majeure pour les campagnes d'échantillonnage en régions éloignées. Pour cette raison, la majorité des études sont menées à partir d'échantillons pris à la base des branches dominantes (Bär et al., 2008; Hallinger et al., 2010; Lu et al., 2016; Uyeda et al., 2016; Weijers, Pape, et al., 2018).

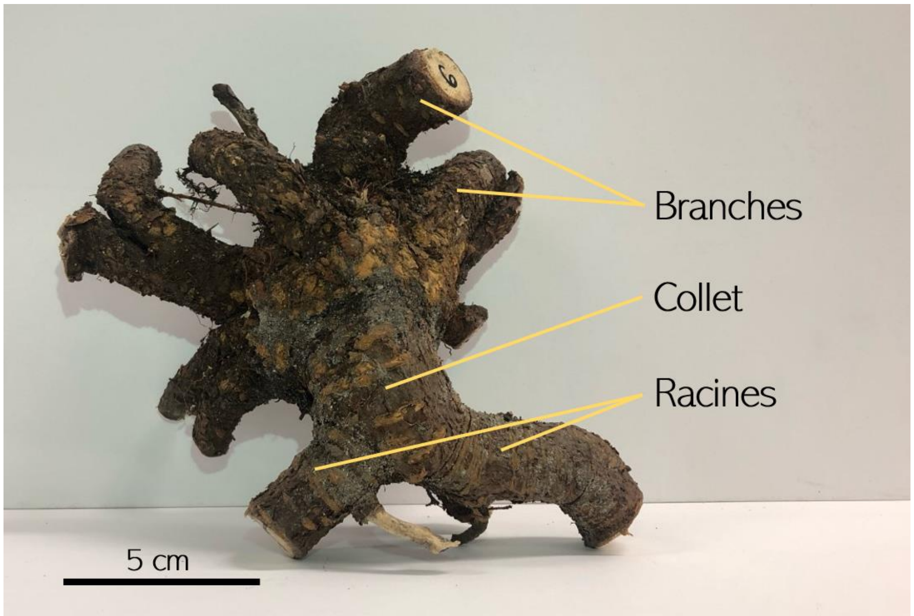

Figure 1 Localisation des branches, du collet et des racines sur un individu de bouleau glanduleux qui a été entièrement déterré et dont une grande portion des branches et des racines a été retirée.

Toutefois, l'utilisation des branches au lieu des collets peut être problématique. En effet, Ropars et al. (2017) ont démontré que la sensibilité climatique des branches de bouleau glanduleux (*Betula glandulosa* Michx.) est plus faible qu'au niveau du collet et que l'identification des déterminants climatiques de la croissance des branches est plus variable. Ils concluent que le plus faible signal climatique enregistré par les branches pourrait être dû à une compétition entre les différentes branches d'un même individu, ce qui engendrerait des inégalités dans l'accès aux ressources (Sadras & Denison, 2009) et masquerait en partie le signal climatique. Or, il est également possible que cette différence de signal climatique entre les branches et les collets résulte de l'utilisation de méthodes de standardisation traditionnelles. En effet, les méthodes de standardisation traditionnelles ont été développées pour des chronologies de croissance plus longues, construites à l'aide d'espèces arborescentes. Ainsi, ces dernières seraient possiblement inappropriées pour standardiser de plus courtes chronologies de croissance construites à partir de branches d'espèces arbustives. À l'opposé, la perte de signal climatique associée à l'utilisation de méthodes de standardisation conventionnelles serait moins importante lors de l'utilisation de collets, puisque, tel que confirmé par Ropars et al. (2017), les chronologies de croissance construites à partir de collets sont significativement plus longues.

L'un des principaux défis de la standardisation est de supprimer l'effet de la taille et de l'âge des individus tout en conservant l'effet du climat, puisque les deux opèrent à des échelles multi-décennales. Dans des séries ne couvrant que quelques décennies (branches d'arbustes), la standardisation conventionnelle, i.e. avec des fonctions mathématiques, nécessite de raccourcir les fenêtres de lissage, ce qui entraîne la perte de signaux de moyenne et de basse fréquence qui correspondent en général au signal climatique à long terme (Nicault et al., 2010). Il serait donc nécessaire de développer une méthode pour standardiser de courtes chronologies de croissance qui permettrait de retirer les tendances associées à l'âge des individus, tout en conservant celles reliées aux facteurs environnementaux.

Parmi les différentes méthodes de standardisation existantes, la conversion des valeurs de largeur annuelle de cernes en valeurs de surface est une approche robuste qui compense pour l'augmentation constante du périmètre de la tige (Hornbeck & Smith, 1985; Phipps, 1984). Les valeurs de surface de cernes ont largement été utilisées dans les études visant à caractériser la réponse des espèces arborescentes aux changements environnementaux, et certaines de ces études démontrent l'efficacité de cette conversion en tant que méthode de standardisation (Hornbeck et al., 1986; Linares et al., 2009; Sullivan et al., 2016). Leblanc (1994) a démontré que la standardisation conventionnelle des mesures de largeur de cernes à l'aide de fonction de lissage a tendance à masquer la relation entre la croissance radiale de certaines espèces et les variables environnementales. Baral et al. (2019) ont également obtenu de plus fortes relations entre les variables climatiques et la croissance lorsqu'ils utilisaient des chronologies de surface de cernes plutôt que de largeur de cernes, possiblement en raison des méthodes de standardisation. Bien que les mesures de surface de cernes soient largement utilisées pour les arbres, elles ne sont que marginalement utilisées pour les espèces arbustives (Buchkowski et al., 2020; Lu et al., 2016). Néanmoins, cette méthode pourrait être une alternative intéressante aux méthodes conventionnelles de standardisation, puisque la conversion des valeurs de largeur de cernes en surface représente une simple correction géométrique de l'accroissement en diamètre des échantillons. Ainsi, en remplaçant les méthodes de standardisation conventionnelles avec de courtes fenêtre de lissage par une méthode faisant appel à une simple correction géométrique, l'effet du climat serait préservé, et les différences de sensibilité entre les branches et les collets pourraient être minimisées.

Contexte de l'étude

Contexte théorique

Bien que le verdissement des régions arctiques soit un phénomène largement documenté, un nombre restreint d'études est parvenu à identifier les facteurs à l'origine de l'hétérogénéité du verdissement (Campbell et al., 2021; Chen et al., 2021; Lemay et al., 2018). Améliorer notre connaissance de ces facteurs est cependant nécessaire pour tenter de prévoir la direction et l'ampleur du verdissement à venir, de même que ses futurs impacts sur les écosystèmes arctiques et subarctiques. À notre connaissance, très peu d'études se sont intéressées aux différences de sensibilité climatique entre les groupes fonctionnels. Or, des différences au niveau de l'avancée vers le nord des espèces arborescentes et arbustives suggère qu'il serait possible qu'une réponse différentielle de ces deux groupes fonctionnels aux changements climatique soit au moins partiellement responsable de l'hétérogénéité du verdissement. Pour parvenir à comparer la sensibilité climatique de la croissance radiale des arbres et des arbustes, il est toutefois nécessaire d'optimiser les méthodes en dendrochronologie des espèces arbustives. Notamment, l'élaboration de méthodes de standardisation mieux adaptées aux courtes séries dendrochronologiques est nécessaire.

Aire d'étude : le Nunavik

Le Nunavik est la portion du territoire québécois qui se trouve au nord du 55^e^ parallèle. Du sud au nord, le Nunavik est divisé en quatre domaines bioclimatiques : la pessière à lichens, la toundra forestière, la toundra à arbustes dressés, et la toundra à arbustes prostrés (Ministère des Forêts de la Faune et des Parcs, 2021). La pessière à lichens est caractérisée par la présence de forêts ouvertes d'épinette noires (*Picea mariana* (Mill.)) et de tapis de lichens au sol. La toundra-forestière correspond à la zone de transition entre la forêt boréale ouverte et la toundra arbustive. Le paysage constitue une mosaïque dominée par des landes subarctiques entrecoupées de peuplements forestiers et arbustifs. La limite nordique de ce domaine bioclimatique, au 58^e^ parallèle approximativement, correspond également à la limite nordique des arbres. La toundra à arbustes dressés est dominée par des arbustes érigés, de même que plusieurs espèces de plantes herbacées, de graminées, de mousses et de lichens. La toundra à arbustes prostrés, le domaine bioclimatique le plus nordique du Nunavik, est caractérisée par la présence de graminées, de mousses, de lichens, de roches et de sol minéral dénudé. La présence d'arbustes y est généralement limitée à ceux qui adoptent une forme de croissance prostrée (Ministère des Forêts de la Faune et des Parcs, 2021). Au Nunavik, les espèces arborescentes et arbustives dominantes sont l'épinette noire et le bouleau glanduleux, respectivement.

Le Nunavik a connu un important réchauffement atmosphérique depuis les années 1990 (Allard et al., 2007; Chouinard et al., 2007). Il s'agit également de l'une des régions ayant connu les plus importantes augmentations de NDVI en Amérique du Nord entre 1984 et 2012 (Ju & Masek, 2016). De plus, McManus et al. (2012) ont observé que les augmentations de NDVI entre 1986 et 2010 se produisaient préférentiellement dans les peuplements herbacés ou arbustifs. Bien que le verdissement au Nunavik soit généralement attribué au phénomène d'arbustation par le bouleau glanduleux (Provencher-Nolet et al., 2014; Ropars et al., 2015; Ropars & Boudreau, 2012; Tremblay et al., 2012), certaines études ont démontré que l'épinette noire répond également positivement aux augmentations de température. En effet, en réponse aux changements climatiques, l'épinette noire y a connu des augmentations de sa croissance radiale (Nicault et al., 2015) et de sa croissance en hauteur (Gamache & Payette, 2004; Truchon-Savard et al., 2019). Elle produit également davantage de graines viables (Dufour-Tremblay & Boudreau, 2011) et sa colonisation des combes à neige semble s'accélérer (Truchon-Savard et al., 2019). Ainsi, en plus de l'arbustation par le bouleau glanduleux, il est fort probable que l'épinette noire contribue également aux augmentations de NDVI au Nunavik.

Objectifs de l'étude et hypothèses

Cette étude a pour objectif de déterminer si une différence au niveau de la réponse des groupes fonctionnels aux changements climatiques pourrait expliquer en partie l'hétérogénéité du verdissement des régions arctiques et subarctiques. Puisque des analyses dendrochronologiques seront effectuées, nous devons au préalable trouver une alternative aux méthodes conventionnelles de standardisation des séries dendrochronologiques dans le but de préserver les tendances climatiques dans de courtes séries, comme celles construites à partir de branches d'arbustes.

Plus précisément, le premier objectif principal de cette étude était de déterminer si la conversion des mesures de largeur de cernes en surface de cernes permet de réduire l'écart de sensibilité climatique entre les branches et les collets chez le bouleau glanduleux. Cet objectif a été divisé en deux sous-objectifs, soit (1) d'évaluer si une estimation de la surface des cernes, à partir de leur largeur, représente adéquatement la surface réelle des cernes de croissance et (2) de déterminer si l'utilisation des mesures d'accroissement annuel en surface, plutôt que des valeurs de largeur de cernes standardisées de façon conventionnelle, permet de réduire l'écart de sensibilité climatique entre les branches et les collets chez le bouleau glanduleux. Pour ce faire, nous avons utilisé les mêmes échantillons que Ropars et al. (2017) qui ont démontré une différence significative de sensibilité climatique entre les branches et les collets. Nous avons refait les mêmes analyses après avoir converti les valeurs de largeur de cernes en valeurs de surface de cernes. Nous prédisons qu'il y aura une forte corrélation entre les surfaces estimées et réelles des cernes de croissance et que les déterminants climatiques de la croissance radiale et la sensibilité climatique seront similaires entre les branches et les collets lorsque les valeurs de surface de cernes seront utilisées.

Le second objectif principal de l'étude était de déterminer s'il existe des différences au niveau de la réactivité aux changements climatiques entre les espèces dominantes d'arbres et d'arbustes au Nunavik. Cet objectif a été divisé en trois sous-objectifs, soit (1) d'évaluer les tendances NDVI dans trois types de formations végétales : pessières à lichens, arbustaies et landes subarctiques, et à deux stations de recherche : du Lac à l'Eau Claire (56°20' N, 74°25' O) et de la Rivière Boniface (57°45' N, 76°15' O), (2) d'identifier et de comparer les déterminants climatiques de la croissance radiale du bouleau glanduleux et de l'épinette noire de même que la force du lien entre le climat et leur croissance radiale, et (3) de caractériser la relation entre le NDVI et la croissance radiale de ces deux espèces. En raison de l'avancée quasi-généralisée des espèces arbustives dans les régions nordiques et puisque McManus et al. (2012) ont démontré que le NDVI augmentait préférentiellement dans les peuplement arbustifs ou herbacés, nous prédisons que la force de la relation entre le climat et la croissance radiale du bouleau glanduleux sera supérieure à celle de l'épinette noire, bien que les déterminants de leur croissance radiale devraient être semblables. Finalement, nous prédisons qu'il existe une relation positive entre le NDVI et la croissance radiale des deux espèces, bien que cette relation devrait être plus forte pour le bouleau glanduleux.

Chapitre 1 The use of basal area increment to preserve the multi-decadal climatic signal in shrub growth ring chronologies: a case study of *Betula glandulosa* in subarctic Québec

1.1 Résumé

Les changements climatique accélérés dans les régions nordiques ont contribué à l'intérêt grandissant pour l'analyse des cernes de croissance des espèces arbustives. Or, la forme de croissance particulière des arbustes présente un nouveau défi pour le domaine de la dendrochronologie des arbustes, et il a été démontré que leur sensibilité climatique serait plus faible au niveau de leurs branches que de leurs collets (l'interface entre les branches et les racines). Les branches des arbustes pourraient donc être considérées comme inadéquates pour étudier les relations entre le climat et la croissance radiale des arbustes. Dans cet article, nous proposons que la sensibilité climatique plus faible des branches pourrait être causée par l'utilisation de méthodes de standardisation inadéquates pour des chronologies couvrant des décennies plutôt que des siècles. Nous émettons l'hypothèse que la conversion de la largeur des cernes (RW) en de surface de cernes (BAI) est mieux adaptée que les méthodes traditionnelles de standardisation pour éliminer les tendances associées à l'âge et à la taille des échantillons sans supprimer le signal climatique. Nous avons comparé les relations climat-croissance radiale obtenues à l'aide de ces deux approches pour les branches et les collets. La sensibilité climatique était en moyenne 4,9 et 2,7 fois plus élevée en utilisant les valeurs de BAI qu'avec les valeurs de RW standardisées (droite de pente nulle) pour les branches et les collets, respectivement. L'utilisation de valeurs de BAI a permis d'identifier des déterminants climatiques de la croissance radiale identiques pour les branches et les collets, tandis que les résultats obtenus avec des valeurs de RW standardisé étaient inconstants. Des résultats semblables ont été obtenus lors de l'utilisation de splines avec des fenêtres de lissage de différentes longueurs. De futures études s'intéressant à différentes espèces évoluant dans différents milieux sont nécessaires avant que la conversion des largeurs de cernes en surfaces ne puisse être largement utilisées comme méthode de standardisation en dendrochronologie avec les arbustes.

1.2 Abstract

Climate warming at high latitudes has contributed to the growing interest in shrub tree-ring analysis. Shrub architecture presents new challenges for dendrochronology, such as the seemingly lower and inconsistent climatic sensitivity of stems vs root collars. Shrub stems may thus be considered as sub-optimal to study climate-growth relationships. In this paper, we propose that the lower climatic sensitivity of stems could be caused by the use of unsuitable detrending methods for chronologies spanning decades rather than centuries. We hypothesize that the conversion of ring width (RW) to basal area increment (BAI) is better suited than traditional detrending methods to remove the age/size-related trend without removing the climate signal. We compared climate-growth relationships of these two approaches for stems and root collars. Climate sensitivity was on average 4.9 and 2.7 times higher with BAI than with detrended (mean-centered) RW chronologies for stems and root collars, respectively. The climatic drivers of radial growth were identical for stems and root collars when using BAI but were inconsistent when using detrended RW series. Detrending with splines of various lengths yielded similar results. Further studies focusing on different species and locations are needed before the use of BAI can become broadly used in shrub dendrochronology.

1.3 Introduction

Harsh climatic conditions and short growing seasons limit plant productivity across the Arctic and subarctic (Chapin, 1983; Jia et al., 2009; Vicente-Serrano et al., 2020). Cold temperatures reduce photosynthetic activity (Taiz et al. 2015) and slow down plant phenological processes such as bud burst and seed development (Aerts et al., 2006; Meunier et al., 2007; Sirois et al., 1999). Over the last decades, however, warming in Arctic and subarctic regions, which is nearly three times greater than the global average (Bush & Lemmen, 2019), has substantially reduced the limiting effect of temperature on primary productivity (Menzel et al. 2003; Zeng et al. 2011; Charron 2015). Although some studies have found browning trends in the boreal or lower Arctic regions (Baird et al., 2012; Verbyla, 2008; Wang & Friedl, 2019), the improved climatic conditions during the growing season has resulted in the widespread "greening" of the circumpolar region of the northern hemisphere (Bunn et al. 2007; Ju and Masek 2016; Tape, Sturm, and Racine 2006). The expansion of shrub species, either through the densification of existing stands or through the colonization of new habitats, contributes to this phenomenon (Lemay et al., 2018; Myers-Smith et al., 2011; Ropars & Boudreau, 2012; Wang & Friedl, 2019). North of the treeline, shrubs are the only woody plants (Buras & Wilmking, 2014; Lu et al., 2016) and their growth rings are a valuable ecological archive with a yearly resolution. Therefore, dendrochronological studies on shrub species can provide precious insights on the drivers of climate and landscape change across the entire circumpolar region.

Shrub growth and architecture present new challenges for dendrochronology. For example, subarctic shrubs such as *Betula glandulosa* Michx. individuals, when they originate from sexual reproduction, present multiple stems that grow from the often-buried root collar, i.e. the interface between the stems and the roots (Fig. 1.1a). From a dendrochronology standpoint, the root collar is therefore the anatomical equivalent of the base of the primary axis of a tree as it integrates the growth of all stems. In the field, shrub root collar sampling necessitates shrub excavation, a time-consuming and destructive manipulation that can interfere with the complex logistic of fieldwork in remote areas. For these reasons, many dendrochronological studies are conducted on samples taken at the base of the dominant stems (Bär et al. 2008; Hallinger, Manthey, and Wilmking 2010; Lu et al. 2016; Uyeda et al. 2016; Weijers et al. 2018). However, stems can be substantially younger than their root collar as they are continually replaced throughout the shrub life, resulting in shorter growth chronologies. Such sampling design could be problematic since Ropars et al. (2017) demonstrated that, for *B. glandulosa* stems, a dominant shrub species in North-Eastern North America, climate sensitivity recorded at the stem level is lower and more variable than the one recorded at the root collar just a few centimeters below (Ropars et al., 2017). Although this was not yet proven for other shrub species, there is a need to better understand the difference in climate sensitivity between stems and root collars in order to improve shrub dendroclimatology.

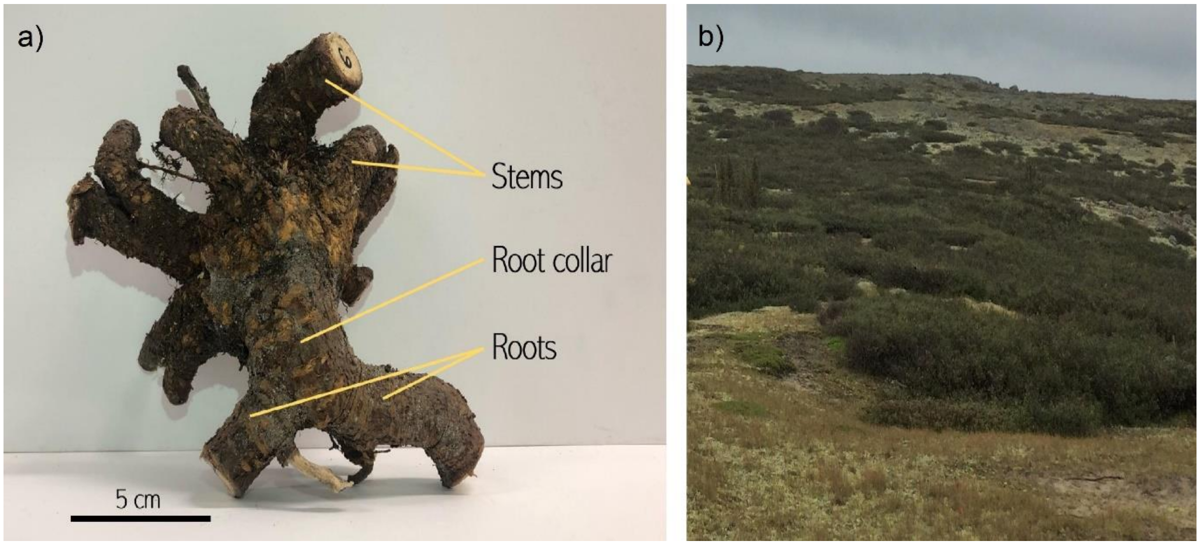

Figure 1.1 a) Position of the root collar, roots, and stems of an uprooted *Betula glandulosa* individual with most of the roots and stems removed. b) Landscape around the Boniface River research station, showing patches of shrubs interspersed in a matrix of tundra vegetation.

Although Ropars et al. (2017) argued that the weaker climatic signal registered by stems could arise from competition between the different stems of a single individual, another likely explanation relies on a technical issue associated with the detrending of growth ring chronologies. Detrending, also called standardization, is necessary to remove age/size related trends from tree-ring series in order to isolate and amplify signals of interest such as high-frequency or low-frequency climatic trends, forest disturbances, or stand dynamics (Cook et al., 1990). One of the trends that is almost systematically removed is the age/size effect, observed as a gradual decrease in ring width from the center of the stem towards the bark. This trend, which results from the increasing perimeter of the cambium as new rings are produced, is removed using a variety of detrending approaches that each have their benefits and drawbacks

(Briffa & Melvin, 2011; Dietrich & Anand, 2019; Peters et al., 2015). One of the challenges of detrending is to be able to remove the age/size trend while keeping the low-frequency (long term) variations associated to climate change as both operate at a multi-decadal scale. For example, in time series spanning decades rather than centuries, detrending to remove any age/size related trends will likely also remove at least part of the long-term increase in ring width associated to climate warming.

The conversion of ring width (RW) to ring area, or basal area increment (BAI), is a robust detrending approach that compensates for the ever-increasing perimeter of the cambium (Hornbeck & Smith, 1985; Phipps, 1984). BAI has been used in studies aiming to characterize tree responses to environmental changes, and some of these studies confirm the effectiveness of converting RW into BAI as a detrending method (Boakye et al., 2022; Hornbeck et al., 1986; Linares et al., 2009; Sullivan et al., 2016). Leblanc (1994) demonstrated that RW measurements of pine and spruce species tend to cloud the relationship between a growth trend and its potential cause, and that BAI measurements are more closely related to stem volume increment than RW data. Moreover, based on the results of Baral et al. (2019) who demonstrated that climate-tree growth relationships were stronger when using BAI rather than standardized RW in short chronologies, we believe that the use of BAI might be of high interest when analyzing shrub species growth rings . Indeed, even though BAI measurement has been used mainly with trees, it remains only marginally used for shrub species (Bär et al., 2006; Buchkowski et al., 2020; Buras & Wilmking, 2014; Le Moullec et al., 2020; Lu et al., 2016).

In this study, conducted in Nunavik (subarctic Québec, Canada), our main objective was to determine if the conversion of RW to BAI can reduce the discrepancies found in *B. glandulosa* detrended chronologies built from shrub stems vs root collars, both in terms of growth patterns and relationship to the multi-decadal climate trends. If so, climatic drivers and climatic sensitivity of growth chronologies should be comparable, regardless of the nature of the sample (stem or root collar), when using BAI data instead of detrended RW data (mean-centered or spline detrended). A secondary objective was to determine if BAI estimations (i.e. calculated from raw ring-width measurements) are correlated to the actual measurements of BAI (i.e., measured on scanned cross-sections using image analysis) for *B. glandulosa*. Indeed, both approaches have been used in previous studies but never compared (calculated: Baral et al., 2019; Buchkowski et al., 2020; Linares et al., 2009; measured: Bär et al., 2006; Buras & Wilmking, 2014). Calculating BAI from RW measurements is significantly faster but might generate inaccurate values in presence of eccentric growth form or irregular rings (Lu et al., 2016).

1.4 Methods

Using the same dataset as Ropars et al. (2017), we calculated BAI values to perform a direct climate sensitivity comparison between growth ring chronologies built with either detrended RW or BAI for both stems and root collars. For that reason, only a brief overview of the sampling methods and analyses will be provided here (but see Ropars et al. 2015, 2017 for more detailed descriptions). However, during our analyses, we realised that the detrending methods applied in Ropars et al. (2017) were sometimes inconsistent between samples and sites. Therefore, we decided to redo the detrending process using the same detrending methods for all samples. Uniformity in the standardization process is in fact necessary to show how traditional detrending methods can remove climatic trends in dendrochronological series. Consequently, results showed in this paper are slightly different from the ones published in Ropars et al. (2017).

1.4.1 Study area

Samples were collected in the vicinity of the Boniface River research station (57°45’ N, 76°10’ W) in Nunavik (subarctic Québec, Canada). Located at the forest-tundra ecotone, approximately 10 km south of the treeline (Ropars et al. 2017), this region showed a significant greening trend between 1984 and 2012 (Ju & Masek, 2016). The landscape is dominated by shrub tundra, with *B. glandulosa* being the dominant shrub species (Fig. 1.1b). Open lichen woodlands dominated by black spruce (*Picea mariana* Miller) cover *ca.* 30% of the landscape. Wetlands, exposed hilltops, and sandy terraces are also common. The fire frequency in the region is very low, with a fire rotation period of 1800 years (Payette et al., 2008). The study area is also located at the southern limit of the summer range of the Leaf River Caribou Herd, but the caribou density is low and grazing evidences have mostly been found on *Salix* species (Dufour-Tremblay & Boudreau, 2011).

The closest meteorological station is located 130 km northwest of the Boniface River research station, at the Inukjuak airport (Environment Canada, 58°28’ N, 78°05’ W). Mean annual air temperature was -6.8 ºC for the 1950-1994 period but increased to -5.2 ºC in the 1995-2019 period. Over the 1995-2019 period, total annual precipitation was 500 mm on average, 42% of which fell as snow (Environment Canada, 2019).

1.4.2 Field sampling

Field sampling was conducted in the summer of 2010 (Ropars et al., 2015, 2017). Samples were collected at three sites in each of the following environment types: sandy terraces, exposed hilltops, and snowbeds. Sandy terraces, located on well-drained sites next to the river, are dominated by lichens, graminoids and large patches of shrub species (Ropars et al., 2017) whereas exposed hilltops are dominated by arctic-alpine vegetation and mineral soil as a result of harsher winter conditions (Ropars et al., 2015). Snowbeds are characterized by greater snow accumulation during winter and later snowmelt in the spring, resulting in shorter growing seasons (Payette et al., 1985). At each site, 20 large, circular, and isolated *B. glandulosa* individuals were selected as they were believed to represent older individuals that originated from seed. Each shrub was excavated to collect the root collar, as well as two of its main stems. If the root collar of an individual could not easily be identified, it was discarded, and another shrub was excavated. Samples were cleaned and left to dry at room temperature for further analysis. Ropars et al. (2017) randomly selected one site per environment type (sandy terrace, exposed hilltop and snowbed) to conduct their analyses. We used the same sites and samples in this study.

1.4.3 Dendrochronological analysis

Root collars and stems were boiled for 3 hours before being sliced (25μm) with a microtome. Thin sections were stained with 1% safranine, dried and mounted on microscope glass slides with a 66% toluene solution. Root collars that could not be sliced perpendicularly or that were rotten were discarded, along with their corresponding stems. At the end of this process, 46 shrubs were kept in the study, for a total of 138 analysed cross-sections (46 root collars and 92 stems). Mean diameter of the stems and root collars were respectively 7 and 21 mm.

Digital pictures of each sample were taken with a camera mounted on a binocular at 40x magnification. Most samples showed little to no eccentricity. Ring width measurements were conducted with the LIGNOVISION software (v. 1.36) on two opposite radii for each sample. RW chronologies were crossdated using the COFECHA software (Holmes, 1983) and standardized in the Dendro 2019 software (v. 3.2.8, Centre for northern studies, Université Laval) to produce RWI chronologies. The first detrending method used was the mean-centering method since it is the most commonly used method when studying multi-decadal growth trends. However, to show how other detrending methods can alter climatic signal, we also detrended RW data with cubic splines of different wavelengths (20-year, 30-year, and 66% of the length of the series). Only the comparison between BAI and RWI obtained from the mean-centering method is showed in the text, but results obtained with the various spline lengths are presented in supplemental material (Tables S.1.1-S.1.3).

BAI were first calculated using raw (non-standardized) RW measurements according to the following equation, which assumes that all growth rings are perfectly circular and concentric:

$$(1)\quad \text{Calculated BAI} = (\pi \text{ x } r^2 \text{ of current year}) - (\pi \text{ x } r^2 \text{ of previous year})$$

BAI were also measured by image vectorisation with the Image J software. For this part of the study, only samples for which the complete thin section could fit on a microscope slide were used, resulting in the measurement of 56 samples, mostly stems (terrace: 18; hilltop: 18; snowbed: 20) with a mean and maximum diameter of 5.0 and 11.5 mm, respectively. Each outer ring was delineated by hand, and annual ring area was computed by subtracting the cumulative ring area of the previous year from the cumulative ring area of the current year.

EPS values were computed in Dendro 2019, and rbar and AR1 values were computed using the dplR package in R (Bunn et al., 2022). All individual RWI and calculated BAI chronologies are available as supplemental material (Figures S.1.1-S.1.3), as well as mean chronologies divided by age cohorts (Figure S.1.4-S.1.6).

1.4.4 Statistical analyses

To determine whether the BAI values calculated from raw RW were representatives of the BAI values measured by image vectorisation, two mean chronologies were produced for each site using the calculated and measured BAI data. The similarity of the chronologies was then evaluated with the Pearson correlation coefficients (r).

To evaluate climate sensitivity, mixed-effects models were performed using the lme4 package in the R software (v. 4.0.2; R Core Team, 2020). For each environment type (terrace, hilltop, and snowbed), we ran 4 separate series of models using individual growth series constructed with (1) either root collar or stem data and (2) either RWI (detrended by mean-centering or various spline wavelength) or BAI calculated from raw RW measurements. RWI and calculated BAI were used as response variables, monthly total precipitation, monthly mean temperature, and their various combinations were used as fixed effects. Year was considered as a random effect. Null models using only growth measurements (BAI or standardized RW; response variable) and year (random effect) were used as a baseline to calculate climatic sensitivity. The models were run with data from 1947 to 2009, the period for which both climatic and radial growth data were available.

The Akaike information criterion (AIC) was used to determine the best models and to compare climatic sensitivity (Ropars et al. 2017). To do so, we calculated the ΔAIC_{null} by subtracting the AIC of each model built with climatic data from the AIC of the corresponding null model. A higher ΔAIC_{null} represents a greater sensitivity to climate (Myers-Smith et al. 2015). To assess the goodness of fit of the models, the marginal and conditional R^2 were calculated using the MuMIn package and the r.squaredGLMM function (Nakagawa and Schielzeth 2013; Ropars et al. 2017) in R. Marginal R^2 represents the proportion of growth that is influenced by fixed effects (climate) whereas the conditional R^2 represents the proportion of growth that is influenced by both fixed and random effects (Nakagawa & Schielzeth, 2013).

1.5 Results

RWI results included in the results section come from RW series detrended by the mean-centering method. Climate sensitivity results obtained with RWI detrended by the various spline lengths were place as supplemental material (Tables S.1.1-S.1.3).

Age of the sampled root collars ranged from 13 to 96 years, with an average age of 41.4 ± 20.5 years (Fig. 1.2). On average, root collars were 18 years older than their two corresponding stems. Stem age ranged from 10 to 64 years, with an average age of 23.4 ± 13 years (Fig. 1.2). Age distributions were however skewed towards younger individuals, with 68.4 % of stems being younger than 25 years.

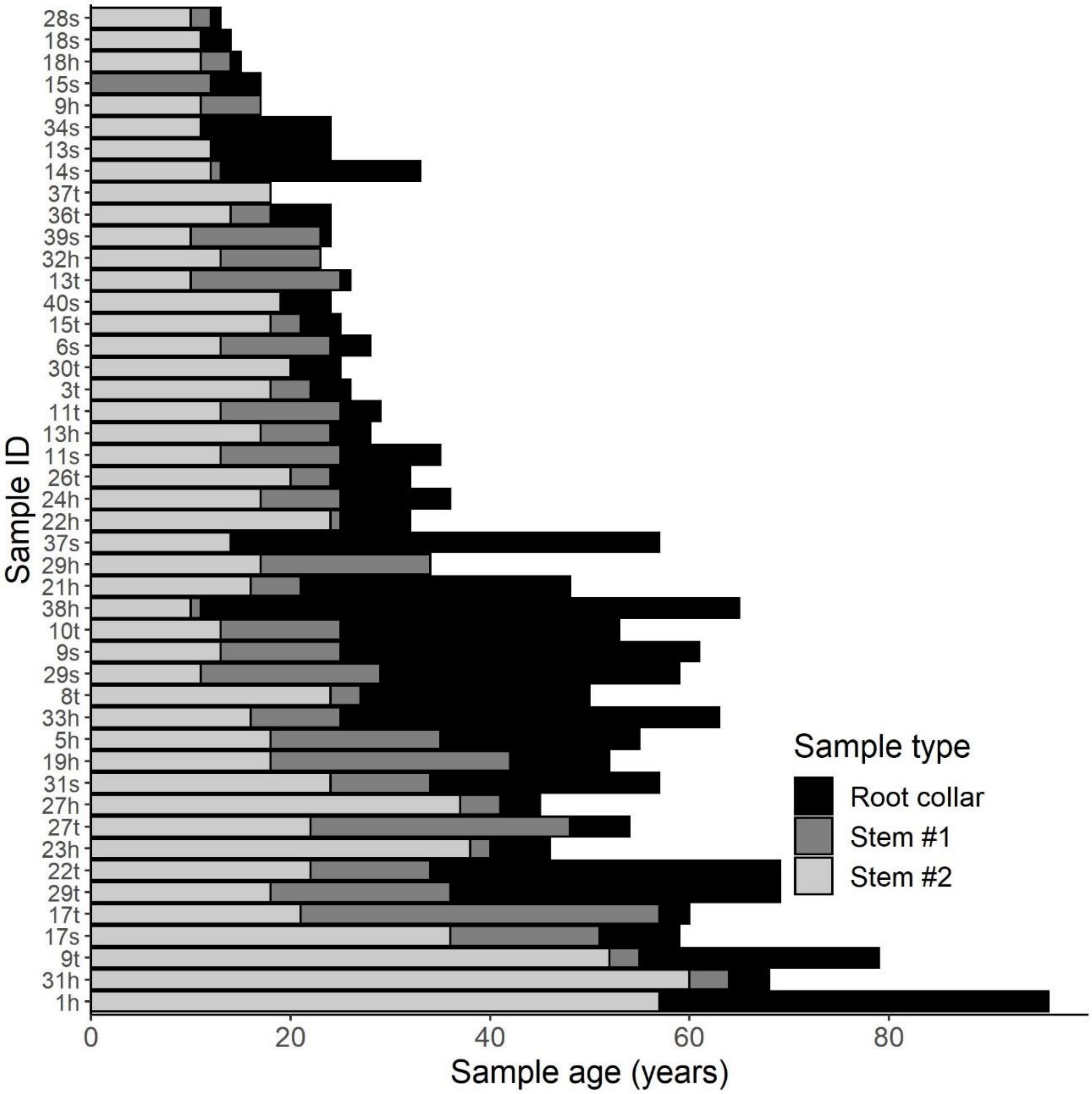

Figure 1.2 Age of the root collar (black) and stems (grey) of each sampled shrub (horizontal lines). Letters at the end of the shrub IDs represent the site from which they come (t = terrace, h = hilltop, s = snowbed).

1.5.1 Growth chronologies

There was a strong correlation ($p < 0.001$) between BAI calculated with a perfect circle equation and BAI measured by image vectorization, as revealed by correlation coefficients > 0.9 (Fig. 1.3).

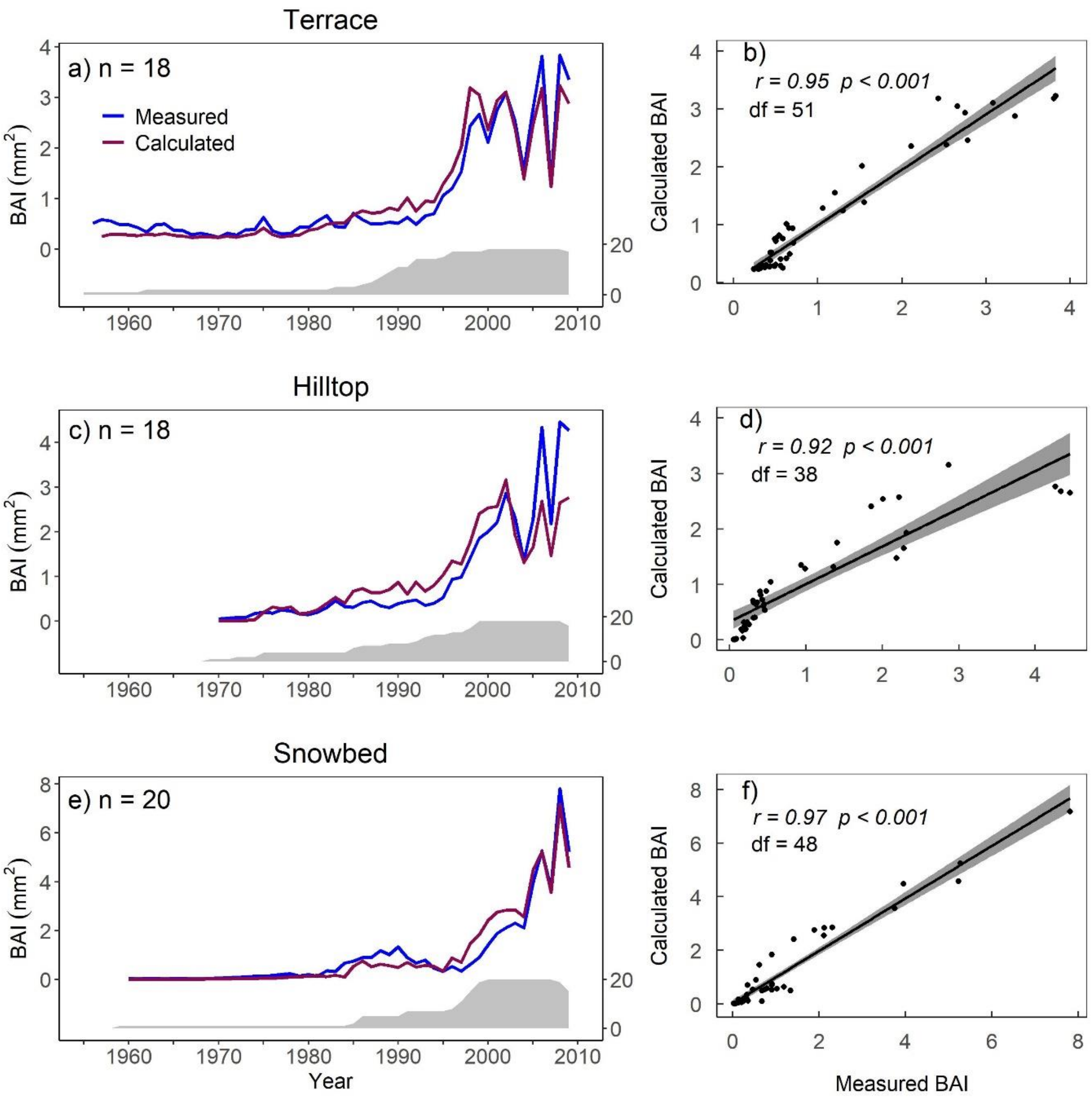

Figure 1.3 Growth chronologies based on calculated (red) and measured (blue) BAI data. Number of cross-sections used (n), correlation coefficients (r), and degree of freedom of the correlations (df) are given for the three sites. Shaded areas represent sample depth of the series.

All growth chronologies had high EPS (expressed population signal) values, between 0.92 and 0.98, with average of 0.95 (see Table S.1.4 for other growth chronologies statistics). Growth chronologies built from RW data were characterized by high variability (large confidence intervals) in their oldest portion and a significant radial growth increase in the mid-1990s (Fig. 1.4). Compared to RW chronologies, BAI chronologies were much less variable at their onset but also showed a significant increase in growth in the mid-1990s. As a result, the main difference between RW and BAI chronologies was found in the oldest portion of the chronologies. Examination of individual chronologies (Figs. S.1.1-S.1.3) and of chronologies separated by age groups (Figs. S.1.4-S.1.6) suggest that the high variability in the early RW chronology is caused by the gradual inclusion of new individual series that destabilize the mean because of the age/size effect found in each individual series. Such effect is not seen in the BAI chronologies because the age/size effect is effectively removed by the transformation of RW to BAI.

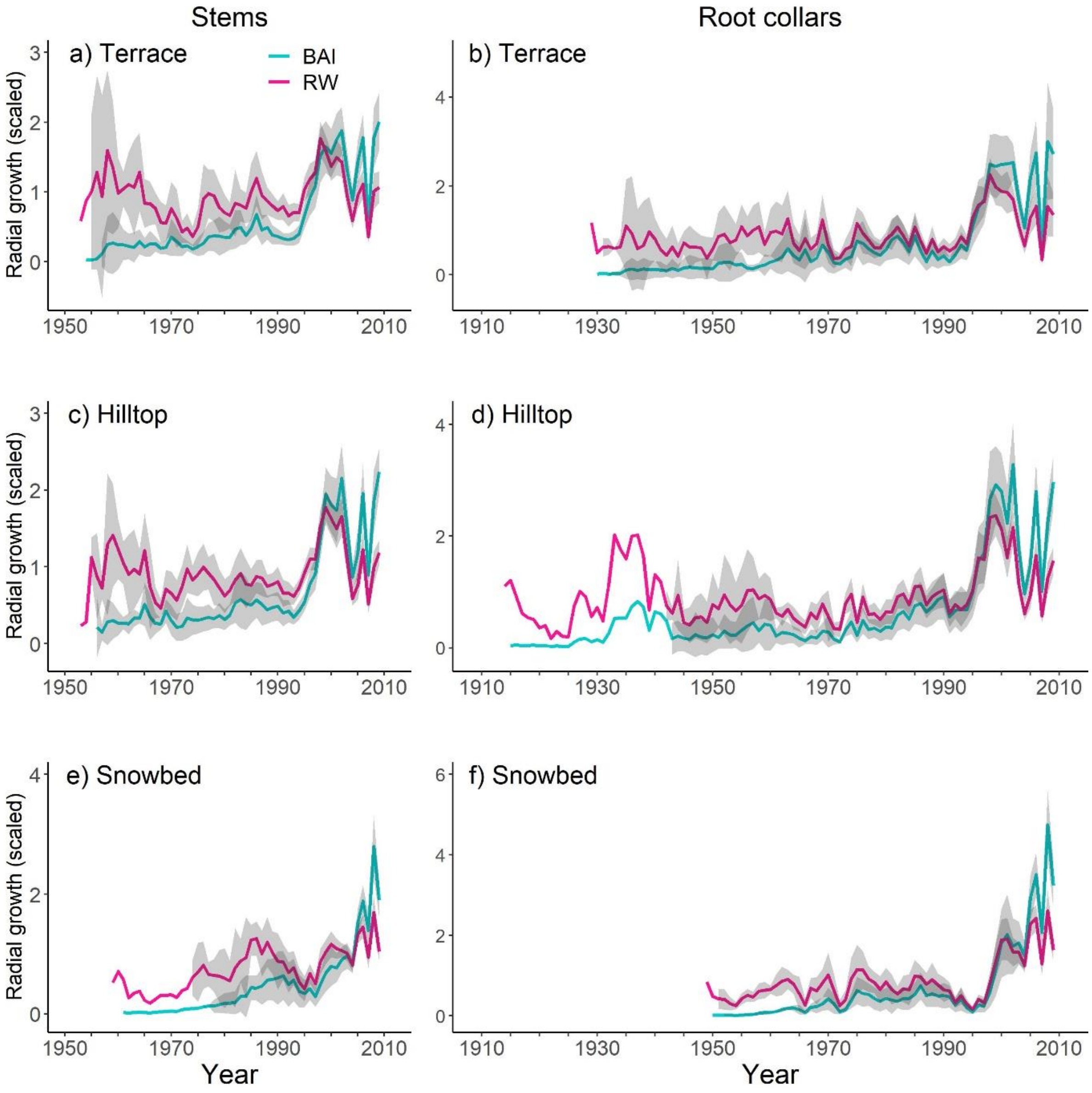

Figure 1.4 Mean growth chronologies of stems (a, c, e) and root collars (b, d, f) using mean-centered ring width (RW; pink) and calculated basal area increment (BAI; blue). Shaded areas represent 95% confidence intervals.

1.5.2 Climatic drivers and sensitivity to climate

When using RW index data, model selection found that climatic drivers were different for stem and root collar growth chronologies (Table 1.1). Moreover, climatic drivers of stem chronologies were also different between the different habitats. However, when using BAI instead of RW, our analyses generated identical climatic drivers of *B. glandulosa* growth, regardless of sample type/shrub part and habitat (Table 1.1). For all BAI chronologies, July temperature and March precipitation were the best predictors and had positive impacts on *B. glandulosa* growth. In fact, BAI was more responsive to July temperature and March precipitation than RW index (Table 1.1, Fig. 1.5). These results contrast sharply with those presented by Ropars et al. (2017) in which the climatic drivers of stem radial growth varied from site to site.

BAI chronologies also showed greater climatic sensitivity than RWI chronologies (Table 1.1). For stems, the use of BAI increased climate sensitivity by 5.2 times on terraces, 7.5 on hilltops, and 1.9 in snowbeds (average increase across all environment types: 4.9 times higher). Even the climatic sensitivity of root collar chronologies appeared to benefit, although to a lesser extent, from the use of BAI (3.6 times higher on terraces: 2.6 on hilltops; 1.8 in snowbeds; average: 2.7).

Differences in climate sensitivity between root collars and stems were greatly reduced by the use of BAI values. This was exemplified by the overlapping predictive responses of stems and root collar growth to July temperature and March precipitation (Fig. 1.6). Other detrending approaches (spline of various wavelengths) did not have the same positive impacts as BAI conversion since they did not reduce the differences in climate sensitivity between root collars and stems and between habitats (Tables S.1.1-S.1.3). Therefore, the conversion of RW into BAI leads to the highest climate sensitivity results amongst the five detrending methods tested (Fig. S.1.7). Lastly, the substantial increases in marginal and conditional R^2 values revealed that climatic variables explained a larger portion of BAI than RW index (Table 1.1).

Table 1.1 Climate sensitivity values (ΔAIC_{null}), model fit statistics (R^2) and residual degree of freedom (residual df) for the best climatic variables explaining RW index (RWI; detrended by mean-centering) and calculated BAI of *Betula glandulosa* root collars and stems over the 1947-2009 period.

Environment	**Data type**	**Sample type**	**Best climatic model**	**Climatic sensitivity (ΔAIC_{null})**	**Marg. R^2**	**Cond. R^2**	**Residual df**
Terrace	RWI	Root collars	T Jul + P Mar	9.8	0.07	0.14	413
		Stems	T Apr	6.4	0.04	0.06	403
	BAI	Root collars	T Jul + P Mar	34.8	0.29	0.39	400
		Stems	T Jul + P Mar	33.5	0.39	0.46	354
Hilltop	RWI	Root collars	T Jul + P Mar	16.3	0.13	0.25	471
		Stems	T Apr	4.9	0.03	0.08	486
	BAI	Root collars	T Jul + P Mar	43.1	0.43	0.56	458
		Stems	T Jul + P Mar	36.7	0.40	0.48	449
Snowbed	RWI	Root collars	T Jul + P Mar	18.9	0.28	0.50	339
		Stems	T Jun	10.6	0.15	0.24	246
	BAI	Root collars	T Jul + P Mar	33.5	0.52	0.75	325
		Stems	T Jul + P Mar	20.2	0.39	0.52	228

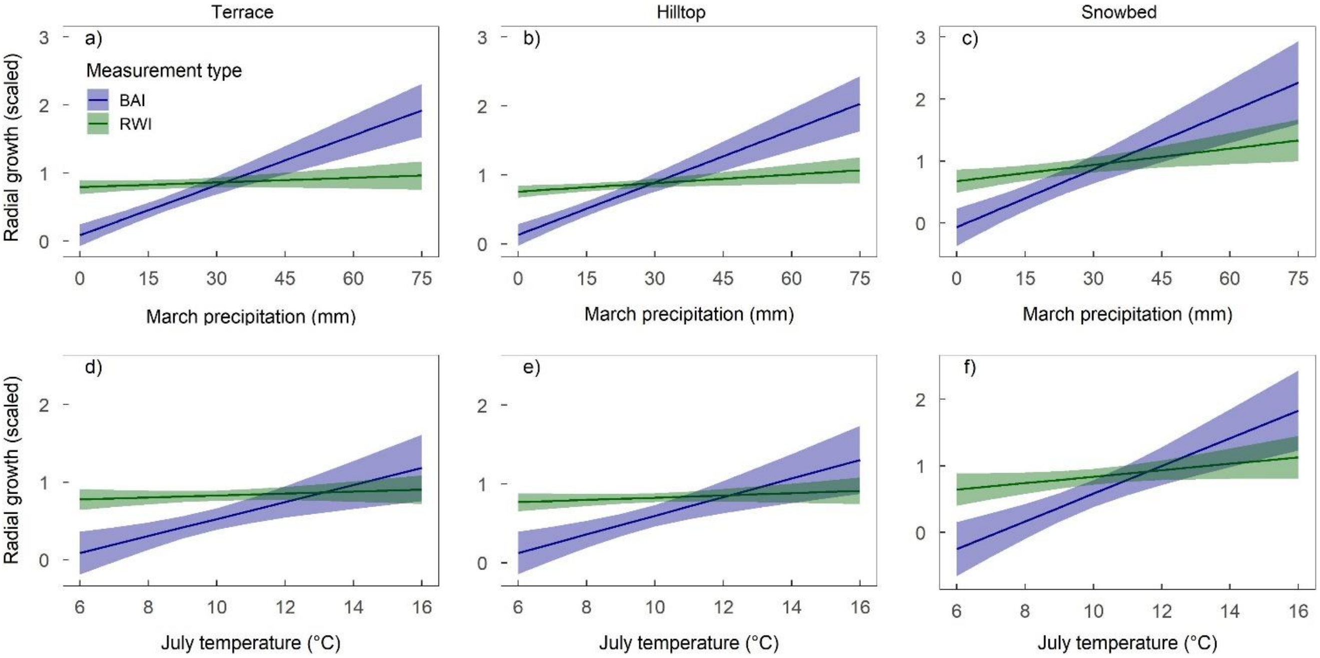

Figure 1.5 Predicted responses of *Betula glandulosa* stem growth and 95% confidence intervals when using calculated BAI values (blue) and RW index obtained by the mean-centering method (green) according to the best climatic models: March precipitation (a-c) and July temperature (d-f) for the 1947-2009 period

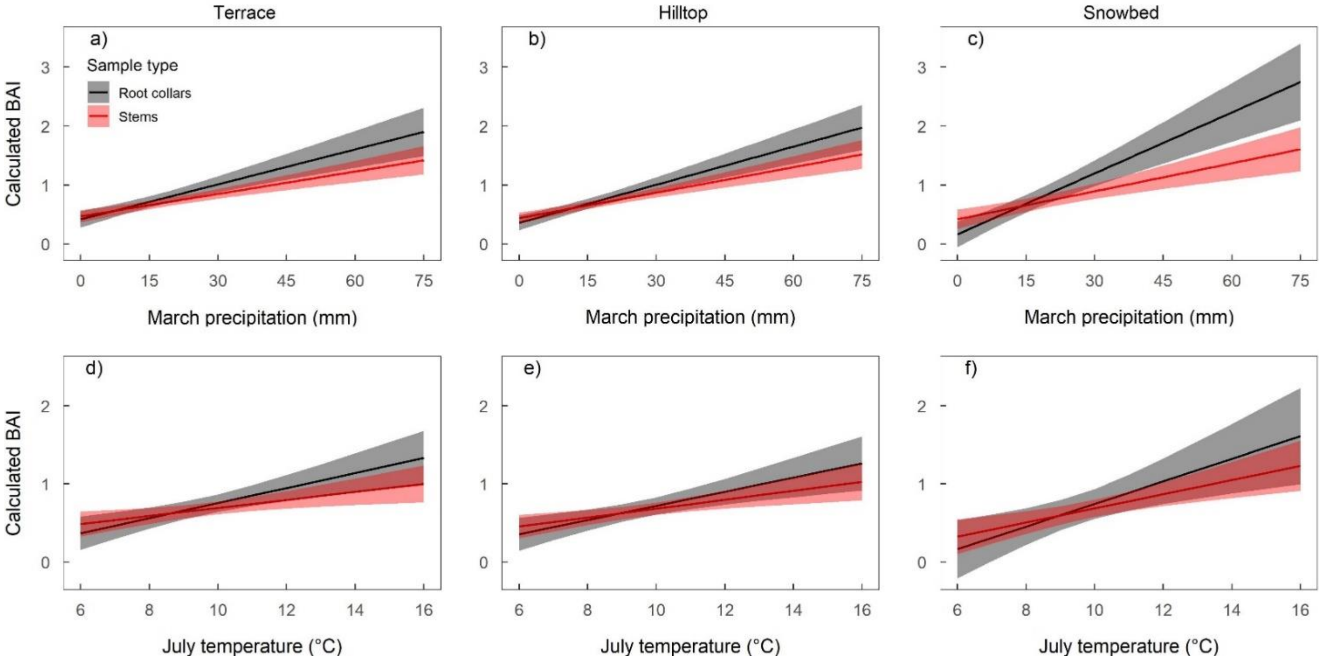

Figure 1.6 Predicted calculated BAI values and 95% confidence intervals for root collars (black) and stems (red) of *B. glandulosa* according to the best climatic models: March precipitation (a-c) and July temperatures (d-f) for the 1947-2009 period.

1.6 Discussion

In this study, we showed that the use of basal area increment (BAI) to remove the age/size related growth trend is an effective detrending procedure for *B. glandulosa* as it yielded consistent results regardless of the nature of the samples (stems or root collars). First, the use of BAI allowed us to identify with consistency July temperature and March precipitation as the most important climatic drivers of *B. glandulosa* radial growth. Secondly, using BAI increased the climate sensitivity of stem growth to a level comparable to the root collars. Therefore, our results strongly support the use of BAI when interested by the impact of climate change on shrub species radial growth at the multi-decadal scale.

1.6.1 Calculated vs measured BAI

Calculated BAI values from raw *B. glandulosa* RW measurements were strongly correlated to the measured BAI values. This result suggests that ring width can be used to estimate BAI for species with regular and concentric growth rings like *B. glandulosa* (see Fig. S.1.8 for pictures of *B. glandulosa* cross-sections). For such species, it appears therefore not necessary to conduct the time-consuming BAI measurements on scanned images, although we would recommend to always verify the strength of the correlation between calculated and measured BAI before using this short-cut approach with another species as shrubs growing in Arctic and subarctic regions under extreme growth conditions often produce irregular, off-centered, or discontinuous growth rings. For such species, further tests would be needed prior to using ring width to estimate BAI. A lower correlation between calculated and measured BAI could necessitate various adjustments. For example, ring width could be measured on at least four radii to improve the accuracy of BAI estimation (Buras & Wilmking, 2014). The use of equations considering growth rings as elliptical instead of circular could also be a solution for some species (Visser, 1995). However, for species with very important eccentric growth, BAI measurements (instead of calculation) would be the most appropriate approach.

1.6.2 BAI conversion as a detrending method for shrub chronologies

BAI is already widely used in studies aiming to analyze the relationship between climate and tree growth (Alfaro-Sánchez et al., 2020; Baral et al., 2019; Boakye et al., 2022; Bouriaud et al., 2005; Hornbeck & Smith, 1985; Linares et al., 2009; Rozenberg et al., 2020). In fact, many studies have demonstrated that the use of BAI instead of RW generates higher correlations to tree biomass and wood volume gain (Biondi and Qeadan 2008; Bouriaud et al. 2005; LeBlanc 1994). Similar results were also reported for some shrub species (Uyeda et al. 2016). In most cases, the conversion of raw RW to calculated BAI values is used as a detrending method to remove non-climatic growth trends related to stem age/size in trees (Hornbeck and Smith 1985; Linares et al. 2009; Nehrbass-Ahles et al. 2014; Sullivan et al. 2016). When both RW and BAI values are compared, the latter systematically yield better correlations between climate and radial growth (Lu et al. 2016; Baral et al. 2019; Dietrich and Anand 2019; Alfaro-Sánchez et al. 2020).

Our results corroborate these previous studies, even though they were mainly conducted on tree species. They strongly suggest that the use of BAI is an efficient method to remove non-climatic growth trends related to age or size of shrub stems while preserving the climatic trends. The conversion of RW to BAI had a noticeable effect in the earliest portion of our growth chronologies, where BAI series were less variable (narrower confidence intervals) than RW ones. This greater variability in RW data arises from the different period of establishment of the samples used to build the growth chronologies, resulting in asynchronous age/size growth trends (see figures S.1.1 to S.1.3 for individual chronologies). On the other hand, climatic growth trends are generally synchronous in a given region because they are associated to climatic drivers acting at the regional scale. In our chronologies, these trends, mostly found in the recent period in response to the substantial warming observed in the study region since the mid 1990s (Chouinard et al., 2007), were not removed by the conversion to BAI. Moreover, the reduced variability at the beginning of the BAI chronologies, evidenced by narrower confidence intervals in BAI chronologies, reveal that growth estimations are more robust when BAI measurements are used.

An alternative hypothesis for the simultaneous increase in growth observed during the 1990s is the manifestation of a strong recruitment pulse with young stems growing rapidly. However, most individuals showed an increase in radial growth during the 1990s, regardless of their establishment year (see Figs. S.1.4 to S.1.6). Such synchrony between individuals (or stems) of different ages suggests a generalized growth trend that cannot be solely due to a sudden recruitment pulse. Also, since the conversion of RW into BAI is a simple geometric correction removing the effect of the increasing stem diameter (Le Moullec et al., 2020), it fails to remove growth fluctuations related to population dynamics and disturbance. This is not an issue in most Arctic and subarctic environments with low inter-individual competition and disturbance regime. However, in environments where disturbances and competition affect growth trends, researchers should be aware of the limits of the BAI detrending method.

1.6.3 Influence of BAI on *Betula glandulosa* climatic drivers and sensitivity

Ropars et al. (2017) found that growth chronologies built from stem samples instead of root collars resulted in inconsistent climatic drivers of *B. glandulosa* and in reduced climatic sensitivity. As many shrubs species, such as *B. glandulosa*, have a multi-stem growth form, Ropars et al. (2017) hypothesized that competition between stems of a single individual could overshadow at least partially the climatic signal. Under this hypothesis, the available resources for growth might be unevenly allocated to the different parts of a single individual according to a competition-like mechanism (Sadras & Denison, 2009). It would therefore be possible that all stems do not get their fair share of resources, a pattern that can lead to differential radial growth between stems for any given year. Nonetheless, we would still expect growth trends in stems and root collars to be influenced by the same climatic variables, which was not the case in Ropars et al. (2017).

While intra-plant competition is a potential contributor to the observed differences in climate-growth relationship between stems and root collars, we showed that the detrending method that is used to remove age/size trends could be another factor to consider. In fact, the correlation between climate and woody species growth is strongly influenced by the detrending procedure applied (Dietrich and Anand 2019; Nehrbass-Ahles et al. 2014; Sullivan et al. 2016). For example, in young chronologies (ca. 22 years old on average), Baral et al. (2019) found that the use of splines and negative exponential functions tended to eliminate the climatic signal of RW chronologies. When using a smoothing detrending method for shorter chronologies, the use of shorter time windows tends to eliminate mid- and low-frequency variations, which usually comprise most of the long-term climatic signal (Nicault et al., 2010). Such a detrending procedure could therefore explain the lack of radial growth increase in the mid-1990s in our dataset following standardization with cubic splines (Fig. S.1.9-S.1.11). Although detrending by mean-centering data enables to preserve the multi-decadal climatic trends, is fails to remove, or even amplifies, the asynchronous age/size growth trends, which can cloud the climatic signal and strongly influence the results of such analysis.

The conversion of raw RW to BAI could solve many of the inconsistencies related to the chosen detrending method. In our study, the use of BAI resulted in greater consistency in the identification of the climatic drivers of *B. glandulosa* growth. Using BAI, the best climatic model combined July temperature and March precipitation, regardless of site or sample type (root collar or stem). Analysing the Inukjuaq meteorological station data, we found that July temperature increased by 0.14°C/year between 1980 and 2009 (p=0.002) while no significative trend was observed between 1947 and 1980 (p=1). Before 2000, March precipitation only increased by 0.25mm/year, while it increased by 4.1mm/year after 2000 (p=0.003 and p=0.1, respectively). In addition to corroborating the climatic trends in the regions, such results also corroborate previously published dendroclimatological analyses that revealed the importance of summer temperature and winter precipitation for shrub growth. In fact, a strong relationship was found between *Empetrum hermaphroditum* radial growth and summer temperature (Bär et al., 2008), and the growing season temperature was found to be the main growth driver in 9 circumpolar countries (Myers-Smith et al., 2015). At sites located at high latitudes, warmer summer temperatures contribute to the lengthening of the growing season (Zeng et al., 2011), allowing the formation of more wood cells and resulting in an overall increase in radial growth

(Deslauriers et al., 2010). Snow precipitations were also found to have a positive impact on shrub radial growth (Hallinger et al., 2010). This is in line with our results since March precipitation falls as snow in our study region. March precipitation could lead to a deeper snow cover that provides greater protection against freeze-thaw cycles in the spring (Bokhorst et al. 2009), creates higher water availability at the onset of the growing season, and stimulates soil organic matter decomposition (Chapin, 1983; Hallinger et al., 2010), all of which have positive effects on primary productivity.

Another notable effect of using BAI is the increased climate sensitivity of the chronologies, regardless of the analysed shrub part/cross-section type (i.e., root collar or stem). Indeed, in Ropars et al. (2017) as well as in our study, RWI chronologies built with stem samples had substantially lower climate sensitivity than those using root collar samples. However, when using calculated BAI values, our results show that these differences almost disappeared. Thus, the use of BAI appears to be a more robust approach for climate sensitivity analyses at the multi-decadal scale than traditional detrending methods (mean-centering or spline), at least for *B. glandulosa*. Although we only tested this approach on *B. glandulosa*, we believe that the use of BAI would yield similar results for other erected subarctic shrubs species displaying similar concentric growth ring. Further studies should therefore focus on other species and could be expanded to include prostrate shrub species growing in the High Arctic.

1.7 Conclusion

In this study, we demonstrated that the conversion of raw RW to BAI should be favored over mean-centering or spline-fitting detrending methods for the dendroclimatological analysis of multi-decadal growth trends in *Betula glandulosa* growth chronologies spanning decades rather than centuries. When using BAI instead of RWI, chronologies have stronger and more consistent relationships with climate, especially for stems. Our results support the hypothesis that standardization of short chronologies using unsuitable detrending methods might be responsible for the observed lower climate sensitivity of stems compared to root collars. Since climate sensitivity of root collars and stems are similar when BAI is used, the only difference remains in the length of the series, which is longer for root collars than for stems. Otherwise, the time-consuming and destructive process of collecting shrub root collars may no longer be necessary for dendroclimatological analysis, as long as BAI values are used. We showed that the calculation of BAI from raw RW is an accurate estimate of the true basal area increment measured on an image for samples whose rings are mostly circular and concentric. This study contributes significantly to the still fast-developing field of shrub dendrochronology. First, from a logistical perspective, the ability to use stems instead of root collars while still getting robust and consistent results greatly simplifies and quickens sampling in the field. Second, the use of BAI instead of RW for shrub stems should allow for a more accurate identification of the climatic drivers of shrub growth and expansion across the Arctic and subarctic. In the light of these results and since our study was conducted on only one shrub species (*B. glandulosa*), further studies need to investigate the use of BAI with different species and detrending methods before it becomes broadly used in shrub dendrochronology.

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Chapitre 2 Radial growth of subarctic tree and shrub species: relationship with climate and contribution to the greening of the forest-tundra ecotone

2.1 Résumé

Le réchauffement climatique a entraîné une augmentation généralisée de la productivité primaire dans les régions nordiques. Ce "verdissement", qui modifie la dynamique des écosystèmes terrestres et peut potentiellement accentuer le réchauffement climatique, est toutefois spatialement hétérogène. Parmi les nombreuses études qui ont tenté d'identifier les causes de cette hétérogénéité du verdissement, très peu se sont concentrées sur les réponses différentielles des groupes fonctionnels végétaux au réchauffement climatique. Notre objectif était de déterminer si la relation climat-croissance spécifique aux espèces peut expliquer l'hétérogénéité des taux de verdissement subarctiques. Nous avons comparé la relation climat-croissance et la contribution au NDVI des espèces dominantes d'arbres (*Picea mariana*) et d'arbustes (*Betula glandulosa*) à deux endroits de l'écotone forêt-toundra au Nunavik (Québec, Canada). Les coefficients de corrélation de la relation climat-croissance variaient selon les espèces et les sites, étant plus élevés pour *P. mariana* et dans le site le plus au nord. L'association plus faible entre le NDVI et la croissance radiale de *P. mariana* à la station la plus au nord semble être compensée par une association plus forte entre le NDVI et la croissance radiale de B. *glandulosa*. Nos résultats montrent que la réponse au climat varie dans l'espace et entre les espèces, ce qui pourrait expliquer en partie l'hétérogénéité des taux de verdissement subarctiques. Cette meilleure compréhension de l'hétérogénéité du verdissement dans les régions subarctiques aidera à prévoir la direction et les potentielles conséquences du verdissement dans le futur.

2.2 Abstract

Global warming has resulted in a widespread increase in primary productivity in northern regions. This "greening", which alters terrestrial ecosystems dynamics and triggers positive feedback on climate, is however spatially heterogeneous. Few studies have focused on the differential responses of plant functional groups to warming as a potential driver of greening rates heterogeneity. Our objective was to determine if the species-specific climate-growth relationship can explain the heterogeneity of the subarctic greening rates. We compared climate-growth relationship and contribution to NDVI of the dominant tree (*Picea mariana*) and shrub (*Betula glandulosa*) species at two locations in the forest-tundra ecotone in Nunavik (Québec, Canada). Correlation coefficients of the climate-growth relationship varied between species and locations, being higher for *P. mariana* and at the northernmost location. The lower association between NDVI and *P. mariana* radial growth at the northernmost location appeared to be compensated by a stronger association between NDVI and *B. glandulosa* radial growth. Our results show that response to climate varies spatially and between species, which could partially explain the heterogeneity of subarctic greening rates. This improved understanding of the greening heterogeneity will help predict forthcoming changes in primary productivity and their potential positive feedback on global warming.

2.3 Introduction

Over the last century, the Arctic has warmed at more than twice the rate of the global average (AMAP, 2017), and mean Arctic temperatures have increased by 0.75ºC during the last decade alone (Post et al., 2019). Since high latitude ecosystem primary productivity is mainly limited by the harsh climate that prevails in these regions (Jia et al., 2009), the milder conditions experienced over the last decades have triggered an increase in plant growth. In fact, several studies have shown that warmer temperatures (Myers-Smith et al., 2015), longer growing season (Charron, 2015; Menzel et al., 2003), and greater precipitation (Bush & Lemmen, 2019; IPCC, 2014) have led to higher plant productivity in Artic and subarctic regions.

The increase of plant productivity under this new climatic regime has triggered the greening of the Arctic and subarctic regions (Tape et al., 2006), a pan-Arctic phenomenon mainly studied through the Normalized Difference Vegetation Index (NDVI). As a proxy of plant photosynthetic biomass derived from satellite imagery (Epstein et al., 2012; Goetz et al., 2005; Vicente-Serrano et al., 2020; Walker et al., 2012), NDVI allows researchers to track the expansion of vascular plant cover, as its values are closely associated to the amount of photosynthetic biomass in a given site (Wang & Friedl, 2019). Although observed throughout the circumpolar region, this greening trend displays high heterogeneity across different spatial scales (Myers-Smith et al., 2020). For example, Arctic and subarctic North America displays one of the most rapid greening rate compared to other regions at the circumpolar scale (Epstein et al., 2013). NDVI heterogeneity is also observed at the continental scale with Nunavik (northern Québec, Canada) displaying higher greening rates than any other regions in Arctic and subarctic North America (Ju & Masek, 2016). Heterogeneity of greening rates is also observed at the landscape scale in Nunavik, with some plant cover types contributing more to the greening than others (McManus et al., 2012).

The mechanisms underlying such heterogeneity in the greening of the northern regions are still poorly understood. Although large herbivores were found to negatively affect NDVI values (Blanco et al., 2008; Te Beest et al., 2016), most studies have linked the greening heterogeneity to the abiotic environment, including both topographic (elevation, exposition) and edaphic factors. For example, higher-elevation sites facing northwards were reported to be more suitable for greening (Berner et al., 2020; Choler et al., 2021), while other studies suggest that greening preferentially occurs in sites that are less exposed to wind (Lemay et al., 2018; Ropars & Boudreau, 2012) or with warmer and more mesic soils (Berner et al., 2020; Tape et al., 2012).

Another potential driver of the greening heterogeneity is the specific response of various plant species to similar changes in growth conditions. Such differential responses to climate can be assessed by studying the relationship between their radial growth (annual growth rings) and climate (Myers-Smith, Elmendorf, et al., 2015; Weijers, Beckers, et al., 2018) and by evaluating the strength of the relationship between their radial growth and NDVI trends (Andreu-Hayles et al., 2011; Ropars et al., 2015; Vicente-Serrano et al., 2020). Fast-growing erect shrub species tend to respond more rapidly than trees to better growth conditions associated with milder climatic conditions (Aerts et al., 2006). This differential response is reflected by the widespread expansion of shrub species in Arctic and subarctic regions over the last decades (Elmendorf et al., 2012; Myers-Smith et al., 2011; Myers-Smith & Hik, 2018; Tape et al., 2006) compared to the more variable northward expansion of treeline during the same period (Holtmeier & Broll, 2007). Indeed, both Harsch et al. (2009) and Rees et al. (2020) found that treelines were expanding northward in only 52% of their 166 and 151 study sites, respectively. Also, after finding significant increases in NDVI in only 15% of forested sites in comparison to 50-60% in shrub sites, McManus et al. (2012) concluded that shrubs are more likely to contribute to the greening trends in subarctic Québec (Canada) than trees. Yet, the impact of such intrinsic differences in plant functional groups' response to climate warming has not yet been linked to the heterogeneity of greening in the subarctic region.

As the greening of the northern regions and the northward expansion of woody species are expected to alter Arctic and subarctic ecosystem dynamics and composition (Fraser et al., 2014; Provencher-Nolet et al., 2014) and to trigger a positive feedback loop feeding global warming (Pearson et al., 2013), it is therefore essential to better understand the drivers responsible for the greening of Arctic and subarctic regions. Since studies assessing the impact of abiotic factors on greening rates have come to contradicting conclusions (Berner et al., 2020; Choler et al., 2021; Lemay et al., 2018), we believe that greening heterogeneity might, at least partially, come from biotic factors such as species-specific response to global warming. Because differences in the expansion of shrub and trees species are already observed in northern regions subjected to rapid warming (Harsch et al., 2009; Tape et al., 2006), and because NDVI increases are more frequent in shrub-dominated plant communities (McManus et al., 2012), one would expect shrub species to be more reactive to improved climate conditions and to contribute to a greater extend to the NDVI increases in these regions.

Thus, in this study, we aim to determine if the climate-growth relationship and the strength of the relationship between NDVI and radial growth differ between the dominant tree and shrub species near the treeline in Nunavik (subarctic Québec, Canada). To do so, (1) we identified the 1984 to 2018 NDVI trends of lichen woodlands, shrublands and lichen heathlands, three of the most representative terrestrial plant communities in subarctic Nunavik at two different locations, (2) we identified the main driver of radial growth and compared the climate-growth relationship of the dominant tree (*Picea mariana* Mill.) and shrub (*Betula glandulosa* Michx) species sampled in these plant communities and (3) we quantified the strength of the relationship between NDVI and radial growth of these species at each sampling site. We expected *i.* radial growth of *P. mariana* and *B. glandulosa* to be driven by the same climatic drivers, although *B. glandulosa* radial growth should be more responsive to climate than *P. mariana*, and *ii.* a stronger relationship between NDVI and *B. glandulosa* radial growth, although NDVI should be positively associated to the radial growth of both species.

2.4 Methods

2.4.1 Study area

This study was conducted at two locations in subarctic Nunavik (Québec, Canada; Fig. 2.1a). The southernmost location, near the Clearwater Lake research station (CWL; 56°20' N, 74°25' W), is located in the southern half of the forest-tundra bioclimatic zone (Meunier et al., 2007), in the Tursujuq National Park, and is characterized by the presence of a large lake resulting from a double meteorite impact (1270 km^2; Bégin, 2001). Mean annual temperature and annual precipitation at CWL are respectively -4.0ºC and *ca.* 600 mm for the 2007-2016 period, with the lowest and highest monthly mean temperatures recorded respectively in February (-22.4 ºC) and July (11.8 ºC) (Centre d'études nordiques, 2021). The northernmost location, near the Boniface River research station (BR; 57°45' N, 76°15' W), is located at the northern edge of the forest-tundra bioclimatic zone, approximately 10 km south of the treeline (Ropars et al., 2017). This region is colder (mean annual temperature of -5.0ºC) and drier (annual precipitation of *ca.* 500

mm) than CWL (Centre d'études nordiques, 2021). As in CWL, the coldest and warmest months at BR are February (-24.0 °C) and July (12.5 °C; Centre d'études nordiques, 2021). Both stations are characterized by similar landscape with lichen-shrub tundra dominated by dwarf birch (*Betula glandulosa*) covering *ca*. 70% of the terrestrial environment, mostly on exposed well drained sites or sandy shores. Black spruce (*Picea mariana*) lichen woodlands cover the remaining 30% of the landscape at lower elevation sites (Payette et al., 2008), although black spruce and larch (*Larix laricina* (Du Roi) K. Koch) can also form mixed stands at CWL (Filion & Cournoyer, 1995). In both locations, NDVI have mostly increased during the 1984-2018 period, and moderate greening rate heterogeneity can be seen at the broader scale (Fig. 2.1b-c).

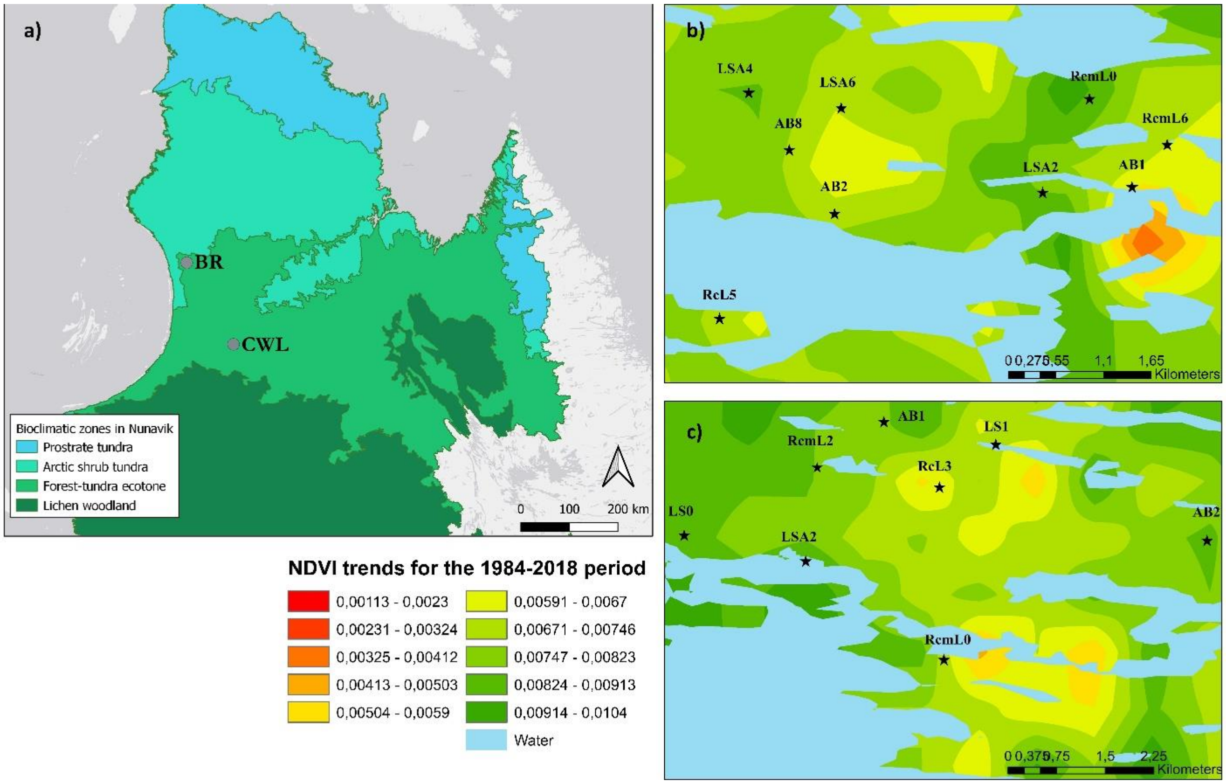

Figure 2.1 a) Location of the two regions sampled in Nunavik (northern Québec, Canada): Clearwater Lake (CWL; 56°20'N) and Boniface River (BR; 57°45'N). (b) NDVI trends (regression slope) in the vegetation polygons found at BR. (c) NDVI trends (regression slope) in the vegetation polygons found at CWL. Black stars represent sampled sites. Bioclimatic zones: Ministère de la forêt, de la faune et des parcs (2021), vegetation polygons: Ministère de la forêt, de la faune et des parcs (2020).

2.4.2 Field sampling

Sampling was conducted in the summer of 2018 (CWL) and 2019 (BR). For both locations, within a radius of 5km, three lichen woodlands, three shrublands, and three lichen heathlands sites were randomly selected prior to fieldwork based on the northern Québec vegetation map produced by the Ministère des Forêts, de la Faune et des Parcs of the government of Québec (MFFP; 2020). Lichen woodlands are defined by Payette and Delwaide (2018) as open-canopy subarctic forests found on dry-mesic, nutrient-poor soils with a tree cover ranging from 10 to 40% and a well-developed lichen cover. Shrublands are characterized by a denser erect shrub cover (>70%) than lichen heathlands (<70%), the latter also harboring a greater lichen cover in open areas. As one of the randomly selected shrublands at CWL was dominated by *Alnus alnobetula* (subsp. *crispa* (Aiton) Raus), it was discarded from subsequent dendrochronological analysis. Description of each research site is available in supplemental material (Table S.2.1).

At each site, the lowest section of the two dominant stems of 20 *B. glandulosa* were harvested, stored in paper bags, and left to dry at room temperature for further analysis. For *P. mariana*, sampling differs between the two stations. At BR, ten *P. mariana* individuals were sampled and 5 cm thick sections were harvested as close as possible to the ground. At CWL, only four *P. mariana* could be harvested since sampling occurred inside the Tursujuq National Park. However, another ten individuals were cored at their base (*ca.* 30 cm above the ground). Both cores and thick sections of *P. mariana* were left to dry at room temperature.

2.4.3 Radial growth data

In the laboratory, *B. glandulosa* stem sections were boiled for 2-3 hours prior to being sliced with a microtome (*ca.* 25 μm thin slice). Slices were then stained with 1% safranin, dried and glued on microscope glass slides with a 66% toluene solution. Once mounted, digital pictures of the thin sections were taken with a binocular-mounted camera (Olympus SZ61 with a SC100 camera; Olympus Imaging America, Center Valley, PA, USA). For every sample, ring widths were measured along two opposite radii with the LignoVision software (v. 1.36, Rinntech, Heidelberg, Germany). Samples of *P. mariana* were finely sanded, and ring widths were measured along one (cores) or two (stem sections) opposite radii using the Dendro 2019 software (v. 3.2.8, Centre d'études Nordiques, Université Laval). To assess the measurement and dating accuracy, crossdating was performed using the COFECHA software (Holmes, 1983).

With short chronologies such as those derived from shrub stems, the use of basal area increment (BAI) yields better correlations between climate and growth than the conventional standardisation method conducted on ring width (Baral et al., 2019; Lu et al., 2016), since detrending short chronologies with a smoothing method tends to eliminate low-frequency growth variations associated with long-term climatic signals (Nicault et al., 2010). Therefore, we converted ring width measurements of both species to basal area increment values in order to eliminate growth trends related to the age and the geometry of the stems (Buchkowski et al., 2020; Linares et al., 2009; Sullivan et al., 2016) by using the following equation:

(1) $BAI = (\pi \text{ x } r^2 \text{ of current year}) - (\pi \text{ x } r^2 \text{ of previous year})$

where "r" stands for the total length of the radius of a sample at a given year. Since most of *P. mariana* and *B. glandulosa* samples were almost perfectly concentrical, we concluded that the simple conversion of RW into BAI could efficiently account for the actual measurement of BAI. Finally, all BAI time series were mean centered and the first order autocorrelation was removed prior to climate-growth analyses with the dplR package of the R software (v.4.0.2; R Core Team, 2020) since autocorrelation in *P. mariana* series was very high (see table S.2.2 for all chronologies' summary statistics). Raw and corrected (autocorrelation removed) BAI chronologies are available in supplemental materials (Figure S.2.1 and S.2.2).

2.4.4 NDVI data

To calculate NDVI values, surface reflectance data were acquired from the Landsat 8 OLI, Landsat 7 ETM+ and Landsat 4-5TM sensors (United States Geological Survey, 2020). From 1984 to 2018, all scenes showing a cloud cover lower than 75% were selected during the period of maximal primary productivity, i.e. between July 1sts. and August 31st. (Ju & Masek, 2016). Based on the surface reflectance data of each scene, NDVI values were calculated in ArcGis to produce a yearly NDVI mosaic according to the following equation:

(2) $NDVI = \frac{NIR-Red}{NIR+Red}$

where "NIR" stands for the near-infrared band reflectance and "Red" stand for the red band reflectance (Myneni et al., 1997). NDVI mosaics were then exported with a resolution of 30 m. To separate NDVI data by plant formation, the ecological mapping of the vegetation of northern

Quebec (MFFP, 2020) was superposed to the NDVI mosaics. Median annual NDVI of each polygon was then calculated using the ArcMap Zonal Statistics tool. Only median annual NDVI of the polygons corresponding to our study sites were used in this study.

2.4.5 Climatic data

Since our study sites are located in remote areas, with the nearest meteorological station at *ca.* 130 km of our sampling locations, we decided to use data from the CRU TS v. 4.05 climate dataset (University of East Anglia Climatic Research Unit et al., 2020). This climate dataset provides high-resolution (0.5° decimal degrees) monthly temperature and precipitation data interpolated from observations of all available weather stations in a given region (Harris et al., 2020).

For both study locations, monthly total precipitation and mean air temperature were downloaded from January 1950 to December 2018. Based on these data, annual total precipitation and annual mean temperature were calculated for each year as well as for summer (July and August), fall (September and October), winter (November to April) and spring (May and June).

2.4.6 Statistical analysis

All analysis were performed using the 4.0.2 version of the R software (R Core Team, 2020).

NDVI trends for the 1984-2018 period

First, we conducted linear regressions between NDVI and years for every site to determine if the increase in NDVI over time was significant ($p < 0.05$). Afterwards, we conducted an ANOVA to test if the greening rate, estimated by the slope of the linear regressions, differs between plant communities (lichen woodland, shrubland and lichen heathland) and locations (CWL and BR), or the interaction between these two factors.

Relationship between climate and radial growth

To identify the climatic drivers of radial growth and to quantify the strength of the climate-growth relationship for both species, we calculated Pearson correlations coefficients (R) between radial growth (BAI) and climate variables for each individual tree/shrub in each plant community (lichen woodland, shrubland and lichen heathland) and location (CWL and BR; see supplemental materials for the list of all the climatic variable tested; Table S.2.3). A greater correlation coefficient means a greater radial growth response to the climatic variables tested.

To test if the strength of the response, i.e. the climate-growth relationship, varies between species, plant communities, or locations (and their respective interactions), we compared the correlation coefficient (R) of the best climatic driver at each site. To compare between *B. glandulosa* and *P. mariana*, we first conducted an ANOVA with data from lichen woodlands only, since it is the sole plant community where both species are found. We also added the effect of the location and the interaction between species and location to the analysis. To determine the impact of the plant community on climate-growth relationship, we conducted a second ANOVA on *B. glandulosa* data only, as it is the only species found in the three plant communities. There also, we added the effect of the location and the interaction between plant community and location to the analysis. When significant, a Tukey HSD test was conducted *a posteriori* to identify significant differences.

Relationship between NDVI and radial growth

To evaluate the strength of the relationship between NDVI and radial growth, we conducted linear regressions between NDVI and mean BAI value for each species at every site. A significant and positive regression slope between NDVI and BAI suggests that increases in radial growth translate into greening at the plant community scale. Since NDVI data were available for the 1984-2018 period, we restricted the analysis to this period. Like for climate-growth relationship, we were interested to determine if the strength of the relationship between NDVI and BAI differs between species, plant communities and locations. Therefore, we used a similar analysis design. The first ANOVA was conducted to compare the strength of the relationship between NDVI and *B. glandulosa* and *P. mariana* BAI in lichen woodlands of both locations (including the species-location interaction) while the second ANOVA was conducted to test whether the strength of the relationship between NDVI and *B. glandulosa* BAI varies across plant community and locations (and their interaction). When the ANOVA was significant, a Tukey HSD test was conducted to identify the significant differences.

2.5 Results

2.5.1 NDVI trends between 1984 and 2018

From 1984 to 2018, NDVI increased significantly at all sites (Fig. 2.2). Neither plant communities nor locations (and their interaction) had an impact on the greening rate (regression slope; Table 2.1). Statistics of all regressions are available in supplemental materials (Table S.2.4).

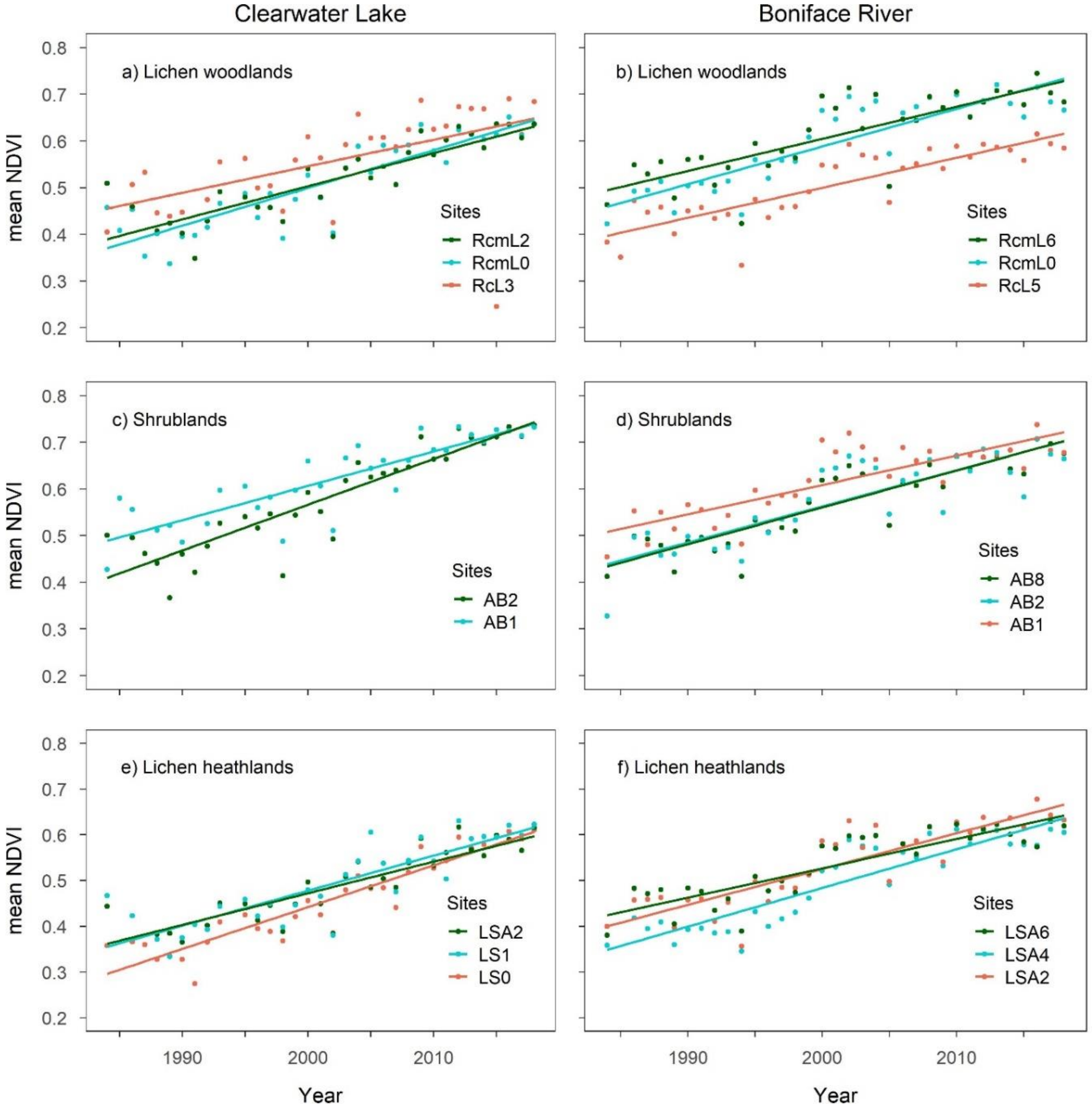

Figure 2.2 Mean NDVI trends for the 1984-2018 period for each plant community (a,b: lichen woodlands; c,d: shrublands; e,f: lichen heathlands) sampled at both locations (a,c,e : Clearwater Lake; b,d,f : Boniface River).

Table 2.1 Effects of sampling location (Clearwater Lake vs Boniface River), plant community (lichen woodlands vs shrublands vs lichen heatlands), and their interaction on the greening rate for the 1984-2018 period in Nunavik, norther Québec.

Effect	F value	*p*-value
Location	0.525	0.484
Community	0.881	0.442
Location: Community	0.589	0.571

2.5.2 Relationship between climate and radial growth

Picea mariana and *B. glandulosa* radial growth are driven by different climatic drivers (Table 2.2). For *B. glandulosa*, regardless of the location or the plant community, the strongest climate-growth relationship is obtained with winter temperature (tWin; November to April), with the sole exception of CWL shrublands, where winter precipitation is better correlated with radial growth. For *P. mariana*, summer temperature (tSum: July and August) represent the best climatic drivers at the southernmost location (CWL) while it is replaced by spring temperature (tSpring; May and June) at the northernmost station (BR).

The strength of the association between climate and radial growth in lichen woodlands differed significantly between species and sampling locations (Table 2.3; Fig. 2.3a-b). First, climate-growth correlation coefficients were higher for *P. mariana* than for *B. glandulosa* at both locations. As for the sampling locations, climate-growth correlation coefficients were higher for both species at BR. While the strength of the association between *B. glandulosa* radial growth and climate did not differ between plant communities, it varied significantly between sampling locations, being higher at BR than at CWL (Fig. 2.3c). Best climatic drivers and climate-growth correlation coefficients for each site are available in supplemental materials (Table S.2.5).

Table 2.2 Climate-growth relationship (Pearson correlation coefficient; R) and p-value for the best climatic drivers of radial growth for *P. mariana* and *B. glandulosa* in the three plant communities sampled at the Clearwater Lake (CWL) and Boniface River (BR) research stations.

Location	**Plant community**	**Species**	**Best climatic driver**	**Pearson correlation coefficient (R)**	***p*-value**
CWL	Lichen woodland	*P. mariana*	tSum	0.18	<0.0001
		B. glandulosa	tWin	0.10	<0.0001
	Shrubland	*B. glandulosa*	pWin	0.15	<0.0001
	Lichen heathland	*B. glandulosa*	tWin	0.11	<0.0001
BR	Lichen woodland	*P. mariana*	tSpring	0.27	<0.0001
		B. glandulosa	tWin	0.15	<0.0001
	Shrubland	*B. glandulosa*	tWin	0.18	<0.0001
	Lichen heathland	*B. glandulosa*	tWin	0.20	<0.0001

Table 2.3 Effect of sampling location, species (in lichen woodlands) and plant communities (for *Betula glandulosa* only) on climate-growth relationship.

Effect	**F value**	***p*-value**
Lichen woodlands		
Species	26.8	**0.001***
Location	15.9	**0.004***
Species: Location	5.43	**0.05***
***B. glandulosa* only**		
Community	0.39	0.687
Location	4.96	**0.05***
Community: Location	0.50	0.621

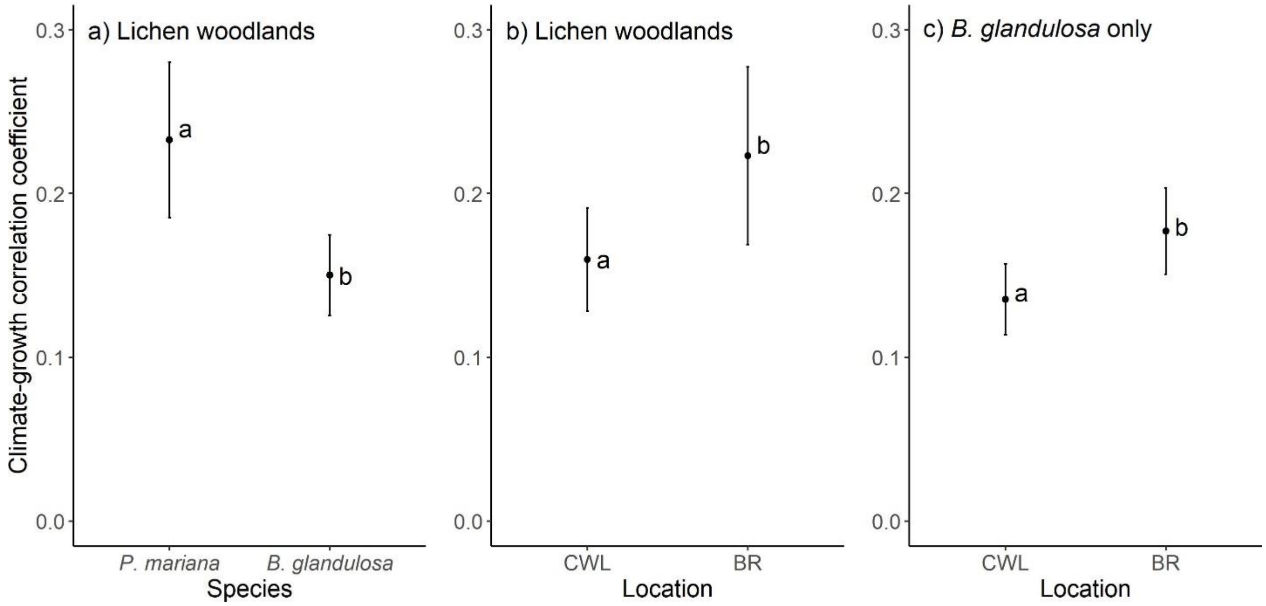

Figure 2.3 (a) Mean climate-growth correlation coefficient of *Picea mariana* and *Betula glandulosa* in lichen woodlands of the two research stations combined. (b) Mean climate-growth correlation coefficient of the two species combined at the lichen woodlands sites of the Clearwater Lake (CWL) and the Boniface River (BR) research stations. (c) Mean climate-growth correlation coefficient of *Betula glandulosa* at the Clearwater Lake (CWL) and Boniface River (BR) research stations. Error bars represent 95% confidence intervals; significant differences (p-value ≥ 0.05) are indicated by a and b indices.

2.5.3 Association between NDVI and radial growth

There is a significant and positive linear relationship between NDVI and radial growth of *P. mariana* and *B. glandulosa* in all sites but one (23 out of 24) as only the regression between NDVI and *B. glandulosa* radial growth in one of the lichen woodlands sampled at the Clearwater Lake station is not significant (Table 2.4). In lichen woodlands, the significant interaction between species and sampling locations reveals that the strength of the relationship between NDVI and radial growth varies from one species to the other according to the sampling location (Table 2.5). Indeed, in lichen woodlands, the strength of this relationship was greater for *P. mariana* at CWL but for *B. glandulosa* at BR (Fig. 2.4). However, we did not detect a significant difference in the strength of this relationship between sampling location or plant communities for *B. glandulosa* (Table 2.5).

Table 2.4 Slope, R^2 and *p*-value of the NDVI-BAI regression for each site at the Clearwater Lake (CWL) and Boniface River (BR) research stations.

Location	Plant community	Species	Site	Slope (NDVI~BAI)	R^2	*p*-value
CWL	Lichen woodland	*P. mariana*	RcL3	0.21	0.22	**0.005***
			RcmL0	0.22	0.67	**< 0.001***
			RcmL2	0.17	0.28	**0.001***
		B. glandulosa	RcL3	0.06	-0.002	0.342
			RcmL0	0.17	0.34	**0.0002***
			RcmL2	0.09	0.32	**0.003***
	Shrubland	*B. glandulosa*	AB1	0.16	0.6	**< 0.001***
			AB2	0.24	0.6	**< 0.001***
	Lichen heathland	*B. glandulosa*	LS0	0.15	0.48	**< 0.001***
			LS1	0.16	0.39	**< 0.001***
			LSA2	0.16	0.45	**< 0.001***
BR	Lichen woodland	*P. mariana*	RcL5	0.09	0.56	**< 0.001***
			RcmL0	0.13	0.63	**< 0.001***
			RcmL6	0.11	0.48	**< 0.001***
		B. glandulosa	RcL5	0.15	0.54	**< 0.001***
			RcmL0	0.22	0.63	**< 0.001***
			RcmL6	0.14	0.51	**< 0.001***
	Shrubland	*B. glandulosa*	AB1	0.14	0.63	**< 0.001***
			AB2	0.15	0.65	**< 0.001***
			AB8	0.25	0.46	**< 0.001***
	Lichen heathland	*B. glandulosa*	LSA2	0.14	0.62	**< 0.001***
			LSA4	0.27	0.64	**< 0.001***
			LSA6	0.13	0.7	**< 0.001***

Table 2.5 Effect of sampling location, species (in woodlands) and plant community (for *Betula glandulosa* only) on the regression slopes between NDVI and radial growth (BAI).

Effect	F value	*p*-value
Lichen woodlands		
Species	0.54	0.485
Location	0.34	0.575
Species: Location	11.3	**0.010***
***B. glandulosa* only**		
Community	1.05	0.383
Location	1.10	0.318
Community: Location	0.77	0.486

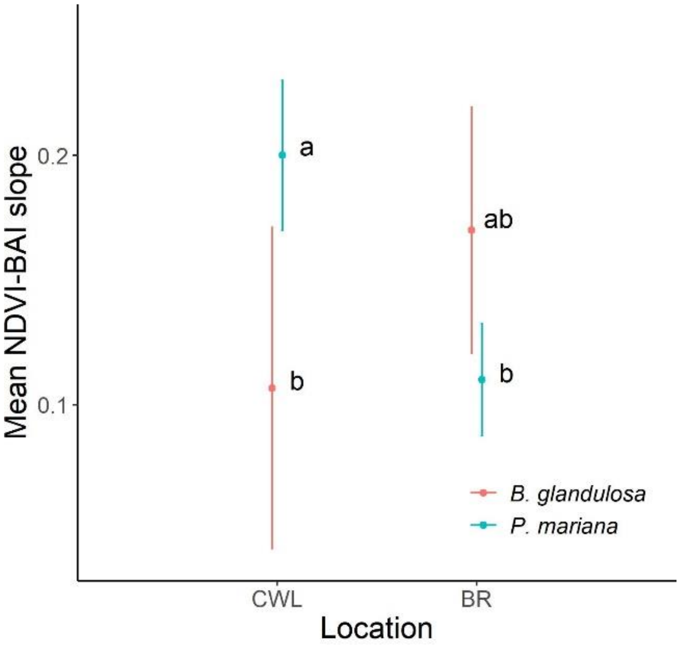

Figure 2.4 Mean NDVI-BAI regression slope for *Picea mariana* and *Betula glandulosa* in the lichen woodlands sites of the Clearwater Lake (CWL) and the Boniface River (BR) research stations. Error bars represent 95% confidence intervals; significant differences (p-value ≥ 0.05) are indicated by a and b indices.

2.6 Discussion

The greening of the Arctic and subarctic is heterogeneous at both the regional and continental scales (Epstein et al., 2012; Ju & Masek, 2016). Although such pattern is usually associated to abiotic factors such as topography and aspect (Berner et al., 2020; Choler et al., 2021; Lemay et al., 2018), we investigated if species-specific response to climate change could also contribute to this heterogeneous pattern. Our analysis revealed that the climatic drivers of radial growth and the climate-growth relationship appears to differ between species. Indeed, while *P. mariana* better responds to growing season temperatures (spring and summer), *B. glandulosa* seems more responsive to winter climatic conditions. Also, overall, *P. mariana* appears to be more responsive to climate than *B. glandulosa*. Lastly, our results suggest that the relationship between NDVI and radial growth is location dependent, with a stronger relationship with *P. mariana* at CWL and with *B. glandulosa* at BR. Overall, our results demonstrate that the species-specific growth response to climate change is site dependent and could therefore contribute to the heterogeneity of the greening.

2.6.1 NDVI trends between 1984 and 2018

The significant NDVI increases in each of our studied sites from 1984 to 2018 corroborates the overall positive NDVI trends observed in Nunavik by McManus et al. (2012) and Ju and Masek (2016) and in other subarctic regions distributed throughout the circumpolar zone (Bunn & Goetz, 2006; Epstein et al., 2012; Walker et al., 2012). In fact, Ju and Masek (2016) identified Nunavik as one of the regions with the highest greening rate in North America for the 1984-2012 period. Such high greening rates have been linked to the rapid expansion of erect shrub species that have been reported throughout Nunavik (Provencher-Nolet et al., 2014; Ropars & Boudreau, 2012; Tremblay et al., 2012), with the notable exception of the Deception Bay region near the Hudson strait where harsh climatic conditions combined with heavy caribou browsing and trampling have been reported to inhibit landscape shrubification (Plante et al., 2014; but see Morrissette-Boileau et al., 2018).

At a finer spatial scale, we did not find any greening rates heterogeneity between neither plant communities nor regions, although such heterogeneity has been observed in other studies that have reported lower NDVI increases in tree-dominated ecosystems (Baird et al., 2012; Beck & Goetz, 2011; Bunn & Goetz, 2006; McManus et al., 2012). The lack of difference between plant communities or sampling locations in our study might result from the spatial scale of our sampling design in which we sampled a relatively low number of plant communities (3 replicates for each of the 3 plant communities) in a *ca.* 75 km^2 circular region at two sampling locations 200 km apart. Other studies have covered much larger regions of North America (Ju & Masek, 2016) and Eurasia (Goetz et al., 2007) or even the whole circumpolar region (Bunn & Goetz, 2006). Therefore, the spatial scale of our study might not have allowed us to capture the greening heterogeneity observed at much larger spatial scale.

2.6.2 Drivers of radial growth

As one of the first studies to compare the climatic drivers of the radial growth of species belonging to different functional groups, our study provides useful insights to better understand the response of subarctic ecosystems to climate change. Our results revealed that the dominant climatic drivers of radial growth differ between *P. mariana* and *B. glandulosa*, suggesting that both species respond differently to changes in growth conditions near the treeline in Nunavik. While

P. mariana is mostly responsive to the temperature found at the onset and during the growing season, *B. glandulosa* radial growth responds the most to winter conditions.

The climatic drivers of radial growth identified in this study corroborate results from previous studies. Firstly, summer temperature was identified as the dominant driver of radial growth of woody species either in Nunavik or in other subarctic regions (Boudreau & Villeneuve-Simard, 2012; Lu et al., 2019; Myers-Smith et al., 2015; Myers-Smith & Hik, 2018; Ropars et al., 2015, 2017). Warmer summer temperature enhances plant productivity, allowing for greater wood cell formation and increases in radial growth (Deslauriers et al., 2010). As for the significance of spring temperature, other studies also found that spring temperature positively affects radial growth of spruce and other tree species (Huang et al., 2010; Wilmking et al., 2004). Indeed, in high latitude regions, spring temperature is critical for the onset of the growing season, because a warmer spring leads to an earlier snowmelt and greater water availability to initiate photosynthetic activity (Bunn et al., 2005; Wilmking et al., 2004). Huang et al. (2010) also found that *P. mariana* individuals located at higher latitudes tend to respond more to spring temperatures than those located in the south, which could explain why *P. mariana* was more responsive to spring temperature at the northernmost station, but more responsive of summer temperature at the southernmost station. These results suggest that radial growth of individuals located in northern regions could be limited by the duration of the growing season, while the radial growth of individuals located southwards might be mostly influenced by the condition experienced during the growing season.

Our analysis also revealed the importance of winter temperature and precipitation as a driver of *B. glandulosa* radial growth. Since shrubs are smaller than trees, they are more vulnerable to damages from windblown ice particles abrasion during cold winters (Bokhorst et al. 2009). Indeed, Panthi et al. (2021) found that shrub growth was primarily affected by winter frost damage at the Himalayan treeline, and that shrub radial growth was best correlated to winter temperature. With warmer winter temperature and more snow precipitation, such frost damage is less frequent, which leads to enhanced shrubs' radial growth (Carrer et al., 2019; Krab et al., 2017). Aside from protecting against frost damage, warmer winter temperature and thicker snow cover enhances winter soil temperature which leads to more microbial activity and nutrient availability as well as a quicker snowmelt and water drainage at the beginning of the growing season (Carrer et al., 2019; Hollesen et al., 2015; Krab et al., 2017; Sturm et al., 2005; Sullivan et al., 2020), all of which are beneficial to shrub growth.

2.6.3 Relationship between climate and radial growth

Just like for the climatic drivers of radial growth, the strength of the climate-growth relationship significantly differs from one species to the other and between sampling locations. Contrary to our predictions, we found stronger climate-growth association for *P. mariana* than for *B. glandulosa*, with both species displaying stronger climate-growth association at BR. While such patterns might appear to be in contradiction with the widespread expansion of erect shrub species and the apparent inertia of tree stands at the treeline, they might arise from the location of the two sampling stations relative to the geographical distribution of both species. First, *Picea mariana* individuals sampled in this study are located towards the (CWL) or at the northern edge (BR) of the species geographical distribution. As a species' growth is more limited by climatic conditions as it is found closer to its northern edge distribution, they often display greater climatic sensitivity (Myers-Smith et al., 2015; Ohse et al., 2012). Our results for *P. mariana* are in accordance with this hypothesis. For *B. glandulosa*, our sampling locations were much further from the northern edge of the species geographic distribution (Blondeau et al., 2010). As a result, *B. glandulosa* displayed weaker climate-growth relationship than *P. mariana*, although we observed an increase in the strength of the relation as we move northwards.

The overall stronger growth-climate relationship at BR is mainly caused by the greater radial growth response of both species at this station. Another potential explanation for the weaker climate-growth relationship of both species at CWL is the influence of the Clearwater Lake, a very large body of water, on the region's climatic conditions. Indeed, Tremblay et Bégin (2000) found that the presence of such body of water generates cooler summer conditions as well as greater wind exposure, both of which results in lower annual wood production.

2.6.4 Association between NDVI and radial growth

Our results showed a positive and significant linear relationship between NDVI and radial growth for both species. Although increases in radial growth, i.e. wood formation, do not directly contribute to the NDVI increase, which results more from an increase of photosynthetic biomass (Kaufmann et al., 2004), radial growth is a good proxy of primary productivity and, therefore, of the overall growth of individuals (Vicente-Serrano et al., 2020). Such positive associations between NDVI and radial growth has been previously reported in other studies (Andreu-Hayles et al., 2011; Ropars et al., 2015; Vicente-Serrano et al., 2020). Based on this relationship, we suggest that one can estimate the contribution of different species to NDVI trends based on the strength of the relationship between radial growth and NDVI, at least in relatively simple subarctic terrestrial ecosystems.

Our results showed that the species' contribution to the greening appears to vary spatially. For *P. mariana*, the lower NDVI-radial growth slopes at BR suggest that a similar increase in radial growth has a lesser positive impact on NDVI values than at CWL. Such result might be explained by multiple factors, including *P. mariana* physiological, populational and structural responses to environmental stresses found at high latitudes. First, the chlorophyll content of *P. mariana* leaves tend to decrease at higher latitudes or altitudes, resulting in yellowish-green leaves (Richardson et al., 2003). It was hypothesized that such decrease in chlorophyll content is part of a protective mechanism to cope with environmental stresses (González-Rodríguez et al., 2019). Therefore, for a given biomass, a yellowish-green foliage should generate lower NDVI values than a healthy foliage. Another explanation resides in the weaker recruitment of *P. mariana* observed at higher latitudes. As the mean thermal sum received at CWL and BR was of 696 and 634 degree-days respectively (2007-2017; Centre d'études nordiques, 2021), it appears that viable seed production is limited at both station since *P. mariana* seed maturation necessitates a thermal sum of *ca.* 800 growing degree-days (Meunier et al., 2007). However, the lower thermal sum received at BR could exacerbate this limitation, resulting in less recruitment in lichen woodlands. In fact, several studies reported that the low production of viable seeds at BR combined with the thick lichen carpet found in lichen woodland result in overall low recruitment (Dufour-Tremblay et al., 2012; Houle & Filion, 2003; Sirois, 2000). Thus, since seedling establishment and stands densification contribute directly to the increases in NDVI (Myers-Smith et al., 2011), the lower reproduction success of *P. mariana* at BR could explain its weaker contribution to NDVI. In stands where *P. mariana* is not even able to adopt an erect growth form, its contribution to NDVI increases can be further diminished. Indeed, contrary to our sampling sites, *P. mariana* individuals found at or north of the treeline often adopt a shrubby growth form (Krummholz; Gamache & Payette, 2005; Meunier et al., 2007; Payette & Delwaide, 1994) for which an increase in radial growth might not transfer as directly to leaf biomass production as for the regular growth form.

Even though our results suggest a lower contribution of *P. mariana* to the NDVI increase in lichen woodland at the treeline, we did not find significant differences in the NDVI trends between locations. Therefore, the lower contribution to NDVI of *P. mariana* appears to be somewhat compensated by *B. glandulosa,* as suggested by the overall higher slope of the NDVI-*B. glandulosa* radial growth relationship at the BR location. It appears likely that *B. glandulosa* take advantage of the lower tree cover in the lichen woodlands at this location to increase its growth and cover, two phenomenon that would increase its contribution to the NDVI trend. Indeed, it was found in a previous study that *B. glandulosa* showed greater volume (i.e. cover x height) and vertical growth rates in the lichen woodlands of BR compared to CWL (Beaupré, 2021).

Finally, caution is needed when interpreting the link between NDVI and radial growth trends, since radial growth does not directly translate to photosynthetic material but is rather a proxy of a species' response to climatic conditions. Also, although *B. glandulosa* and *P. mariana* were the dominant woody species in our study regions, other species also contribute to the increase in NDVI values at our sampling sites. Future studies should incorporate more proxies of species performance when comparing species-specific contribution to NDVI and try to account for the multi-specific composition of research sites when doing so.

2.7 Conclusion

In this study, we demonstrated the differential responses to climate change of the dominant tree (*P. mariana*) and shrub (*B. glandulosa*) species in Nunavik. Even though *P. mariana* radial growth had a stronger association with climate than *B. glandulosa*, *P. mariana* seems to contribute to a lesser extent to the increases of NDVI in high latitude regions, as shown by the weaker association between its radial growth and NDVI at our northernmost sampling location. Because we found similar NDVI trends in both research stations, our results strongly suggest that *B. glandulosa* is compensating for the weaker contribution of *P. mariana* to NDVI at higher latitudes. This study is one of the first to enlighten the differential response of tree and shrub species to global warming and to suggest that such discrepancy between species could at least partially explain the greening heterogeneity of the subarctic regions. Our results represent a new avenue of studies, i.e. comparing the response of different species/functional groups to global warming and their contribution to NDVI, in order to better understand the greening processes and to help predict the upcoming changes in surface reflectance. However, our study was conducted at a rather small spatial scale, on only one species per functional group, and in a region showing very low greening heterogeneity. Therefore, larger scale studies and studies that are focusing on more species per functional groups are needed before extrapolating these results.

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Conclusion

Cette étude avait comme premier objectif d'adapter la méthode dendrochronologique pour optimiser l'utilisation des branches d'espèces arbustives. Avec l'avancée généralisée des peuplements arbustifs vers des régions plus nordiques, un intérêt grandissant pour les analyses dendrochronologiques de la croissance des espèces arbustives s'est développé au cours des dernières décennies. Notre étude visait donc, dans un premier temps, à mieux adapter les méthodes de dendrochronologie, à l'origine développées pour les arbres, aux courtes chronologies construites avec des branches d'espèces arbustives. Des travaux antérieurs ont en effet montré que les cernes de croissances des branches, lorsque analysés avec des méthodes traditionnelles, présentent une plus grande variabilité au niveau du signal climatique ainsi qu'une moins grande sensibilité par rapport aux échantillons prélevés au collet. Nos résultats montrent que la conversion des valeurs de largeur de cernes en valeur de surface, plutôt que la standardisation des données à l'aide de splines cubiques, permet de préserver les tendances climatiques dans les courtes séries dendrochronologiques tout en retirant celles associées à l'âge ou à la taille des échantillons. Cette transformation permet de réduire substantiellement l'écart de sensibilité observé entre les branches et les collets (Ropars et al., 2017).

Notre second objectif était de déterminer, à l'aide de la dendrochronologie, si les espèces arborescentes et arbustives répondent de façon similaire ou différentielle aux changements climatiques. Le cas échéant, une réponse différentielle pourrait expliquer en partie l'hétérogénéité du verdissement des régions subarctiques. Ce verdissement a des répercussions importantes sur la composition du paysage, la mégafaune et même sur le climat planétaire. Notre étude visait donc à améliorer notre compréhension de ce phénomène, en identifiant des facteurs pouvant être à l'origine de l'hétérogénéité du verdissement. Nos résultats sont en accord avec d'autres études qui ont démontré que les espèces ligneuses nordiques répondent positivement aux augmentations des températures durant la saison de croissance mais aussi à celles de l'hiver (Bär et al., 2008; Carrer et al., 2019; Myers-Smith, Elmendorf, et al., 2015). Nos résultats mettent en évidence une différence de sensibilité climatique entre les espèces arborescentes et arbustives, de même qu'une atténuation de la force de la relation entre la croissance radiale de l'épinette noire et les valeurs de NDVI plus on se rapproche de la limite des arbres. Les différences entre ces deux groupes fonctionnels pourraient donc contribuer à l'hétérogénéité du verdissement des régions arctiques et subarctiques.

L'utilisation de la surface des cernes en dendrochronologie des arbustes

La forme de croissance des arbustes présente un défi important pour le domaine de la dendrochronologie, initialement développé pour étudier la croissance radiale des arbres. En effet, l'enjeu principal est de déterminer s'il est convenable d'échantillonner les branches des arbustes, ou s'il est préférable d'aller recueillir leur collet, l'équivalent anatomique du tronc des arbres, qui est comprimé et enfoui dans le sol. Bien que Ropars et al. (2017) aient démontré que la sensibilité climatique est plus importante au niveau du collet des arbustes, la majorité des études présentant des analyses dendrochronologiques d'espèces arbustives utilisent des branches puisqu'elles sont plus faciles à échantillonner sur le terrain (Hallinger et al., 2010; Lu et al., 2016; Uyeda et al., 2016; Weijers, Pape, et al., 2018). Nous pensons que cette différence de sensibilité entre les branches et les collets pourrait être provoquée par l'utilisation de méthodes de standardisation non optimales pour les courtes chronologies construites à partir des branches d'arbustes. Ainsi, notre étude propose une alternative aux méthodes de standardisation conventionnelles, qui permet de réduire l'écart de sensibilité entre les branches et les collets et d'optimiser les analyses dendrochronologiques avec les arbustes. Nous avons démontré que la conversion des valeurs de largeur de cernes en surface de cernes, plutôt que leur standardisation habituelle, permet de réduire les différences entre les branches et les collets.

Dans un premier temps, nous avons démontré que les valeurs de surface de cernes calculées à partir des mesures de largeur de cernes étaient très étroitement corrélées à celles qui avaient été mesurées. Ainsi, une simple conversion des valeurs de largeur de cernes à l'aide d'une équation mathématique permet de représenter adéquatement la surface réelle de cernes de croissance, du moins pour les espèces à croissance concentrique comme le bouleau glanduleux. Cependant, plusieurs espèces arbustives des régions nordiques sont soumises à des conditions de croissance extrêmes qui peuvent engendrer une croissance excentrique ou irrégulière ainsi que la formation de faux-cernes et de cernes discontinus. Pour ces espèces, l'estimation de la surface à partir des largeurs de cernes pourrait être moins fiable. Nous recommandons donc de tester cette relation avant de l'appliquer. Par exemple, l'estimation de la surface pourrait s'effectuer à l'aide de valeurs de largeur de cernes prises sur davantage de rayons, de façon à mieux représenter la croissance radiale sur toute la circonférence des échantillons (Buras & Wilmking, 2014). Également, l'utilisation d'équations considérant les cernes de croissance comme elliptiques plutôt que parfaitement circulaires pourrait être une alternative.

La conversion des valeurs de largeur de cernes en valeur de surface de cernes a bel et bien eu pour effet de standardiser nos séries dendrochronologiques. Cela avait d'ailleurs déjà été démontré pour les chronologies de croissance radiale d'espèces arborescentes (Linares et al., 2009; Nehrbass-Ahles et al., 2014; Sullivan et al., 2016). En effet, la conversion des valeurs de largeur en surface a permis de retirer l'effet de l'âge et de la taille des échantillons, qui est asynchrone à l'échelle d'un site et surtout observable au début des chronologies. Également, cette méthode de standardisation nous a permis de conserver les tendances de croissance associées au climat, qui sont synchrones à l'échelle du site. En effet, suite à la conversion des largeur de cernes en surface, toutes les séries dendrochronologiques montraient une forte augmentation de croissance radiale à partir du début des années 1990, période à laquelle le Nunavik a connu un réchauffement climatique important (Allard et al., 2007; Chouinard et al., 2007).

Cette méthode de standardisation a également permis d'obtenir des résultats similaires pour les branches et les collets d'arbustes. En effet, en utilisant des valeurs de largeur de cernes standardisées de façon conventionnelle, Ropars et al. (2017) avaient démontré que les déterminants climatiques de la croissance radiale des branches variaient entre les sites et étaient différents de ceux des collets. De plus, leur sensibilité climatique était plus faible que celle des collets. Or, dans notre étude, l'utilisation des valeurs de surface nous a permis d'obtenir des déterminants climatiques similaires pour la croissance radiale des branches et des collets dans tous les sites. De plus, cela a permis d'augmenter les valeurs de sensibilité climatique, diminuant ainsi la différence de sensibilité entre les branches et les collets. Nos résultats suggèrent fortement que la différence de sensibilité entre les branches et les collets est le résultat de l'utilisation d'une méthode de standardisation inappropriée pour de courtes chronologies. Ainsi, nous recommandons de prioriser la conversion des valeurs de largeur de cernes en surface de cernes pour les courtes chronologies, puisque cette méthode permet d'obtenir des résultats plus constants et plus robustes, et qu'elle permet de réduire l'écart de sensibilité entre les branches et les collets.

La réactivité des arbres et des arbustes aux changements climatiques

Puisque le verdissement des régions arctiques et subarctiques a des répercussions importantes sur les écosystèmes terrestres et le climat planétaire, de nombreuses études ont tenté d'identifier ses déterminants (Jia et al., 2009; Myers-Smith et al., 2011; Myers-Smith & Hik, 2018). D'autres études se sont plutôt intéressées aux facteurs responsables de son hétérogénéité. Cette dernière a principalement été expliquée par des facteurs liés à la topographie (Berner et al., 2020; Choler et al., 2021; Lemay et al., 2018; Ropars & Boudreau, 2012) ou à l'herbivorie (Blanco et al., 2008; Te Beest et al., 2016). Toutefois, peu d'études ont tenté de déterminer si une différence au niveau de la réactivité aux changements climatiques des différents groupes fonctionnels pourrait expliquer, du moins partiellement, l'hétérogénéité du verdissement. En réalisant cette étude à l'écotone forêt-toundra du Nunavik, l'une des régions ayant connu les plus importantes augmentations de NDVI en Amérique du Nord au cours de la période 1984-2012 (Ju & Masek, 2016), nous avons pu comparer la réponse de l'épinette noire et du bouleau glanduleux aux changements de leurs conditions de croissance, de même que la relation entre leur croissance radiale et les augmentations de NDVI. Notre étude est l'une des premières à démontrer qu'il existe une différence au niveau du lien entre le climat et la croissance radiale de ces espèces. De plus, nos résultats démontrent qu'il existe une relation entre la croissance radiale de ces deux espèces et les valeurs de NDVI, mais que, pour l'épinette noire, la force cette relation tend à s'atténuer avec la latitude.

Contrairement à nos prédictions de départ, nous avons observé des différences au niveau des déterminants climatiques de la croissance radiale de l'épinette noire et du bouleau glanduleux. Cela peut possiblement être expliqué par la forme de croissance différentielle des espèces. En effet, le bouleau glanduleux étant situé davantage au niveau du sol, ce dernier est plus vulnérable aux dommages associés aux particules de glaces déplacées par le vent en hiver (Bokhorst et al., 2009). Sa croissance serait donc favorisée par des conditions hivernales plus clémentes. Quant à l'épinette noire, cette dernière est principalement affectée par les températures au début ou pendant la saison de croissance, températures qui affectent la productivité et le nombre de cellules formées (Deslauriers et al., 2010). De plus, nos résultats démontrent que la réponse au niveau de la croissance radiale est plus importante pour l'épinette noire que pour le bouleau glanduleux. Ce résultat peut s'expliquer par le fait que nos stations d'échantillonnage étaient situées près de la limite nordique des arbres, mais loin de celle des arbustes. Tel que démontré par Ohse et al. (2012), la croissance des espèces se trouvant plus près de leur limite de répartition est davantage limitée par les conditions climatiques, et ces espèces sont donc plus réactives à leur amélioration. Cela peut aussi expliquer pourquoi, pour les deux espèces combinées, nous avons observé une plus grande sensibilité climatique à la station la plus au nord, soit celle de la rivière Boniface.

Contrairement à ce qui a préalablement été observé dans de nombreuses études (Beck & Goetz, 2011; A. G. Bunn & Goetz, 2006; McManus et al., 2012) nous n'avons pas observé de différence au niveau des tendances NDVI entre les formations végétales et les stations. L'absence d'hétérogénéité dans nos résultats pourrait être due au fait que notre étude était située dans l'une des régions ayant connu les plus importantes augmentations de NDVI en Amérique du Nord entre 1984 et 2012 (Ju & Masek, 2016) et qu'elle ait été réalisée à petite échelle. Les études ayant précédemment démontré l'hétérogénéité du verdissement couvraient en effet une échelle spatiale beaucoup plus large. Par exemple, l'étude de Ju & Masek (2016) couvrait l'ensemble des régions nordiques de l'Amérique du Nord (Ju & Masek, 2016), et celle de Bunn et Goetz (2006) couvrait l'ensemble de la zone circumpolaire. Nous avons aussi observé un lien positif et significatif entre la croissance radiale des deux espèces et les tendances de NDVI. Bien qu'une augmentation de croissance radiale n'entraîne pas directement une augmentation des valeurs de NDVI, un lien significatif entre ces deux variables a été observé dans d'autres études (Andreu-Hayles et al., 2011; Ropars et al., 2015; Vicente-Serrano et al., 2020), suggérant que les augmentations de croissance radiale peuvent être utilisées comme un proxy de la contribution de différentes espèces au verdissement des régions nordiques. Dans notre station la plus au nord, le lien entre la croissance radiale de l'épinette noire et les valeurs de NDVI s'est atténué malgré une augmentation de sensibilité climatique, suggérant que sa contribution aux augmentations de NDVI serait plus faible dans cette région. Cela pourrait s'expliquer par le fait que les individus d'épinettes noires ont tendances à diminuer le contenu en chlorophylle de leurs aiguilles dans des conditions environnementales stressantes (González-Rodríguez et al., 2019), ce qui leur confère une couleur plus jaunâtre (Richardson et al., 2003). La station de recherche de la rivière Boniface étant située plus au nord que celle du lac à l'Eau Claire, les conditions environnementales y sont plus stressantes, ce qui a possiblement entraîné une diminution du contenu en chlorophylle des aiguilles d'épinettes noires et donc une diminution de leur contribution au NDVI. La formation de graines viables étant dépendante d'une certaine somme de degrés-jours de croissance chez l'épinette noire (Meunier et al., 2007), la plus faible somme de degrés-jours à la rivière Boniface, combinée à l'épais tapis de lichens dans les pessières, pourrait entraîner un plus faible recrutement à cette station de recherche. Puisque le recrutement et la densification des peuplements contribuent directement à l'augmentation du NDVI (Myers-Smith et al., 2011), ce plus faible succès reproducteur pourrait expliquer la diminution de la contribution de l'épinette noire aux augmentations de NDVI à la station de la rivière Boniface. Le fait que nous ayons observé des tendances de NDVI semblables entre les deux stations suggère une certaine compensation par le bouleau glanduleux dans la station la plus au nord. Cette hypothèse de compensation est appuyée par nos résultats démontrant une plus grande sensibilité climatique du bouleau glanduleux dans cette région, de même que par les résultats de Beaupré et al. (2021) qui démontrent une plus grande croissance en hauteur et un plus grand volume arbustif de bouleau glanduleux dans les pessières de la station de la rivière Boniface en comparaison à celles du lac à l'Eau Claire.

Contributions du projet

Le premier volet de mon projet de recherche représente une contribution significative au domaine de la dendrochronologie des arbustes. En effet, nous proposons une méthode de standardisation pour les courtes séries dendrochronologiques construites à partir de branches d'arbustes qui permet de réduire les différences entre les branches et les collets. Conséquemment, en utilisant cette méthode de standardisation, il n'est plus nécessaire d'extraire le collet des individus, ce qui représente un gain de temps et d'énergie considérable lors des campagnes d'échantillonnage très coûteuses en régions éloignées. De plus, cela évite d'avoir recours à l'extraction complète des individus, qui est très destructrice. Les résultats obtenus grâce à cette méthode de standardisation sont plus constants et robustes, ce qui permet donc de connaître plus précisément les facteurs à l'origine du verdissement de régions arctiques et subarctiques. En ce sens, cela permettra aussi de prédire plus fidèlement la direction du verdissement et ses impacts dans le futur. L'optimisation des méthodes en dendrochronologie des arbustes qui découle de ce projet de recherche sera bénéfique pour toute la communauté de chercheurs qui étudient la réponse des espèces arbustives aux changements climatiques, autant dans les régions nordiques qu'ailleurs. Nous avons d'ailleurs pu mettre en application cette méthode pour répondre à l'objectif du second chapitre de ce projet de recherche. L'amélioration des méthodes en dendrochronologie des arbustes sera également bénéfique pour le domaine de la reconstitution climatique. En effet, les arbustes figurent parmi les seules espèces ligneuses au nord de la limite nordique des arbres (Buras & Wilmking, 2014; Lu et al., 2016). Il s'agit donc d'archives écologiques à résolution annuelle d'une très grande valeur pour le domaine de la reconstitution climatique.

Les résultats du deuxième volet de ce projet de recherche représentent une contribution importante au niveau de notre compréhension du phénomène de verdissement des régions circumpolaires. En effet, à notre connaissance, il s'agit de la première étude qui fait un lien entre l'hétérogénéité du verdissement et les différences de sensibilité climatique entre les espèces arborescentes et arbustives et qui compare aussi leurs contributions respectives aux augmentations de NDVI. Nos résultats démontrent que l'hétérogénéité du verdissement n'est pas attribuable qu'à des facteurs externes tels que la topographie ou l'herbivorie, mais qu'elle peut également découler de différences intrinsèques entre les groupes fonctionnels. Nos résultats suggèrent aussi que toutes les espèces n'auraient pas la même contribution aux augmentations de NDVI, et que la contribution d'une même espèce pourrait varier spatialement. Ces connaissances sont essentielles pour tenter de prévoir les changements à venir au niveau de la dynamique et de la composition des écosystèmes terrestres en réponse aux changements climatiques. De plus, une meilleure compréhension du phénomène de verdissement est essentielle afin de prévoir les conséquences de ce dernier à l'échelle locale et planétaire.

Perspectives de recherche

Bien que nous ayons démontré le fort potentiel de l'utilisation des surfaces de cernes en dendrochronologie des arbustes, nous ne l'avons fait que pour une seule espèce arbustive, le bouleau glanduleux, et dans une seule région, le Nunavik. Il serait donc nécessaire de valider cette méthode pour d'autres espèces arbustives et dans d'autres régions circumpolaires, afin de démontrer son efficacité à plus grande échelle. Également, nous avons démontré que, pour le bouleau glanduleux, une simple estimation des valeurs de surface de cernes à partir des données de largeur suffisait à représenter adéquatement la surface réelle des cernes. Toutefois, le bouleau glanduleux est une espèce dont la croissance radiale est généralement concentrique. Il serait donc nécessaire de développer une méthode qui permettrait d'estimer la surface des cernes de croissance à partir de la largeur pour les individus ou les espèces qui adoptent des formes de croissance plus excentriques ou qui ont tendance à former des faux cernes ou des cernes irréguliers ou discontinus. Finalement, cette contribution au domaine de la dendrochronologie ouvre la porte à la réanalyse de nombreuses études déjà publiées. En effet, une réanalyse des chronologies d'arbustes, cette fois en utilisant des valeurs de surface de cernes, pourrait permettre d'expliquer les incohérences parfois observées entre différentes études.

Pour ce qui est du deuxième volet de ce projet de recherche, ce dernier nécessite la réalisation d'études semblables, mais à plus grande échelle. En effet, cette étude était réalisée à petite échelle, soit dans deux stations d'échantillonnage, et elle comparait la sensibilité climatique et la contribution au NDVI d'une seule espèce par groupe fonctionnel, soit une espèce arborescente et une espèce arbustive. Il serait donc nécessaire de réaliser cette étude à plus grande échelle, et sur davantage d'espèces et davantage de groupes fonctionnels, avant de pouvoir généraliser nos interprétations à l'échelle des régions circumpolaires. Également, notre étude n'évaluait que la croissance radiale des individus. Bien que nous ayons démontré un lien significatif entre la croissance radiale et le NDVI, ces derniers ne sont pas directement liés, et des études portant sur le recrutement des espèces permettraient d'encore mieux quantifier leurs contributions aux augmentations de NDVI. Ce projet ouvre également sur de nouvelles perspectives de recherche. En effet, nous avons démontré que le lien entre les augmentations de croissance radiale de l'épinette noire et les augmentations de NDVI tendait à s'atténuer avec la latitude, mais nous n'avons pas observé cela pour le bouleau glanduleux. Il serait donc intéressant d'évaluer la relation entre la croissance radiale du bouleau glanduleux et les valeurs de NDVI à de plus hautes latitudes, pour déterminer si, au même titre que l'épinette noire, cette relation aura tendance à s'atténuer avec la latitude. Dans le même ordre d'idées, il serait intéressant d'effectuer ce type d'étude avec davantage d'espèces, autant arbustives qu'arborescentes, afin d'identifier les espèces pour lesquelles la contribution aux augmentations de NDVI est plus constante.

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Annexe 1: Figures supplémentaires

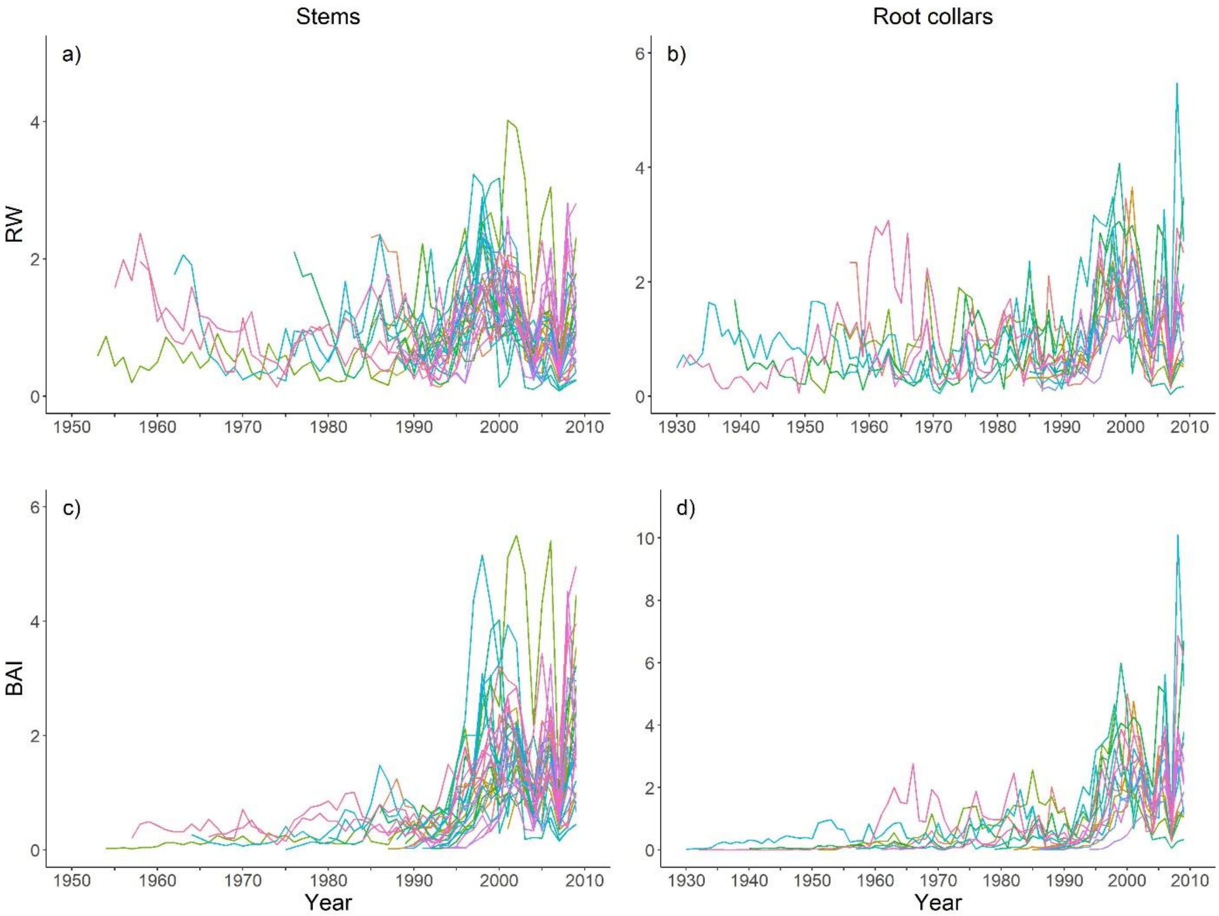

Figure S.1.1 Individual RW and BAI growth chronologies of stems and root collars of *B. glandulosa* individuals growing on terraces at the Boniface River research station.

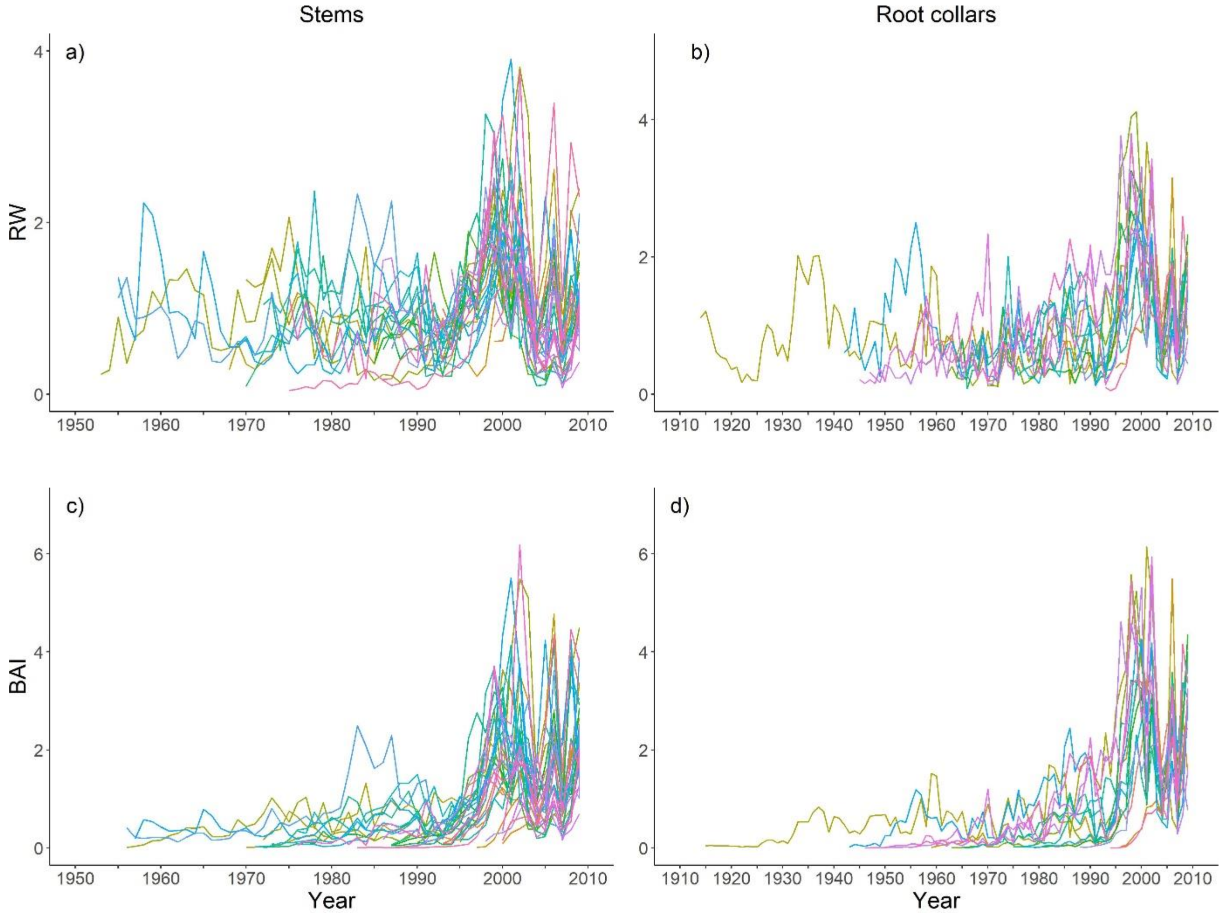

Figure S.1.2 Individual RW and BAI growth chronologies of stems and root collars of *B. glandulosa* individuals growing on hilltops at the Boniface River research station.

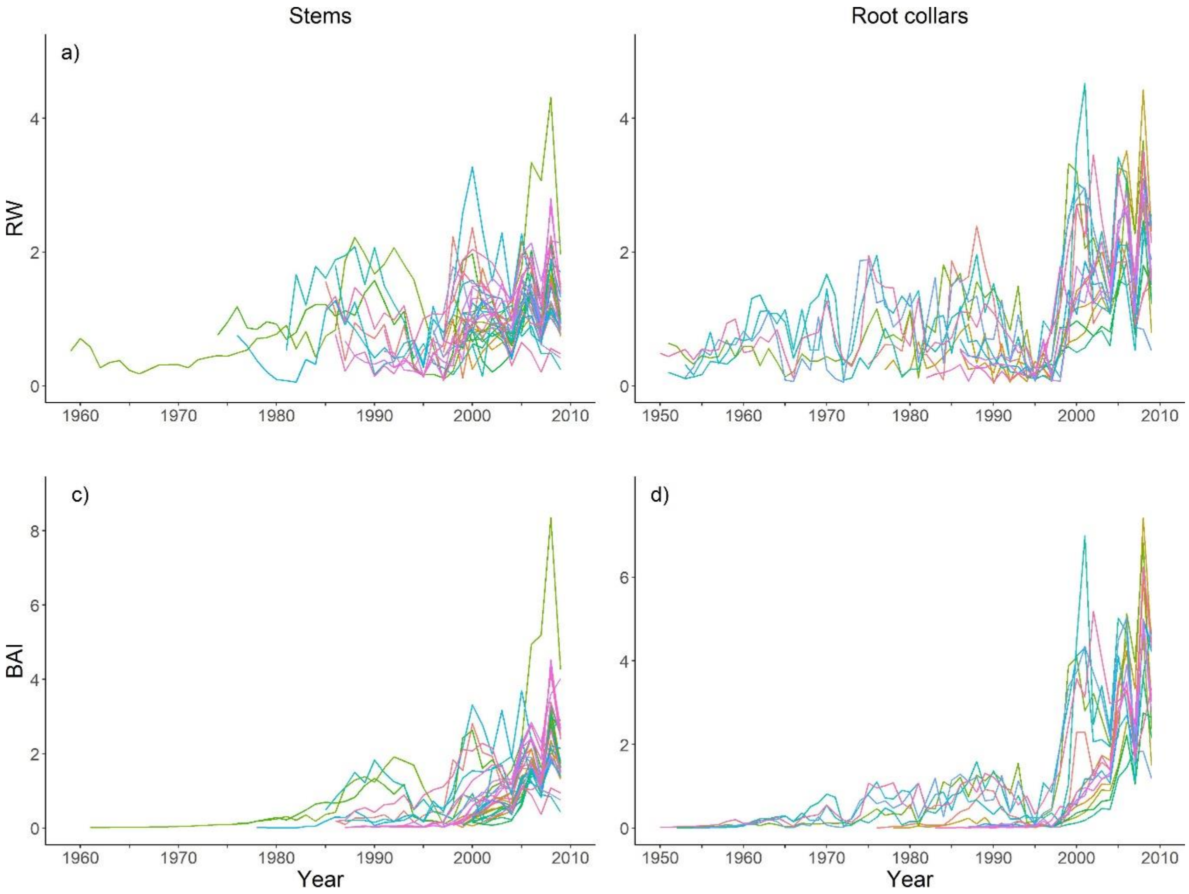

Figure S.1.3 Individual RW and BAI growth chronologies of stems and root collars of *B. glandulosa* individuals growing in snowbeds at the Boniface River research station.

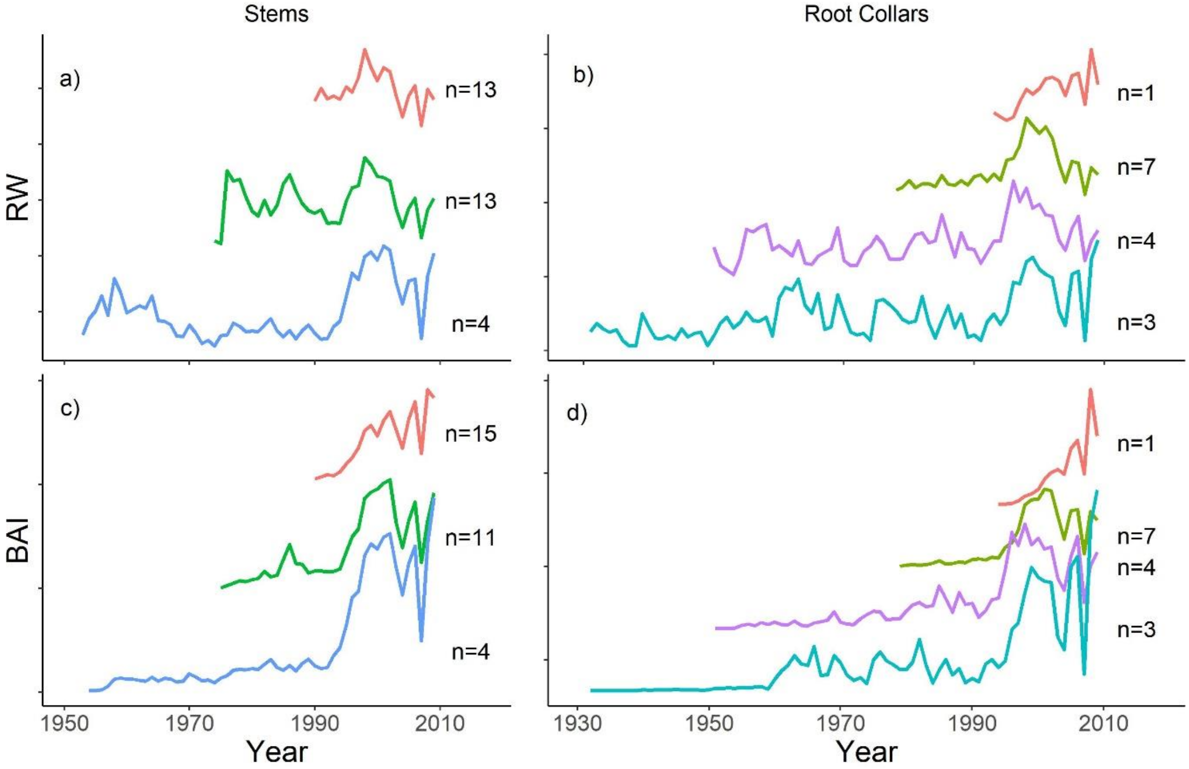

Figure S.1.4 Mean chronologies (RW and BAI) of stems and root collars growing on terraces at the Boniface River research station, separated into 20-year age groups (different colours).

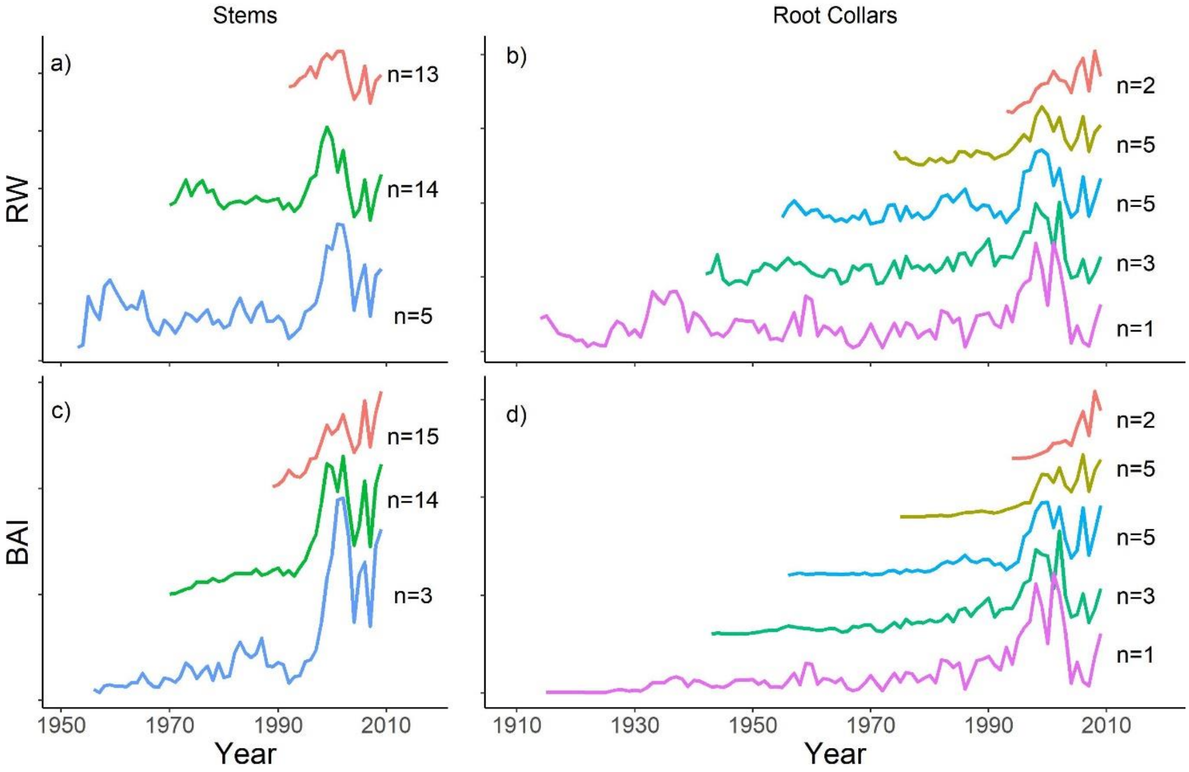

Figure S.1.5 Mean chronologies (RW and BAI) of stems and root collars growing on hilltops at the Boniface River station, separated into 20-year age groups (different colours).

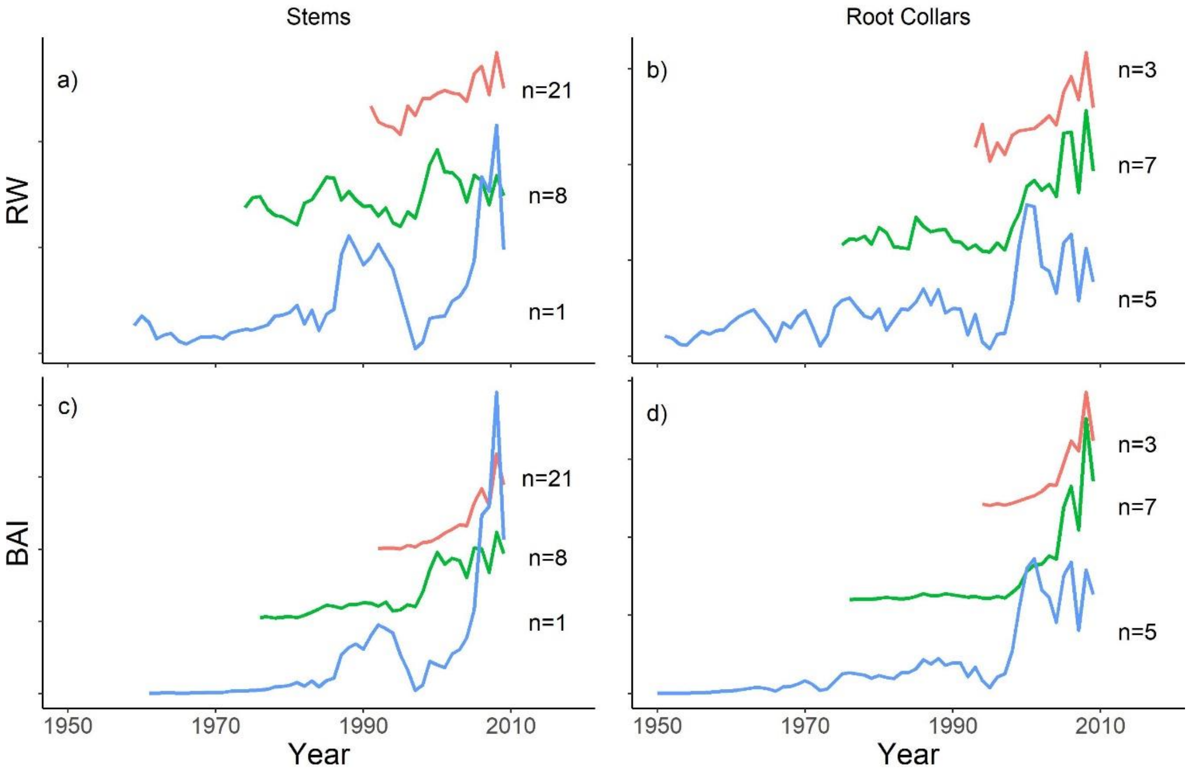

Figure S.1.6 Mean chronologies (RW and BAI) of stems and root collars growing in snowbeds at the Boniface River research station, separated into 20-year age groups (different colours).

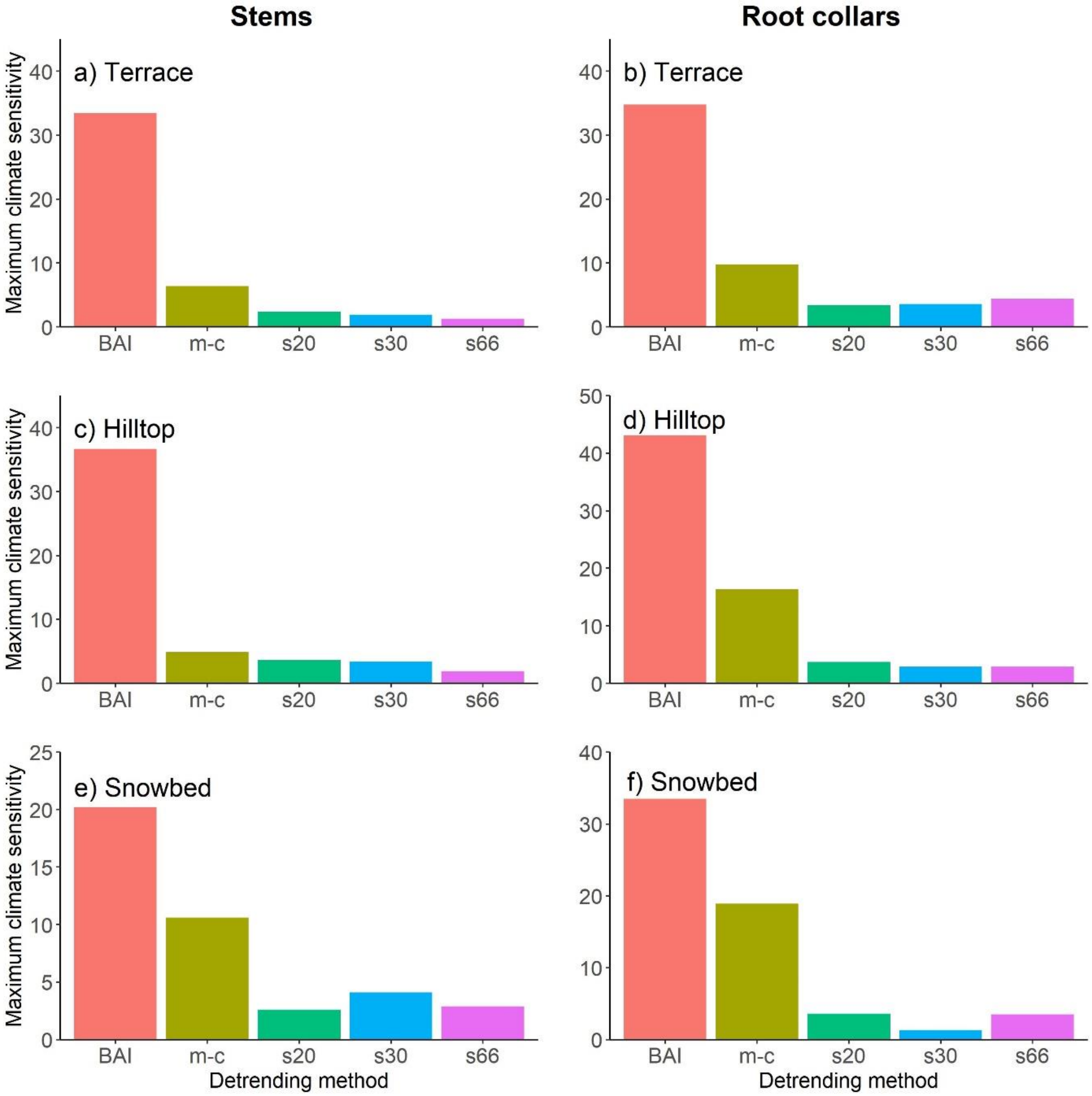

Figure S.1.7 Maximum climate sensitivity (ΔAIC_{null}) of stems and root collars of each environment type obtained with various detrending methods of RW measurements (BAI = conversion into basal area increments, m-c = mean-centering, s20 = 20-year spline, s30 = 30-year spline, s66 = spline with a wavelength of 66% the length of the dendrochronological series).

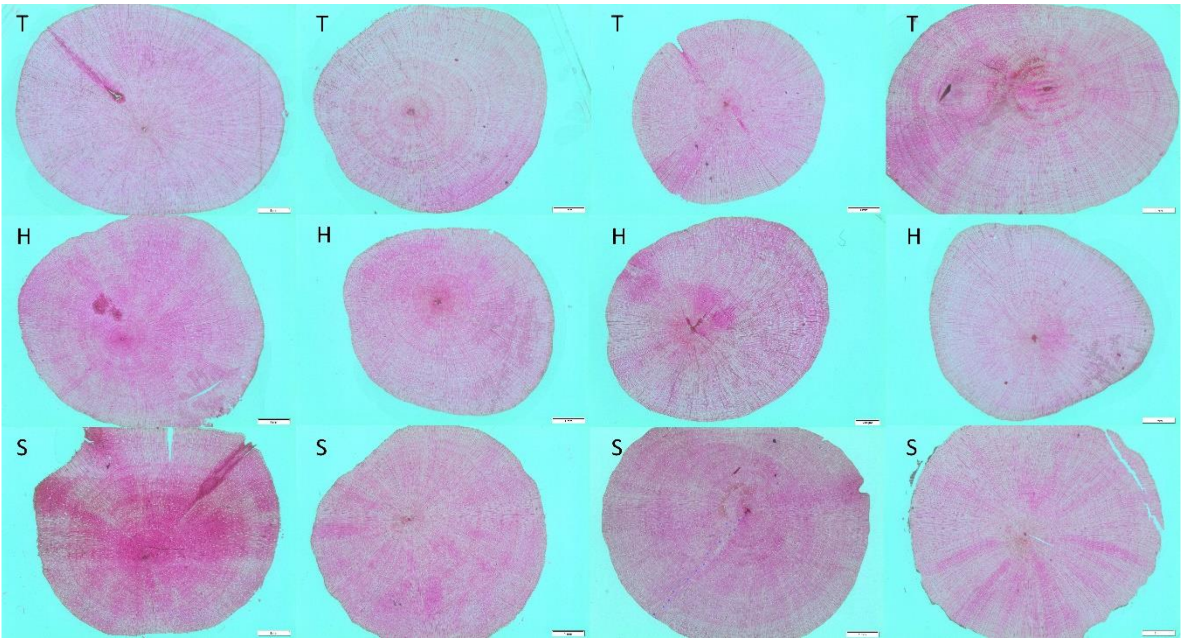

Figure S.1.8 Example of *Betula glandulosa* cross-sections used in this study. Letters represent the environment type in which the samples were collected (T = terrace, H = hilltop, S = Snowbed).

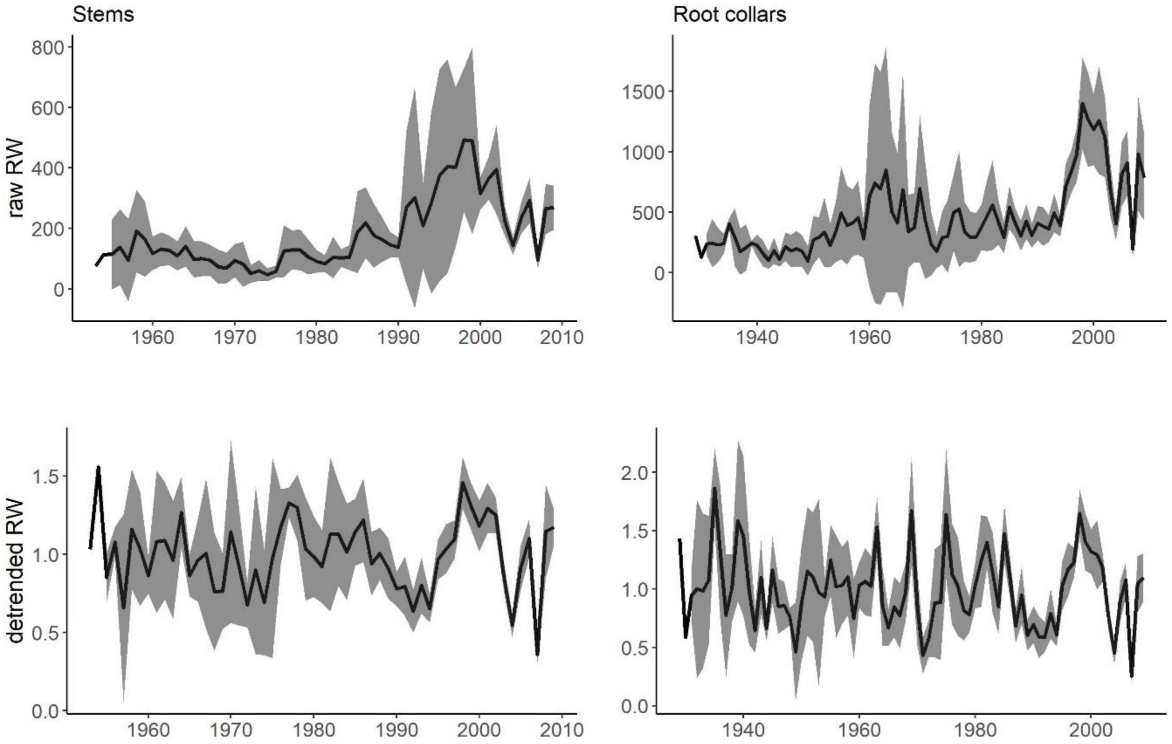

Figure S.1.9 Mean raw and detrended (30-year spline) RW series for stems and root collars collected on terraces at the Boniface River research station. Shaded areas represent 95% confidence intervals.

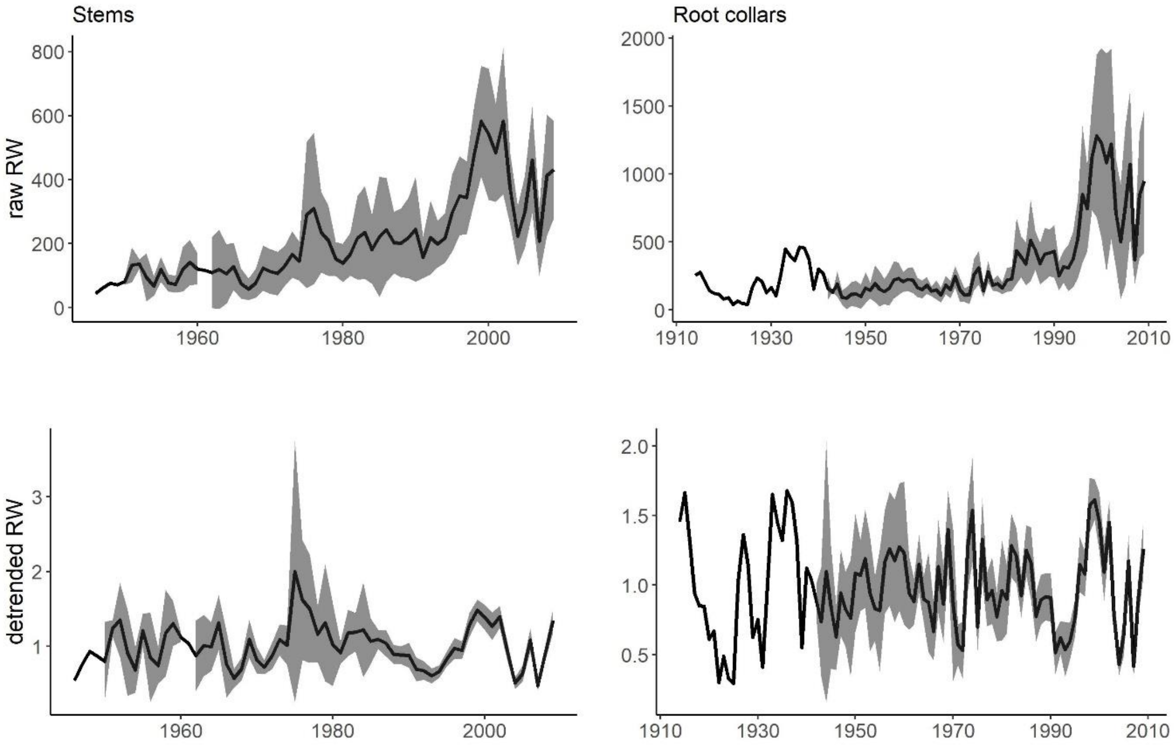

Figure S.1.10 Mean raw and detrended (30-year spline) RW series for stems and root collars collected on hilltops at the Boniface River research station. Shaded areas represent 95% confidence intervals.

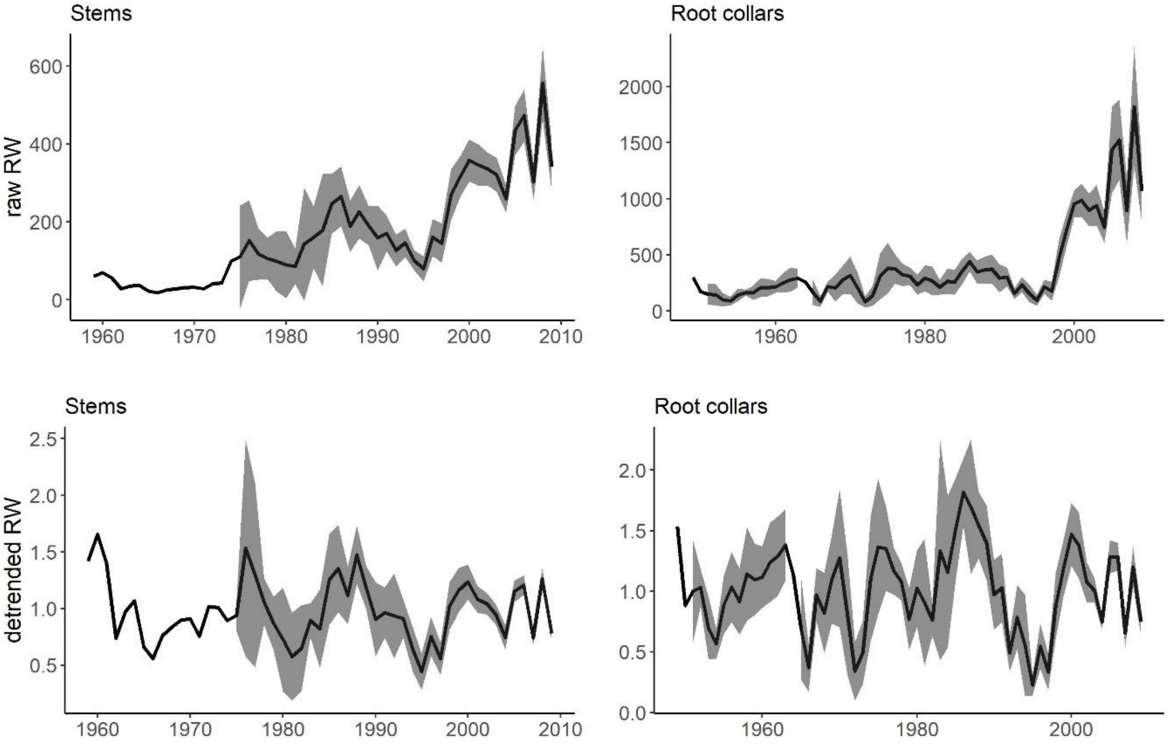

Figure S.1.11 Mean raw and detrended (30-year spline) RW series for stems and root collars collected in snowbeds of the Boniface River research station. Shaded areas represent 95% confidence intervals.

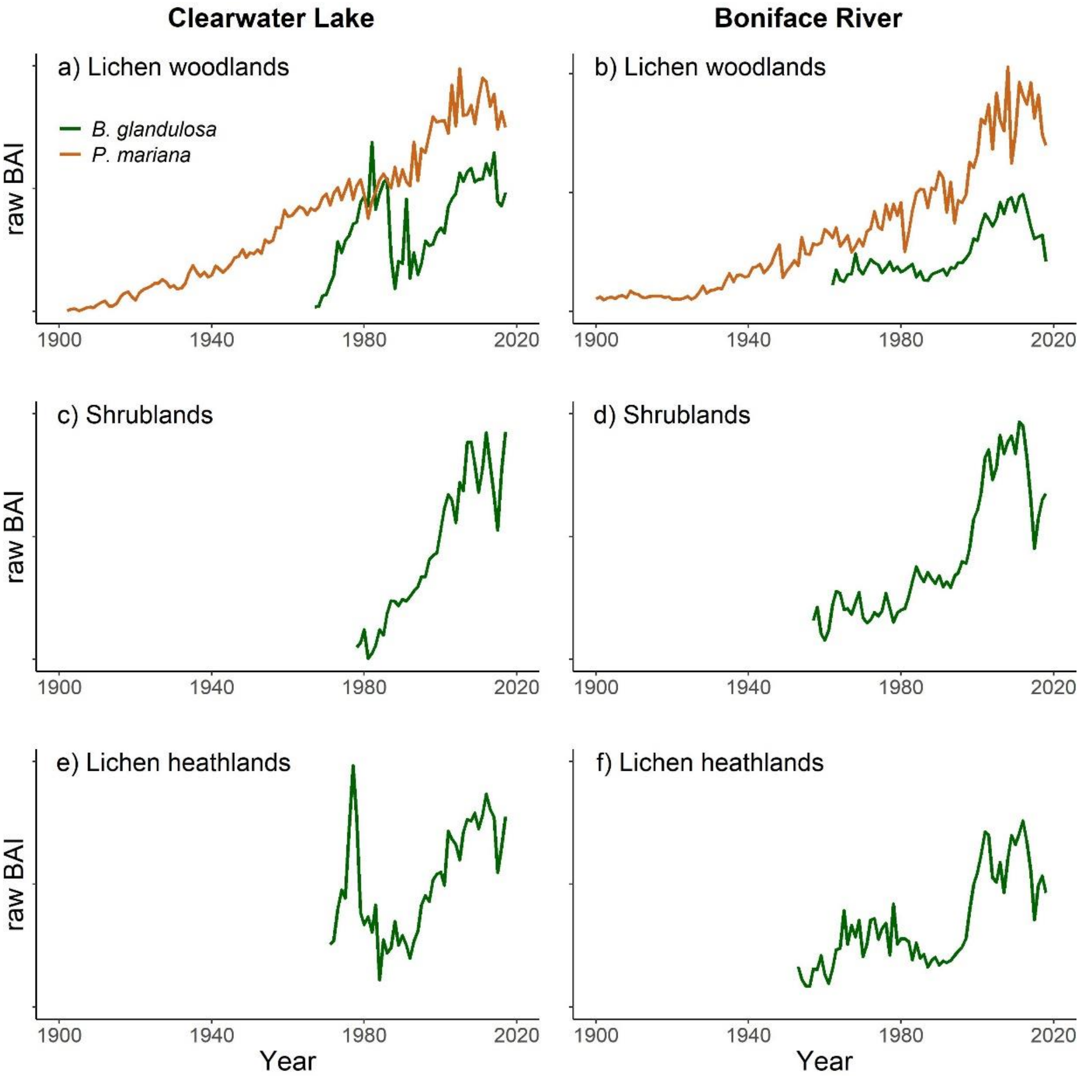

Figure S.2.1 Mean raw BAI chronologies of *B. glandulosa* (green) and *P. mariana* (orange) in each plant community at the Clearwater Lake (a, c, e) and Boniface River (b, d, f).

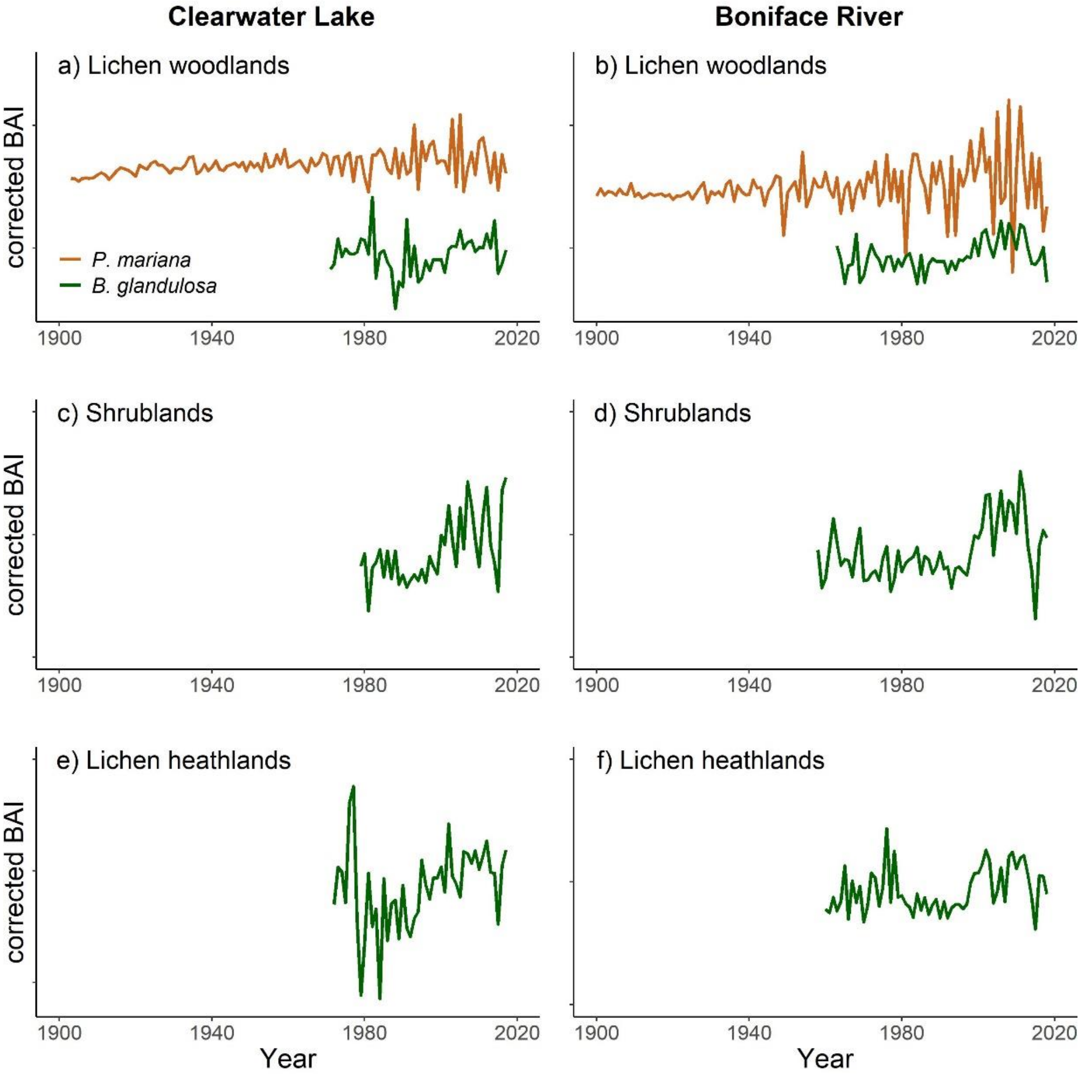

Figure S.2.2 Mean BAI chronologies with first order autocorrelation removed for *B. glandulosa* (green) and *P. mariana* (orange) in each plant community at the Clearwater Lake (a, c, e) and Boniface River (b, d, f).

Annexe 2: Tableaux supplémentaires

Table S.1.1 Climate sensitivity values (ΔAIC_{null}) and model fit statistics (R^2) for the best climatic variables explaining RW index (detrended by a 20-year spline) and calculated BAI of *Betula glandulosa* root collars and stems over the 1947-2009 period.

Environment	**Data type**	**Sample type**	**Best climatic model**	**Climatic sensitivity (ΔAIC_{null})**	**Marg. R^2**	**Cond. R^2**
Terrace	RW index	Root collars	T Feb	3.4	0.04	0.27
		Stems	P Mar	2.4	0.04	0.16
	BAI	Root collars	T Jul + P Mar	34.8	0.29	0.39
		Stems	T Jul + P Mar	33.5	0.39	0.46
Hilltop	RW index	Root collars	pT Sep	3.7	0.04	0.25
		Stems	p Mar	3.6	0.05	0.21
	BAI	Root collars	T Jul + P Mar	43.1	0.43	0.56
		Stems	T Jul + P Mar	36.7	0.40	0.48
Snowbed	RW index	Root collars	P Jul	3.6	0.04	0.30
		Stems	T May	2.6	0.08	0.21
	BAI	Root collars	T Jul + P Mar	33.5	0.52	0.75
		Stems	T Jul + P Mar	20.2	0.39	0.52

Table S.1.2 Climate sensitivity values (ΔAIC_{null}) and model fit statistics (R^2) for the best climatic variables explaining RW index (detrended by a 30-year spline) and calculated BAI of *Betula glandulosa* root collars and stems over the 1947-2009 period.

Environment	Data type	Sample type	Best climatic model	Climatic sensitivity (ΔAIC_{null})	Marg. R^2	Cond. R^2
Terrace	RW index	Root collars	T Feb	3.6	0.04	0.27
		Stems	T May	1.9	0.03	0.12
	BAI	Root collars	T Jul + P Mar	34.8	0.29	0.39
		Stems	T Jul + P Mar	33.5	0.39	0.46
Hilltop	RW index	Root collars	pT Sep	2.9	0.03	0.25
		Stems	pP Sep	3.4	0.02	0.10
	BAI	Root collars	T Jul + P Mar	43.1	0.43	0.56
		Stems	T Jul + P Mar	36.7	0.40	0.48
Snowbed	RW index	Root collars	P Jul	1.3	0.02	0.25
		Stems	T Apr	4.1	0.07	0.24
	BAI	Root collars	T Jul + P Mar	33.5	0.52	0.75
		Stems	T Jul + P Mar	20.2	0.39	0.52

Table S.1.3 Climate sensitivity values (ΔAIC_{null}) and model fit statistics (R^2) for the best climatic variables explaining RW index (detrended by a spline of wavelength = 66% of series length) and calculated BAI of *Betula glandulosa* root collars and stems over the 1947-2009 period.

Environment	**Data type**	**Sample type**	**Best climatic model**	**Climatic sensitivity (ΔAIC_{null})**	**Marg. R^2**	**Cond. R^2**
Terrace	RW index	Root collars	T Feb	4.4	0.04	0.26
		Stems	T Apr	1.3	0.02	0.13
	BAI	Root collars	T Jul + P Mar	34.8	0.29	0.39
		Stems	T Jul + P Mar	33.5	0.39	0.46
Hilltop	RW index	Root collars	pT Sep	2.9	0.03	0.23
		Stems	T Apr	1.9	0.02	0.12
	BAI	Root collars	T Jul + P Mar	43.1	0.43	0.56
		Stems	T Jul + P Mar	36.7	0.40	0.48
Snowbed	RW index	Root collars	P Jul	3.5	0.04	0.25
		Stems	T May	2.9	0.08	0.26
	BAI	Root collars	T Jul + P Mar	33.5	0.52	0.75
		Stems	T Jul + P Mar	20.2	0.39	0.52

Table S.1.4 Number of samples (n), Expressed Population Signal (EPS), mean correlation coefficients (rbar) and first order autocorrelation (AR1) of the BAI and RWI (mean-centered) chronologies of stems and root collars in the three environment types. EPS values were computed in the Dendro 2019 software, rbar and AR1 were computed with the dplR package in R.

Environment	Sample type	Measurement type	n	EPS	rbar	AR1
Terrace	Root collars	BAI	15	0.95	0.57	0.67
		RWI (mean-centered)	15	0.92	0.32	0.58
	Stems	BAI	30	0.96	0.74	0.49
		RWI (mean-centered)	30	0.95	0.33	0.49
Hilltop	Root collars	BAI	16	0.96	0.73	0.70
		RWI (mean-centered)	16	0.93	0.48	0.60
	Stems	BAI	32	0.96	0.62	0.54
		RWI (mean-centered)	32	0.95	0.27	0.45
Snowbed	Root collars	BAI	15	0.98	0.80	0.72
		RWI (mean-centered)	15	0.96	0.57	0.63
	Stems	BAI	30	0.98	0.66	0.61
		RWI (mean-centered)	30	0.94	0.20	0.32

Table S.2.1 Localisation and vegetation composition of every studied site as well as the size of the vegetation polygon from which they were selected at the Clearwater Lake (CWL) and Boniface River (BR).

Location	Plant community	Site	Coordinates (°N; °W)	Plant cover (%)	*B. glandulosa* cover (%)	Relative *B. glandulosa* cover (%)	*P. mariana* cover (%)	Relative *P. mariana* cover (%)	Polygon size (m^2)
CWL	Lichen woodland	RcL3	(56.36; -74.42)	72.917	7.440	10.204	33.333	45.714	1000850
		RcmL0	(56.33; -74.41)	89.881	19.345	21.523	14.286	15.894	160135
		RcmL2	(56,36; -74,43)	73.810	18.155	24.597	19.940	27.016	206556
	Shrubland	AB1	(56.37; -74.42)	99.405	22.917	23.054	0.298	0.299	188301
		AB2	(56.35; -74.38)	99.107	35.417	35.736	0.000	0.000	43814
	Lichen heathland	LS0	(56.35; -74.45)	57.143	5.655	9.896	3.274	5.729	206556
		LS1	(56,37; -74,41)	31.845	25.595	80.374	0.298	0.935	160099
		LSA2	(56,35; -74,43)	66.369	46.131	69.507	3.274	4.933	1000850
BR	Lichen woodland	RcL5	(57,74; -76,21)	92.560	8.631	9.325	27.083	29.260	214089
		RcmL0	(57,76; -76,17)	76.786	25.000	32.558	17.560	22.868	69627
		RcmL6	(57,75; -76,17)	95.238	7.143	7.500	15.774	16.562	69627
	Shrubland	AB1	(57,75; -76,17)	97.321	26.190	26.911	0.000	0.000	1046568
		AB2	(57,75; -76,20)	96.429	82.440	85.494	0.000	0.000	1729257
		AB8	(57,75; -76,20)	97.619	25.595	26.220	2.381	2.439	1046568
	Lichen heathland	LSA2	(57,75; -76,18)	39.583	38.393	96.992	0.000	0.000	1729257
		LSA4	(57,76; -76,21)	66.369	55.655	83.857	0.000	0.000	69627
		LSA6	(57,76; -76,20)	66.369	65.774	99.103	0.000	0.000	1046568

Table S.2.2 Number of samples (n), Expressed Population Signal (EPS), mean correlation coefficients (rbar) and first order autocorrelation (AR1) of the raw BAI chronologies of stems and root collars in each site.

Location	Plant community	Species	Site	n	EPS	rbar	AR1
CWL	Lichen woodlands	*P. mariana*	RcL3	11	0.91	0.55	0.89
			RcmL0	14	0.95	0.66	0.89
			RcmL2	12	0.88	0.46	0.91
		B. glandulosa	RcL3	40	0.90	0.2	0.37
			RcmL0	40	0.84	0.16	0.37
			RcmL2	40	0.80	0.15	0.40
	Shrublands	*B. glandulosa*	AB1	40	0.98	0.70	0.50
			AB2	40	0.97	0.57	0.40
	Lichen heathlands	*B. glandulosa*	LS0	40	0.83	0.22	0.48
			LS1	40	0.84	0.24	0.43
			LSA2	40	0.82	0.22	0.43
BR	Lichen woodlands	*P. mariana*	RcL5	9	0.94	0.72	0.91
			RcmL0	8	0.98	0.87	0.91
			RcmL6	9	0.96	0.79	0.92
		B. glandulosa	RcL5	40	0.90	0.31	0.57
			RcmL0	40	0.98	0.63	0.46
			RcmL6	40	0.92	0.38	0.54
	Shrublands	*B. glandulosa*	AB1	40	0.97	0.62	0.47
			AB2	40	0.91	0.21	0.44
			AB8	40	0.88	0.28	0.50
	Lichen heathlands	*B. glandulosa*	LSA2	39	0.97	0.55	0.53
			LSA4	40	0.83	0.22	0.44
			LSA6	40	0.97	0.66	0.46

Table S.2.3 List of the climatic drivers tested for the climate-growth analysis and their descriptions.

Climatic driver	Description	Months included
tSum	Summer temperature	July and August
tFall	Fall temperature	September and October
tFall^{-1}	Fall temperature of previous year	September and October
tWin	Winter temperature	November to April
tSpring	Spring temperature	May and June
pSum	Summer precipitation	July and August
pFall	Fall precipitation	September and October
pFall^{-1}	Fall precipitation of previous year	September and October
pWin	Winter precipitation	November to April
pSpring	Spring precipitation	May and June

Table S.2.4 Slope, R^2 and p-value of the NDVI-year regressions for each site at the Clearwater Lake (CWL) and Boniface River (BR) research locations.

Location	Plant community	Site	Slope	R^2	*p*-value
CWL	Lichen woodlands	RcL3	0.0057	0.28	**0.001**
		RcmL0	0.0081	0.78	**< 0.001**
		RcmL2	0.0071	0.7	**< 0.001**
	Shrublands	AB1	0.0074	0.75	**< 0.001**
		AB2	0.0098	0.82	**< 0.001**
	Lichen heathlands	LS0	0.0091	0.87	**< 0.001**
		LS1	0.0077	0.73	**< 0.001**
		LSA2	0.0069	0.76	**< 0.001**
BR	Lichen woodlands	RcL5	0.0064	0.73	**< 0.001**
		RcmL0	0.0081	0.77	**< 0.001**
		RcmL6	0.0069	0.64	**< 0.001**
	Shrublands	AB1	0.0063	0.68	**< 0.001**
		AB2	0.0077	0.70	**< 0.001**
		AB8	0.0079	0.80	**< 0.001**
	Lichen heathlands	LSA2	0.0078	0.77	**< 0.001**
		LSA4	0.0085	0.82	**< 0.001**
		LSA6	0.0064	0.75	**< 0.001**

Table S.2.5 Radial growth-climate relationship (Pearson correlation coefficient; R) and p-value for the best climatic drivers of radial growth for *P. mariana* and *B. glandulosa* at each site sampled at the Clearwater Lake (CWL) and Boniface River (BR) research stations.

Location	**Plant community**	**Species**	**Site**	**Best climatic driver**	**Pearson correlation coefficient (R)**	***p*-value**
CWL	Lichen woodlands	*P. mariana*	All	tSum	0.18	<0.0001
			RcL3	tSum	0.16	<0.0001
			RcmL0	tSpring	0.23	<0.0001
			RcmL2	ptFall	0.17	<0.0001
		B. glandulosa	All	tWin	0.10	<0.0001
			RcL3	tWin	0.11	<0.0001
			RcmL0	ptFall	0.12	<0.0001
			RcmL2	tWin	0.18	<0.0001
	Shrublands	*B. glandulosa*	All	pWin	0.15	<0.0001
			AB1	pWin	0.15	<0.0001
			AB2	pWin	0.15	<0.0001
	Lichen heathlands	*B. glandulosa*	All	tWin	0.11	<0.0001
			LS0	tWin	0.15	<0.0001
			LS1	tWin	0.17	<0.0001
			LSA2	tFall	0.09	<0.0001
BR	Lichen woodlands	*P. mariana*	All	tSpring	0.27	<0.0001
			RcL5	tSpring	0.30	<0.0001
			RcmL0	tSum	0.28	<0.0001
			RcmL6	tSpring	0.30	<0.0001
		B. glandulosa	All	tWin	0.15	<0.0001
			RcL5	tWin	0.18	<0.0001
			RcmL0	tWin	0.14	<0.0001
			RcmL6	tFall	0.17	<0.0001
	Shrublands	*B. glandulosa*	All	tWin	0.18	<0.0001
			AB1	tWin	0.17	<0.0001
			AB2	tWin	0.22	<0.0001
			AB8	tWin	0.15	<0.0001
	Lichen heathlands	*B. glandulosa*	All	tWin	0.20	<0.0001
			LSA2	tWin	0.24	<0.0001
			LSA4	tWin	0.15	<0.0001
			LSA6	tWin	0.22	<0.0001