UNIVERSITÉ DU QUÉBEC À MONTRÉAL
ÉCOLE PRATIQUE DES HAUTES ÉTUDES

VARIATIONS DE CROISSANCE ET CAPACITÉ D'ADAPTATION DES POPULATIONS MARGINALES FRAGMENTÉES D'ARBRES DES ZONES BORÉO-MONTAGNARDES, EN RÉPONSE AUX CHANGEMENTS CLIMATIQUES

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

JOHANN HOUSSET

SEPTEMBRE 2015

REMERCIEMENTS

Dans les moments les plus durs de mon doctorat j'aimais prendre du recul en comparant cette épreuve académique à une épreuve sportive, comme la traversée d'un océan à la voile, ou une ascension en alpinisme. Même si par moments l'on est tenté de rebrousser chemin, l'envie de toucher au but nous pousse à continuer. Heureusement, ce projet ne s'est pas fait en solitaire, et j'ai pu compter sur l'aide très précieuse de nombreuses personnes, sans qui je n'aurais pas réussi. Je tiens à remercier ici toutes celles et tous ceux qui ont permis de faire de moi un aspirant chercheur.

En particulier je remercie mes deux directeurs, Yves Bergeron et Christopher Carcaillet pour avoir cru en mes capacités de mener à bien ce projet et pour m'avoir donné une chance de « monter à bord » du projet BOREALP. Vous avez su me guider sur le chemin de ce doctorat et je pense que je me serais perdu en route sans votre aide. Votre patience, votre connaissance du monde scientifique et vos conseils m'ont tiré vers le haut et m'ont permis de mieux aborder les passages délicats.

Je suis aussi reconnaissant envers Martin Girardin pour son aide précieuse tout au long de mon doctorat et pour son accueil en stage au sein du Centre de Foresterie des Laurentides. Merci également à Renzo Motta qui m'a accueilli dans son laboratoire à Grugliasco en Italie pour la mesure des échantillons de pin cembro, mais surtout qui m'a fait partager sa passion pour les écosystèmes d'altitude alpins. Je remercie également Francine Tremblay et Huaitong Xu, pour leurs conseils et leur collaboration pour le volet génétique de mes recherches.

Mes remerciements vont également vers le consortium Ouranos pour m’avoir accueilli dans leurs bureaux à Montréal, le programme FONCER MCF, pour son support financier, Christian Messier, Virginie Arielle-Angers, grâce à qui je n’ai plus peur de la complexité de mes données, et le Centre d’Étude des Forêts (CEF) pour son aide financière lors de la participation à des congrès et la réalisation de stages. Je remercie tout particulièrement les professionnels de recherche du CEF, bras armés de la réussite académique des étudiants, pour maîtriser les statistiques (Marc Mazerolle et Stéphane Daigle), la cartographie et le GPS (Mélanie Desrochers), les bases de données et Star Wars (Daniel Lesieur), sans oublier bien-sûr le travail quotidien de Luc Lauzon pour nous appuyer et nous faciliter la vie.

Dans la Chaire en Aménagement forestier durable, merci à l’omniprésente Danielle Charron, pour avoir été une aiguilleuse précieuse dans le labyrinthe du doctorat, mais aussi à Marie-Hélène Longpré pour son soutien logistique à l’UQAT, et à Aurélie Terrier, telle l’aînée bienveillante d’une fratrie, pour son implication dans le laboratoire et ses nombreux conseils. Je remercie également le personnel de la station de recherche Duparquet : Raynald, Marie, Igor, le balbuzard pour nous offrir un quotidien lumineux propice à la conduite de nos travaux de recherche.Pour mes séjours en France, merci à l’équipe du CBAE, en particulier à Benoît Brossier pour son assistance précieuse sur le terrain, le prêt de matériel et pour la hotline « SOS Crossdating », Laure Paradis pour son aide avec les données cartographiques dans les Alpes, Chantal Gaine pour son soutien administratif, logistique et mécanique sans faille, et tout le reste de l’équipe pour leur accueil et les discussions autour du café.

La portée de cette thèse a été largement décuplée par les nombreuses personnes qui m’ont assisté sur le terrain et au laboratoire et ont décuplé ma force de travail. En particulier Jam Roy, Benjamin Gadet, Albanie Leduc, Maxime Allard, Maxime Tremblay, Mathieu Baconnet et Cécile Leroy. Merci pour votre aide et surtout pour les moments forts que nous avons partagés et pour l’ambiance de travail chaleureuse qui est si importante à mes yeux. Parmi toutes les autres personnes qui m'ont appuyé, je ne saurais oublier Isabelle Chimani pour son aide concernant l'utilisation des données météorologiques de la base de données Histalp, ainsi que Valantina Garavaglia et l'équipe du programme européen COST sur les populations marginales pour leur cours providentiel qui m'a permis de mieux saisir les enjeux associés à ces peuplements forestiers et à leur génétique.

Sur un tout autre registre, je remercie la nature et ses beautés, le golf du saint Laurent, les cembraie-mélézins des Alpes, les forêts boréales canadiennes et leur immensité pour m'avoir permis de me ressourcer lorsque je ne me souvenais plus pourquoi je faisais cette thèse ou simplement d'échanger la lourdeur du doctorat pour la lourdeur du sac à dos le temps d'une randonnée. La musique qui a rythmé inlassablement mon parcours doctoral, dans les coups durs, les passages à vide, les rushs et les joies, et a inspiré une autre profondeur à mon regard sur la nature.

Enfin et pour finir en beauté, je remercie du fond du cœur ma compagne Cécile, pour son indéfectible soutien qui m'a donné le courage d'avancer à maintes reprises et tout simplement pour faire partie de ma vie. Mes pensées vont aussi vers mes amis, la bande de la Compôte, la gang du Québec, Catherine et Paddy, Etienne et Valérie, Frère Jean, Gérard Thirion qui m'ont inspiré pour vivre une vie pleine et qui a du sens, de même que mes parents Nicole et Michel, Myriam et Hervé et aussi Pauline et Lucile qui ont le don de rendre les pauses joyeuses et légères. Vous avez supporté de façon compréhensive l'accaparement causé par ce doctorat, pas toujours conscient, pas toujours volontaire mais toujours difficile à porter. Merci de votre soutien et de votre compréhension.

À toutes ces personnes et à toutes celles et tous ceux qui m'ont aidé mais que je n'ai pas mentionné ici : je n'y serais jamais arrivé sans vous et je vous remercie du fond du cœur!

AVANT-PROPOS

Ce mémoire de thèse et les articles qu'il contient constituent les contributions originales du doctorat que j'ai effectué en cotutelle au sein de l'Université du Québec à Montréal au Canada (UQAM, programme de sciences de l'environnement) et de l'École Pratique des Hautes Études en France (EPHE, école doctorale 472, mention Systèmes Intégrés, Environnement et Biodiversité).

Cette thèse est constituée d'une introduction générale (texte original), de trois chapitres, et d'une conclusion générale. Il s'agit d'une thèse sur articles, ce qui signifie que chacun desdits chapitres est un article scientifique qui peut être lu indépendamment du mémoire dans son ensemble. Les chapitres I à III correspondent aux trois publications suivantes :

1. Housset, Johann M., Martin P. Girardin, Mathieu Baconnet, Christopher Carcaillet and Yves Bergeron. « Unexpected warming-induced growth decline in *Thuja occidentalis* at its northern limits in North America ». *Journal of Biogeography*, in press; doi:10.1111/jbi.12508.
2. Housset, Johann M., Martin P. Girardin, Huaitong Xu, Francine Tremblay, Christopher Carcaillet and Yves Bergeron. « Climatic control on radial growth of *Thuja* occidentalis is modulated by its genetic structure ». Soumis.
3. Housset, Johann M., Francine Tremblay, Martin P. Girardin, Renzo Motta, Yves Bergeron and Christopher Carcaillet. « Growth-climate relationships in western marginal populations of *Pinus cembra* in relation with genetic, tree-size and the environment ». En préparation.

Le paragraphe qui suit vise à préciser mon rôle ainsi que celui des coauteurs dans la réalisation de ces articles. En tant que premier auteur de ces articles, et dans le cadre de ma thèse, j'ai mis au point le dispositif expérimental avec mes directeurs, Yves Bergeron et Christopher Carcaillet. Ce dispositif a été également validé par deux autres chercheurs membres de mon comité de thèse, le Dr Martin P. Girardin (Service Canadien des Forêts, Canada) et le Prof. Renzo Motta (Università degli studi di Torino, Italie), dans le cadre de la présentation de mon projet de thèse à l'UQAM. J'ai conduit la récolte de données et d'échantillons sur le terrain et les mesures dendrochronologiques. J'ai pour cela bénéficié du matériel et des équipements des laboratoires de dendrochronologie de la station de recherche de Duparquet (Université du Québec en Abitibi Témiscamingue) pour l'espèce *Thuja occientalis* L. (thuya). Pour le pin cembro (*Pinus cembra* L.) en Europe, c'est grâce aux équipements et aux laboratoires du Centre de Bio-Archéologie (Montpellier, France) et du département DISAFA de l'université de Turin (Università degli studi di Torino, Italie) que j'ai pu effectuer le travail de terrain et de laboratoire. Yves Bergeron et Christopher Carcaillet ont financé et supervisé tout le travail de la thèse. Martin Girardin a guidé l'analyse des données dendrochronologiques et statistiques pour les trois chapitres et participé à l'amélioration de versions antérieures des articles. Mathieu Baconnet a participé aux mesures dendrochronologiques pour le thuya et à l'analyse statistique des données. Huaitong Xu a fourni les données génétiques pour le thuya qui ont été utilisées dans le chapitre II et a participé à l'amélioration de l'article par des commentaires sur les versions précédentes. Francine Tremblay a fourni les données génétiques pour le pin cembro qui ont été utilisées dans le chapitre III, a aidé à l'interprétation génétique des chapitres II et III, et a fourni des critiques constructives ayant permis d'enrichir les articles de ces deux chapitres. Renzo Motta a aidé à la conduite des mesures dendrochronologiques sur le pin cembro et à l'interprétation de l'écologie de cette espèce dans les Alpes occidentales. Je suis très reconnaissant aux coauteurs d'avoir amélioré cette thèse par leurs commentaires et leurs suggestions.

La réalisation de cette thèse a été rendue possible grâce à l'obtention de plusieurs financements doctoraux : bourse FONCER « modélisation de la complexité des forêts » NSERC (Natural Sciences and Engineering Research Council of Canada), bourse de la Chaire industrielle UQAM-UQAT en aménagement forestier durable, bourse d'excellence de la fondation UQAM et contrat doctoral de quatrième année du programme français Paris Nouveau Monde porté par le consortium heSam. Les travaux de terrain et de laboratoires ont été financés par la bourse de recherche stratégique « BOREALP » du NSERC (STPGP336871), le Laboratoire International Associé MONTABOR (LIA France-Canada CNRS-UM2-EPHE-UQAT-UQAM-UQAC), le Programme de soutien à des initiatives internationales de recherche et d'innovation du gouvernement du Québec, le Centre d'Étude de la Forêt et par la Chaire industrielle UQAM-UQAT en aménagement forestier durable.

TABLE DES MATIÈRES

LISTE DES FIGURES

LISTE DES TABLEAUX

RÉSUMÉ

La réponse des espèces végétales aux changements climatiques devrait conjuguer des ajustements physiologiques, l'adaptation génétique et la migration pour suivre le déplacement des enveloppes bioclimatiques. Ces modifications seront en théorie plus visibles aux marges de distribution des espèces, où les populations sont plus éloignées de leur optimum climatique. Vers les marges froides de la forêt boréale dans l'hémisphère nord, ou dans les forêts d'altitude en montagne, le réchauffement climatique continu devrait intuitivement permettre une plus longue saison de croissance. Mais pour une même quantité de précipitations, l'accroissement des températures au-delà d'un seuil peut aussi avoir un impact négatif sur la croissance des arbres en raison d'une augmentation de l'évapotranspiration aboutissant à un stress hydrique. Le réchauffement pourrait aussi causer une diminution de croissance en raison de la respiration de maintenance, réquisitionnant une part relativement plus importante de la production brute de carbohydrates par la photosynthèse. Ces modifications physiologiques se traduiront vraisemblablement par des variations dans les pressions de sélection exercées sur les populations d'arbres. En raison de leur isolement, de leurs petites tailles et de leur marginalité, les populations périphériques ont en théorie une diversité génétique réduite et des taux plus élevés de « consanguinité ». Ces caractéristiques pourraient nuire à leur capacité d'adaptation génétique vis-à-vis des conditions climatiques à venir. Cependant, il n'existe pas de modèle permettant de projeter la vitesse d'adaptation des espèces, en raison notamment d'un manque de recul temporel sur l'adaptation des populations.

Cette thèse a pour objectif d'apporter des éléments de réponse sur le devenir des populations marginales d'espèces d'arbres boréo-montagnardes dans le contexte des changements climatiques. Seuls les effets du climat sur la croissance radiale des arbres qui est un indicateur de réponses physiologiques, et les capacités d'adaptation ont été abordés dans ce travail au niveau de la population. L'analyse de la réponse dendroclimatologique des populations marginales est couplée à la structure génétique des espèces, sur des gradients allant des zones de distribution continues aux populations marginales. Deux modèles biologiques ont été choisis pour tester cette approche : le thuya (*Thuja occidentalis* L.) en limite nordique dans la forêt boréale de l'est du Canada (47-50°N, 74-80°W) et le pin cembro (*Pinus cembra* L.) à sa limite occidentale dans les Alpes françaises et italiennes (44.2-46.0°N, 5.9-7.1°E). Les hypothèses suivantes ont été testées : (1) le réchauffement climatique au cours du

XX^{e} siècle s’est accompagné d’une augmentation de la croissance des populations marginales nordiques du thuya ; (2) la variabilité inter-sites des relations climat-croissance (signal dendroclimatique) est corrélée à la structure génétique des espèces ; (3) la variabilité de croissance (synchronisme entre les arbres d’un même site) est corrélée à la diversité génétique intra-populationnelle.

Une baisse de la croissance du thuya a été observée à partir de 1980 en zone marginale. Les analyses dendroclimatiques sur cette espèce révèlent que la croissance est limitée par la sécheresse dans la deuxième moitié du XX^{e} siècle. Les populations marginales nordiques de thuya auraient donc déjà atteint un seuil de température optimale pour leur croissance radiale. Pour le thuya, la structure génétique module de façon significative les valeurs de corrélation entre la croissance radiale et les température de mai d’une part, et les précipitation de juin de l’année précédant la formation du cerne d’autre part. Ce résultat suggère qu'il existe un potentiel d'adaptation de la croissance radiale au réchauffement climatique, mais cette adaptation dépendra de la diversité génétique intra-populationnelle disponible pour la sélection naturelle. Concernant le pin cembro, un effet de la structure génétique sur la corrélations avec les températures de novembre de l’année précédant la formation du cerne a été observé. Toutefois, pour les deux espèces, les relations climat-croissance étaient essentiellement modulées par des variables environnementales, en premier lieu le volume des précipitations, mais également par des variables édaphiques et par la morphologie des arbres. La réponse des populations marginales au réchauffement futur sera fortement tributaire de la saisonnalité et du volume des précipitations. Par ailleurs, le synchronisme de croissance entre les arbres était à la fois influencé par la diversité génétique intra-populationnelle et par le volume des précipitations. En conclusion, il apparaît très difficile de distinguer les effets du climat et de la génétique sur la croissance des arbres étudiés.

Mots-clés : Adaptation génétique, changements climatiques, croissance radiale des arbres, dendroclimatologie, forêt boréale, forêt de montagne tempérée, limites de distribution.

INTRODUCTION

Le devenir des écosystèmes et des ressources naturelles dans le contexte des changements climatiques constitue une préoccupation scientifique et politique majeure au niveau international (IPCC, 2013 ; Thompson *et al.,* 2009). Dans ce contexte de changement, l'incertitude est particulièrement problématique pour les gestionnaires forestiers, car la foresterie durable implique, par définition, une planification à long terme : les arbres qui se régénèrent aujourd'hui seront récoltés après une longue période de croissance dépassant généralement 100 ans. Cela impose d'être en mesure d'anticiper la réponse des forêts à ces changements pour guider la gestion forestière actuelle de cette ressource. Il convient donc de bien connaître les processus biologiques régissant les interactions entre les écosystèmes forestiers et le climat, qu'ils soient directs ou indirects.

Le climat agit de façon directe sur les processus physiologiques des arbres comme la photosynthèse, l'équilibre hydrique, la germination, le recrutement, la croissance de la tige et des racines. Les effets des températures et des précipitations sur la croissance des arbres varient à travers la zone de répartition des espèces. Dans les zones froides, comme les limites nordiques des espèces de la zone boréale dans l'hémisphère nord ou vers les limites altitudinales des forêts de montagnes, des températures plus basses et des saisons de croissance plus courtes ont tendance à contraindre la physiologie des plantes (Boisvenue et Running, 2006 ; Kramer *et al.*, 2000). Par ailleurs, vers les limites chaudes des espèces, c'est surtout la disponibilité en eau qui contraindrait la croissance des arbres (Boisvenue et Running, 2006 ; Soja *et al.*, 2007), ainsi qu'une plus grande dépense de ressources carbonatées allouée à la respiration de maintenance dans des températures élevées (Chapin *et al.*, 2011 ;

Lavigne et Ryan, 1997). Le climat agit également sur la reproduction des espèces en régulant la production de graines, les taux de germination et de survie des semences (Greene *et al.*, 1999 ; Tremblay *et al.*, 2002). Au niveau du paysage, le climat influence indirectement la distribution des espèces en agissant sur les compétitions interspécifiques (Aitken *et al.*, 2008) ainsi que sur les régimes de perturbations tels que les feux (Carcaillet *et al.*, 2001 ; Girardin *et al.*, 2010), les avalanches (Bebi *et al.*, 2009) ou les attaques d'insectes (Logan *et al.*, 2003). Les conditions édaphiques influencent également la distribution des espèces

La réponse des arbres aux changements climatiques se conjugue avec différents processus biologiques et écologiques (Aitken *et al.*, 2008) : persistance *in situ* (accommodation des individus par plasticité phénotypique, maintien des populations localement par adaptation génétique ou plasticité génétique), migration (processus de dispersion des semences) ou extinction locale (mortalité). La capacité de persistance *in situ* des populations est fonction de la plasticité des espèces. Une espèce spécialisée est plus vulnérable à des changements environnementaux. La capacité des individus à s'accommoder d'un changement de conditions environnementales par leur plasticité phénotypique peut aussi réduire l'impact des changements climatiques (Chapin *et al.*, 1992 ; G. De Jong, 2005). À partir d'un même génotype, la plasticité phénotypique permet des ajustements physiologiques aux changements de conditions environnementales qui confèrent de la résilience aux arbres. Il a été démontré récemment que la plasticité phénotypique avait un contrôle génétique par le biais de régulations épigénétique (Pigliucci, 2005 ; Yakovlev *et al.*, 2011). Les ajustements liés à la plasticité phénotypique ont néanmoins une certaine limite. Par exemple, un stress hydrique exceptionnel sur une année peut conduire à une extinction locale de populations par mortalité si le seuil de tolérance ou de résistance de l'espèce est dépassé altérant ainsi la résilience du système (Breshears *et al.*, 2008). Des mortalités liées à la sécheresse peuvent aussi être induites par des températures extrêmes (Van Mantgem et Stephenson, 2007). Toutefois, la mortalité est généralement causée par une conjonction entre l’entrée dans une phase de morbidité et la venue d’un facteur déclencheur létal comme une attaque d’insectes ou un stress climatique (Franklin *et al.*, 1987). Une grande diversité génétique existante dans les populations est source de résilience, en augmentant la probabilité de disponibilité de génotype adapté à de nouvelles conditions climatiques (Bradshaw, 1991 ; Chapin *et al.*, 1992 ; Savolainen *et al.*, 2007). La reproduction sexuée participe à la fois à la migration des espèces par la dispersion des propagules et à une adaptation génétique par la sélection des semences à chaque génération. La pollinisation met en œuvre des flux de gènes sur l’ensemble de l’aire de répartition (Aitken *et al.*, 2008 ; Davis et Shaw, 2001) et contribue à l’adaptation sélective de l’espèce. Les populations au nord reçoivent des gènes des populations situées au sud, plus adaptées à des climats chauds (Davis et Shaw, 2001). Des études scientifiques basées sur des observations directes indiquent que les changements climatiques récents induisent déjà une montée des aires de répartition en altitude dans les Alpes (Lenoir *et al.*, 2008) ou en latitude dans les forêts boréales (Payette, 2007) bien que d’autres études suggèrent une certaine inertie (Hättenschwiler et Körner, 1995). Les études montrant un changement sont toutefois limitées par un faible recul temporel, ainsi que par la difficulté à distinguer les effets du climat sur la végétation des conséquences de changements dans les activités humaines (Chauchard *et al.*, 2010). Les cycles passés de glaciation et de déglaciation ont déjà induit des changements importants dans la distribution des espèces (Davis et Shaw, 2001 ; Williams *et al.*, 2004) ou localement dans la composition forestière (Blarquez *et al.*, 2012 ; Carcaillet *et al.*, 2010) ont probablement résulté de changements climatiques significatifs. Ainsi, on peut s’attendre à un changement futur des limites d’aires des espèces en altitude et en latitude (Jump *et al.*, 2009), induite par le réchauffement du climat tout en se confondant partiellement avec les effets des activités anthropiques (changements d’usage des sols et des pratiques sylvo-agropastorales).

Si certaines espèces présentent des aires de distribution continues, d'autres comportent des populations marginales éloignées des populations centrales (voir figure 0.1). Ces populations marginales peuvent être relictuelles, issues d'une aire de distribution plus vaste dans le passé. C'est par exemple le cas au Québec pour le sapin baumier, *Abies balsamea* L., (Lafontaine et Payette, 2010 ; Sirois, 1997). De telles populations marginales, situées au-delà de la zone de distribution continue d'une espèce, pourraient faciliter la migration de l'espèce en jouant le rôle d'avant-poste forestier. Par exemple les refuges glaciaires ont accéléré la recolonisation des espèces au cours des périodes interglaciaires (Davis et Shaw, 2001 ; McLachlan *et al.*, 2005). Toutefois, le devenir de ces populations marginales sera dépendant de l'adéquation de ces populations avec les nouvelles conditions climatiques locales. En cas de différence entre le futur climat et l'optimum climatique de l'espèce, il s'exercera une pression de sélection sur les populations marginales et leur devenir dépendra de leur capacité d'adaptation à ces nouvelles conditions. La capacité d'adaptation génétique d'un trait en réponse à une pression de sélection nécessite deux conditions : (1) l'existence d'un contrôle génétique sur ce trait et (2) l'existence d'une variabilité génétique intra-population et d'une variabilité phénotypique pour ce trait (Violle *et al.*, 2012).

Néanmoins, les populations marginales ont théoriquement des caractéristiques génétiques qui diminuent leur capacité d'adaptation en raison de leur isolement et de leur taille démographique généralement réduite (Eckert *et al.*, 2008 ; Lesica et Allendorf, 1995). Les populations marginales ayant théoriquement des nombres d'individus bien plus faibles que les populations situées au centre de l'aire d'une espèce, le flux de gènes net a donc lieu de manière prédominante depuis le centre vers les marges d'une espèce (modèle central-marginal). Cela a pour conséquence d'apporter des gènes inadaptés aux populations périphériques (Bridle *et al.*, 2010 ; Sexton *et al.*, 2009). La diversité génétique intra-populationnelle de populations aux petits effectifs est susceptible d'être réduite par les effets combinés de la dérive génétique[1], de la consanguinité et par des événements démographiques passés tels que des effets fondateurs ou des goulots d'étranglement génétiques.

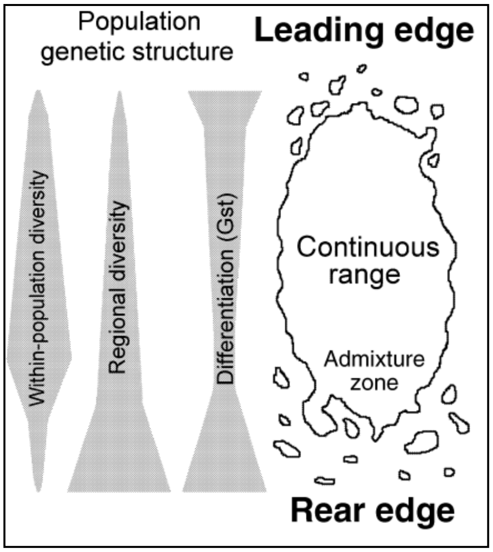


Figure 0.1 Caractéristiques génétiques des populations marginales (Adapté de Hampe et Petit, 2005). Within-population diversity = diversité génétique inrapopulation. Regional diversity = diversité génétique au niveau du paysage. Continuous range = aire de distribution continue. Leading edge, rear edge = populations marginales du front de colonisation, de la queue de migration, dans le contexte d'un réchauffement.

Bien que beaucoup d'efforts de modélisation aient été déployés pour étudier la dynamique évolutive des limites de distribution des espèces (Bridle *et al.*, 2009 ; Kirkpatrick et Barton, 1997 ; Sexton *et al.*, 2009), aucun des modèles théoriques développés n'a de réel pouvoir prédictif en raison d'un manque de connaissances empiriques sur l'architecture génétique des espèces et sur leur réponse à la sélection (Polechová *et al.*, 2009 ; Sexton *et al.*, 2009 ; Shaw et Etterson, 2012). Des études empiriques *in situ* documentant à la fois la structure génétique et la réponse des arbres au climat sont donc nécessaires pour mieux calibrer ces modèles d'adaptation dans le temps et dans l'espace (Polechová *et al.*, 2009 ; Sexton *et al.*, 2009). Pour

---

[1] Perte aléatoire d'allèles liée à la reproduction sexuée dans une population isolée de taille finie.

appréhender de manière complète l'adaptation au climat des espèces, il est nécessaire de faire des recherches sur de vastes gradients incluant la limite de répartition des espèces (Aitken *et al.*, 2008).

Ainsi les capacités d'adaptation génétiques peuvent être déterminantes pour la résilience des populations forestières vis-à-vis du climat (Alberto *et al.*, 2013 ; Thompson *et al.*, 2009). Les caractéristiques génétiques des populations marginales pourraient donc affecter leurs capacités de réponses aux changements climatiques rapides pour la fin du XXIème siècle. Ma question de recherche est donc de déterminer le comportement de populations marginales d'arbres au regard des changements climatiques en cours. Par l'étude des cernes annuels d'accroissement radial du tronc, la dendrochronologie permet d'obtenir des enregistrements de la croissance radiale passée des arbres. En corrélant ces archives naturelles avec les données météorologiques, il est possible de caractériser la réponse des arbres au climat (Fritts, 1976 ; Schweingruber, 1996). Les variations de largeur de cernes dans le temps renseignent indirectement l'adéquation entre un arbre et les variations du climat. La génétique et la dendrochronologie sont donc deux voies empiriques complémentaires pour évaluer la réponse des arbres aux changements climatiques. L'objectif de ce projet est de caractériser la réponse dendroclimatique de populations marginales et de tester le lien entre la structure génétique d'une espèce et les relations climat-croissance. Mon hypothèse de travail est que les populations marginales présenteraient des relations dendroclimatiques et des caractéristiques génétiques différentes de celles des populations centrales qui les rendraient plus sensibles au changement du climat. Il s'agit d'une stratégie innovante – probablement singulière à ma connaissance - qui vise à tester le lien entre la structure génétique *in situ* des populations marginales et leurs réponses à la variabilité climatique interannuelle en termes de croissance radiale. Les variables génétiques utilisées dans cette comparaison seront constituées à la fois par des indicateurs de diversité génétique intra-populationnelle et par des descripteurs de la structure génétique interpopulationnelle. Cette dernière sera caractérisée par des indicateurs basés sur des analyses de groupements – *clustering* - sur l'ensemble des génotypes de la zone d'étude. Cette étude se concentre uniquement sur les effets directs du climat en utilisant la croissance radiale des arbres comme indicateur de la réponse aux variations du climat. Idéalement, il serait nécessaire de prendre en compte la migration et les effets indirects du climat via les régimes de perturbations pour appréhender complètement ce problème, mais ces processus ne seront pas couverts dans ma thèse.

Deux modèles biologiques présentant des traits communs ont été choisis, à savoir des espèces d'arbres croissant dans deux régions différentes du monde mais dont les comportements sont proches, analogues en bien des points voire convergents. Ces deux espèces, le pin cembro (*Pinus cembra* L.) dans les Alpes européennes et le thuya (*Thuja occidentalis* L.) dans l'est du Canada, ont fait l'objet de nombreuses études mettant en évidence des corrélations significatives entre la croissance et les variables climatiques pour les populations centrales de pin cembro (Carrer *et al.*, 2007 ; Carrer et Urbinati, 2004 ; Saulnier *et al.*, 2011) et celles de thuya (Archambault et Bergeron, 1992b ; J Tardif et Bergeron, 1997). Ces deux espèces de conifères sont très peu affectées par les attaques d'insectes et sont tolérantes à l'ombre, ce qui permet de supposer que leurs variations de croissance sont *a priori* plus directement influencées par le climat (Contini et Lavarelo, 1982 ; Hofmeyer *et al.*, 2009).Par ailleurs, la longévité de ces deux espèces permet des reconstitutions dendrochronologiques de plusieurs siècles, voire de plus de 1000 ans (Archambault et Bergeron, 1992a ; Buckley *et al.*, 2004 ; Büntgen *et al.*, 2005 ; Carrer *et al.*, 2007), ce qui en fait des espèces particulièrement intéressantes pour la dendroclimatologie. La croissance radiale du pin cembro est généralement favorisée par des températures chaudes durant l'automne de l'année précédant la formation du cerne et durant l'été de l'année en cours. Il existe cependant des variations spatiales de la relation au climat (Carrer *et al.*, 2007). Par exemple les populations situées au sud des Alpes françaises semblent plus sensibles aux sécheresses estivales, comme le montrent un impact négatif des températures moyennes élevées des mois d'été et l'influence positive des précipitations du mois d'août de l'année antérieure au cerne (Saulnier *et al.*, 2011). Plusieurs études dendroclimatique du thuya autour du Lac Duparquet au Québec montrent que la croissance est contrainte par un stress hydrique en été, en étant favorisée par les fortes pluviosités estivales, et défavorisée par les températures élevées du mois d'août de l'année antérieure (Archambault et Bergeron, 1992a ; J Tardif et Bergeron, 1997). Cela s'explique en partie par le fait que les populations étudiées se situaient essentiellement sur des sites mésiques à xériques, c'est-à-dire plus sensibles aux variations des précipitations et des interactions entre précipitations et températures. Les sites les plus xériques présentent d'ailleurs une relation négative avec l'indice de sécheresse de juin et juillet (J Tardif et Bergeron, 1997).

Il existe encore peu de connaissances sur la réponse dendroclimatologique des populations marginales de ces deux espèces. Une étude sur les populations isolées de thuya en limite nord-ouest de son aire de répartition au Manitoba (J. Tardif et Stevenson, 2001) révèle les mêmes relations climatiques que celles citées précédemment, avec en plus une influence positive des températures de novembre précédant la formation du cerne. Les populations marginales de ces deux espèces correspondraient à des populations relictuelles, puisque des études paléoécologiques indiquent une diminution de leurs abondances après un maximum durant l'Holocène pour le pin cembro dans les Alpes occidentales (Ali *et al.*, 2005 ; Blarquez *et al.*, 2012 ; Genries *et al.*, 2009) et le thuya (Carcaillet *et al.*, 2001, 2010 ; Liu, 1990). Les résultats des études génétiques sur le pin cembro semblent corroborer cette hypothèse, puisque des forts niveaux de diversité génétiques sont observés, probablement hérités de populations de très grandes tailles dans le passé (Höhn *et al.*, 2009). On peut compléter cette hypothèse en indiquant que les activités anthropiques passées, comme le pastoralisme, ont fortement contribué à la fragmentation actuelle des populations de pin cembro en altérant des régimes de perturbations (ex. feux et coupes de bois) et en générant des contraintes (pastoralisme) qui seraient défavorables au maintien du pin cembro. Pour le thuya, la fragmentation anthropique par la coupe est plus récente (deuxième moitié du XXe siècle), et la fragmentation naturelle par les feux a dû se mettre en place suite à l’accroissenment de la fréquence des feux et de l’activité de combustion de biomasse entre 3000 et 2000 ans avant nos jours dans la forêt coniférienne de l’est (Carcaillet *et al.*, 2010 ; Carcaillet et Richard, 2000), bien que les feux existent depuis la mise en place des premiers boisements (Carcaillet *et al.*, 2001 ; Higuera *et al.*, 2009).

Le pin cembro est un gymnosperme boréo-montagnard, caractéristique des étages de végétation subalpins dans les Alpes et les Carpates en Europe méridionale (EUFORGEN, 2015) et de la forêt boréale asiatique, des monts Oural au Kamchatka. Le thuya est un gymnosperme de l’est de l’Amérique du Nord, dont l’aire de répartition s’étend au nord jusque dans la forêt boréale (Little, 1971). Ces deux espèces partagent des traits fonctionnels similaires : longévité, croissance lente, tolérance à l’ombre, généralement dominant le couvert et la biomasse des communautés de fins de successions (Burns et Honkala, 1990 ; Hofmeyer *et al.*, 2009 ; Lingua *et al.*, 2008 ; Motta et Edouard, 2005 ; Risch *et al.*, 2008). De plus, ces deux espèces sont peu exigeantes quant aux conditions édaphiques de croissance et poussent aussi bien sur sol basique ou acide, sur milieux rocheux, dans des milieux humides à xériques, avec ou sans matières organiques. Le thuya et le pin cembro revêtent des enjeux multiples. Bien que représentant de petits volumes exploités, leurs valeurs économiques sont non négligeables, et leurs bois sont appréciés pour leurs qualités technologiques. Les principaux enjeux de préservation de ces espèces sont d’ordres culturels et écologiques : usages ancestraux du bois de pin cembro dans l’art traditionnel montagnard européen, valeur médicinale et spirituelle du thuya pour les Premières Nations, grande valeur écologique des communautés végétales d’altitude du pin cembro (e.g. directive européenne Natura 2000).

Il convient de préciser que le but de cette étude n’est pas de comparer ces deux espèces entre-elles, mais de tenter de tirer de leurs relations au climat et de leur structure génétique en conditions marginales un enseignement commun ou complémentaire sur ces dites relations. Les analyses concernant la marginalité des populations seront donc conduites séparément sur ces deux espèces. La conclusion du mémoire visera à faire l’amalgame des travaux menés avec une approche identique sur ces deux espèces et faire émerger des processus communs ou différentiels. Ce travail de recherche sera décomposé en trois chapitres, dont les objectifs et hypothèses spécifiques sont détaillés ci-après.

0.1 Chapitre 1 : Objectif et hypothèses (thuya)

Evaluer la réponse du thuya à la variabilité climatique inter-annuelle et inter-décennale sur un gradient latitudinal allant de sa zone de distribution continue vers sa zone marginale nordique au Québec.

H1.1: La croissance de thuya est significativement et positivement corrélée avec les variations des températures. La croissance augmente au cours du XXème siècle en fonction du réchauffement climatique, et cette augmentation est la plus forte dans la zone marginale nordique.

H1.2: La réponse de la croissance du thuya aux variations climatiques dépend localement du régime régional de précipitations, de la qualité du site et des conditions associées d'humidité de sol.

0.2 Chapitre 2 : Objectif et hypothèses (thuya)

Tester la capacité de réponse adaptative du thuya à la pression de sélection induite par le réchauffement climatique sur les traits de la croissance radiale annuelle (i.e. la production annuelle de xylème), du centre de la répartition de l’espèce vers sa limite nordique.

H2.1: La réponse de la croissance radiale à la variabilité du climat est influencée par la structure génétique des populations de thuya. L'existence d'un contrôle génétique sur le phénotype observé est une condition préalable pour que la sélection naturelle puisse avoir lieu. L'hypothèse alternative est que la variabilité dans les réponses climatiques entre les sites est due à des conditions environnementales uniquement (pas d'effets de la structure génétique).

H2.2: La variabilité phénotypique intra-population pour les caractères liés à la croissance radiale et la diversité génétique intra-population est plus faible pour les populations marginales, selon l’hypothèse du modèle central-marginal.

H2.3: Le synchronisme de croissance radiale entre les arbres d'un même site diminue avec la diversité génétique intra-populationnelle. Une autre hypothèse est que le synchronisme de croissance est plus lié aux conditions climatiques ; en plaçant une contrainte de croissance commune sur tous les arbres d'un site, un climat local plus stressant devrait théoriquement conduire à un plus grand synchronisme (Schweingruber, 1996).

0.3 Chapitre 3 : Objectif et hypothèses (pin cembro)

Caractériser les relations climat-croissance du pin cembro, à sa limite occidentale de distribution dans l’arc alpin et tester le lien entre la structure génétique et cette réponse au climat. A noter que, *a contrario* du thuya, les relations climat-croissance sont assez bien décrites pour cette espéce dans les Alpes. L’originalité de cette thèse concernant le cembro concerne donc uniquement le lien entre la croissance radiale et la génétique.

H3.1: Le synchronisme de croissance radiale entre les arbres d'un même site est lié à la diversité génétique intra-populationnelle. L’hypothèse alternative est que le synchronisme de croissance serait lié aux conditions climatiques. Un climat local plus stressant pourrait conduire à un plus grand synchronisme en plaçant une contrainte de croissance commune sur tous les arbres d'un même site (Schweingruber, 1996; King et al, 2013.).[1]

H3.2: Les relations climat-croissance sont modulées par la structure génétique du pin cembro. L'hypothèse alternative est que la variabilité dans les réponses climatiques sont dues à des conditions environnementales (pas d'effets de la structure génétique)[2]

---

[1] Hypothèse analogue à H2.3, transposée au pin cembro

[2] Hypothèse analogue à H2.1, transposée au pin cembro

CHAPITRE I

UNEXPECTED WARMING-INDUCED GROWTH DECLINE IN *THUJA OCCIDENTALIS* AT ITS NORTHERN LIMIT IN AMERICA

(UNE BAISSE DE CROISSANCE INATTENDUE INDUITE PAR LE RÉCHAUFFEMENT CLIMATIQUE À LA LIMITE NORD DE *THUJA OCCIDENTALIS* EN AMÉRIQUE DU NORD)

Johann Housset[1,2,3,4*], Martin Girardin[2,5], Mathieu Baconnet[1], Christopher Carcaillet[3,4], Yves Bergeron[1,2]

[1]Natural Sciences and Engineering Research Council of Canada, Industrial Chair in Sustainable Forest Management, Forest Research Institute, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC, J9X 5E4, Canada, [2]Centre d'Étude de la Forêt, Université du Québec à Montréal, Montréal, QC, H3C 3P8, Canada, [3]École Pratique des Hautes Etudes (EPHE), F-75014 Paris, France, [4]LEHNA (UMR5023, CNRS), Université Lyon 1, F-69622 Villeurbanne, France, [5]Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, Stn Sainte-Foy, Québec, QC, G1V 4C7, Canada.

*Auteur correspondant: Johann Housset, Centre d'Étude de la Forêt, CP 8888, Montréal, QC, H3C 3P8, Canada. E-mail: housset.johann@courrier.uqam.ca

Article publié dans *Journal of Biogeography* (2015, doi:10.1111/jbi.12508).

1.1 Abstract

Aim: Towards the cold margins of the Northern Hemisphere boreal zone, continuing warming should theoretically provide a longer vegetative season, favouring growth and a northward shift in tree species distribution. The northern distribution of Thuja occidentalis L. (eastern white cedar) is marked by the presence of isolated marginal populations distant from the continuous distribution. If those populations proved to be well adapted to their future local climatic conditions, their expansion could accelerate cedar poleward migration. We tested the hypotheses that (H1.1) there will be a growth increase in cedar northern marginal populations as a result of global warming and (H1.2) the edaphic conditions and regional precipitation regimes will modulate their response to warming.

Location: Canadian boreal forest, western Québec (47–50° N, 74–80° W).

Methods: We investigated radial growth using tree-ring measurements from dominant and co-dominant eastern white cedar trees (n = 723) distributed along a latitudinal gradient from its northern margin to the centre of its natural range. First, low-frequency growth variations were analysed on whole chronologies (AD 1720–2010). Second, inter-annual growth variations were tested against AD 1953–2010 monthly temperature and precipitation time series with a bootstrapped correlation function. Finally, the impact of environmental variables on the growth–climate relationships was assessed.

Results: Unexpectedly, a growth decline was observed starting from 1980 in marginal sites. Dendroclimatic analyses revealed that radial growth was not only limited by short growing seasons but also by summer droughts in the marginal zone. This response was exacerbated in sites that received less summer precipitation. Counterintuitively, autumn and spring precipitation negatively impacted on growth, especially in wet soil stands.

Main conclusions: Northern marginal populations of cedar may have already reached their optimum temperature threshold for radial growth. Our results suggest that they will probably be facing increasing hydric stress selection pressure under the assumptions of climate change. Their responses to future warming will be highly dependent on the seasonality and magnitude of variation in precipitation regimes.

Keywords: Boreal forest, Canada, climate change, dendroclimatology, tree ring, forest productivity, distribution limit, drought, respiration.

1.2 Résumé

Vers les marges froides de la zone boréale dans l'hémisphère Nord, le réchauffement climatique continu devrait théoriquement permettre une plus longue saison de croissance. Un des résultats attendus est une augmentation de la croissance et une migration vers le nord des espèces d'arbres. La limite nordique de *Thuja occidentalis* L. (thuya) est caractérisée par la présence de populations marginales isolées situées au-delà de la zone de distribution continue de l’espèce. Si ces populations sont bien adaptées à leurs futures conditions climatiques locales, leur expansion géographique pourrait accélérer la migration vers le nord du thuya. Nous avons testé l'hypothèse que (H1.1) il y aura une augmentation de la croissance des populations marginales nordiques du thuya en raison du réchauffement climatique et (H1.2) les conditions édaphiques et les régimes locaux de précipitations influencent leur réponse au réchauffement. Notre zone d’étude se situe dans la forêt boréale canadienne, à l'ouest du Québec (47-50 ° N, 74-80 ° W). La croissance radiale a été étudiée en mesurant les largeurs de cernes d’accroissements annuels des thuyas dominants et co-dominants (n = 723) répartis le long d'un gradient latitudinal allant de la limite nordique de l’espèce au centre de son aire de répartition. Dans un premier temps, les variations de croissance basse fréquence ont été analysées sur les chronologies entières (AD 1720-2010). Puis, les relations entre les variations interannuelles de la croissance et les températures mensuelles d’une part et les précipitations mensuelles d’autre part ont été calculées grâce à des fonctions de corrélation et des fonctions de réponses sur la période AD 1953-2010. De façon inattendue, une baisse de la croissance a été observée à partir de 1980 dans les sites marginaux. Les analyses dendroclimatiques ont révélé que la croissance radiale n’était pas uniquement limitée par les courtes saisons de croissance et le froid, mais aussi par des sécheresses estivales dans la zone marginale. Cette réponse a été exacerbée dans les sites qui reçoivent en moyenne moins de précipitations. Des corrélations négatives ont été observées avec les précipitations à l’automne et au printemps précédant la formation du cerne automne, en particulier pour les peuplements poussant dans des sols humides. Les populations marginales nordiques de thuya ont donc peut-être déjà atteint leur seuil de température optimale pour leur croissance radiale. Nos résultats suggèrent que ces populations marginales seront probablement soumises à une pression croissante de sélection causée par le stress hydrique accru par les changements climatiques. Leur réponse au réchauffement futur sera fortement tributaire de la saisonnalité et de l'ampleur de la variation des régimes de précipitations.

Mots-clés : Forêt boréale, Canada, changement climatique, dendroclimatologie, cernes de croissance annuels, productivité des forêts, limite de distribution, sécheresse, respiration.

1.3 Introduction

Understanding the influences of climate on vegetation is crucial in the context of global climate change, especially at high northern latitudes where the increase in temperature is projected to be the greatest (IPCC, 2013). It is generally accepted that, in the boreal biome of the Northern Hemisphere, northern limits of tree species are linked to climate (Woodward, 1987; Pearson & Dawson, 2003). One of the first expected consequences of projected climate change is therefore a northward shift of species' cold margins (Jump *et al*., 2009; Fisichelli *et al*., 2014). While many studies have focused on the effect of climate change on tree lines (Grace *et al*., 2002; Esper & Schweingruber, 2004; Payette, 2007), the biology of tree limits situated within a forest matrix remains less well understood, partly because it is influenced by complex processes such as interspecific relations, disturbances and biogeochemical cycles (Lafontaine & Payette, 2010; Fisichelli *et al*., 2014). In such contexts, distribution limits tend to be discontinuous, with isolated populations outside the main continuous distributional area of a species. For several boreal tree species, e.g. *Abies balsamea* (L.) Mill. and *Thuja occidentalis* L., poleward marginal populations consist of patches of limited tree occurrences, probably relicts from the contraction of a broader past distribution (Sirois, 1997; Lafontaine & Payette, 2010; Paul *et al*., 2014). The presence of these northern marginal populations isolated from the continuous distribution could accelerate species migration, assuming that such populations are well adapted for their future local climatic conditions and that there are no edaphic (hydrology, soil chemistry, nutrients, etc.) constraints to colonization (McKenney *et al*., 2007).

The influence of climate varies across the distributional area of a plant species, as a result of the complex interplay between temperature and precipitation. Experiments have indicated that populations from the northern limits of boreal species could display better growth under a warmer climate (Rehfeldt *et al*., 1999; Aitken *et al*., 2008; Reich & Oleksyn, 2008), given that local climatic conditions at distribution margins deviate from the species optimum. At the margins of northern distributions, lower temperatures and shorter growing seasons tend to constrain growth (Kramer *et al*., 2000; Boisvenue & Running, 2006). Global warming should relax this constraint, as suggested by studies conducted at high-latitude tree lines

(Innes, 1991; Esper & Schweingruber, 2004; Lloyd *et al*., 2011). In contrast, at the dry limit of a given species, an increase in temperature could theoretically result in growth reduction. Indeed, plant growth could become increasingly limited by water availability with the need to support higher transpiration (Boisvenue & Running, 2006; Soja *et al*., 2007) and sustain a higher maintenance respiration to drive metabolic processes (Lavigne & Ryan, 1997; Girardin *et al*., 2012). While these climatic constraints are now commonly integrated into process-based models, which have been used to forecast climate change impacts on forests (e.g. Richardson *et al*., 2012), it remains a challenge to verify the modelled response with actual field measurements across species' distributional areas. Research using tree-ring data to calibrate and validate forest productivity models has shown promising results (e.g. Babst *et al*., 2013). Nevertheless, information from which the theories have been developed has mostly come from laboratory and controlled experimental studies for a limited number of species, and many models currently misrepresent the seasonality and inter-annual variability of phenological processes (e.g. Richardson *et al*., 2012).

We provide an assessment of the response of the boreal coniferous tree species eastern white cedar (*Thuja occidentalis* L.) (hereafter called cedar) to inter-annual and inter-decadal climate variability over a latitudinal gradient encompassing its northern marginal, discontinuous and continuous distribution zones. The assessment was carried out using analyses of a well-replicated network of annually resolved tree-growth increment data spanning several centuries, combined with meteorological data covering AD 1953–2010. Cedar is a long-lived and shade-tolerant evergreen tree species native to eastern North America, with a latitudinal distribution ranging from James Bay, Canada, to southern New York, Ohio and Michigan, USA (Little, 1971). It displays a very plastic tolerance to edaphic moisture conditions, occupying both poorly drained lowland sites and xeric rocky sites (Hofmeyer *et al*., 2009). Two hypotheses concerning the growth responses of cedar to climate from 1953 to 2010 were postulated and tested statistically. The hypotheses were formulated on the basis of widely accepted evidence that temperatures have been rising in North America over that time period (IPCC, 2013). The hypotheses are:

H1.1: The growth of cedar is significantly and positively correlated with variations in temperature. It increases over time in parallel with climate warming and this increase is greatest in the northern marginal zone.

H1.2: The levels of cedar growth response to climate variations are locally dependent on regional precipitation regimes, site quality and associated soil moisture conditions.

1.4 Materials and methods

1.4.1 Study area

The study area was located in the western regions of Québec (Abitibi-Témiscamingue, James Bay and Chibougamau), Canada. A latitudinal transect was established from 47.3 °N to 50.0 °N and divided into three zones based on cedar abundance: a continuous zone (CZ), where cedars are common; a discontinuous zone (DZ), that marks the northern edge of the continuous distribution and where cedars are less common in the forest matrix; and a marginal zone (MZ), where only a few isolated patches of cedars are found (Fig. 1.1). At the landscape scale, the relative abundance of cedars in the CZ, DZ and MZ was estimated to be 55%, 9% and 3%, respectively (Fig. 1.1b; Xu *et al.*, 2012; Beaudoin *et al.*, 2014). However, sampling was concentrated on dominant and pure cedar stands (on average 82% of the total basal area; see Appendix 1.1 in Supporting Information), to avoid inter-specific competition. A total of 27 cedar stands was sampled along this gradient, with nine stands (or sites) in each biogeographical zone. All cedar stands in the northern marginal distributional zone were found in forest swamps or along lake and river shores. Similar edaphic conditions were sampled in the CZ and DZ. Mean annual temperatures tend to decrease towards the north-east of the study area, while total annual precipitation decreases towards the north-west (Table 1.1). For that reason, the western and eastern parts of the MZ were distinguished as MWZ and MEZ, respectively.

1.4.2 Tree-ring data

During summer 2011, up to 30 dominant and co-dominant cedar trees were selected randomly within a radius of 50 m from the centre of each sampling site. Two cores per tree were collected at 1.3 m above ground level. The cores were sanded, with progressively finer sandpaper, up to a grade of 600. Annual rings of each core were cross-dated visually with skeleton plots and pointer-year identification (Cook & Kairiūkštis, 1990). Ring widths were measured with a Velmex measuring table (Velmex Inc., Bloomfield, NY, USA), with 10^{-3} mm precision under 4.5× magnification, or on a scanned image of the cores using the software COO-RECORDER (Cybis, Saltsjöbaden, Sweden), with 10^{-2} mm precision. Cross-dating was validated with the software COFECHA (Grissino-Mayer, 2001) for each site and zone, and further cross-validated with a published reference chronology from within our study area (Archambault & Bergeron, 1992). Mature cedars often have rotten piths and thus minimum ages were obtained. Our study did not include growth data from young (< 20 tree rings) and immature (20–70 tree rings) cedars because of the difficulties in recovering long-term growth changes in short time series. The average sample size was 27 trees site^{-1} (Table 1.1).

1.4.3 Low-frequency growth variations

The ring-width measurement series were normalized using power transformations and exponential detrending to eliminate noise caused by site and biologically related effects (e.g. competition, self-thinning and ageing). This procedure preserves the variance in low frequencies necessary for the study of long-term growth trajectories (Cook & Peters, 1997). Each individually transformed series was fitted with three growth trend models: linear (L), negative exponential (NE) and generalized negative exponential (GNE). The model retained for detrending was selected by comparing the R^2 of the candidate models. The one with the highest R^2 between L and NE was selected; GNE was selected if its R^2 was more than 5% higher than the one selected between L and NE. Fifty per cent of the ring-width series were fitted with a GNE model, 19% with NE and 31% with L. These calculations were conducted using SAS software (SAS Institute Inc., 2011). After each core was detrended, an average growth time series was computed for each tree. Finally, averaged tree growth index (TGI) time series were computed for each biogeographical zone (CZ, DZ, MWZ and MEZ) by 9999 bootstrapped resampling among the pooled tree samples of each zone, using R software (version 2.15.3, R Development Core Team, 2013). This procedure is robust against the presence of outliers and allowed us to calculate a 90% confidence interval (CI). These low-frequency cedar TGI chronologies were used for the study of low-frequency growth variations over the full chronology of each zone to test the hypothesis H1.1 (growth increase in the last decades).

1.4.4 High-frequency growth variations

To filter out medium- to low-frequency trends (long-term growth) from the ring-width measurements, a second procedure was used. The aim of this procedure was to maximize the high-frequency growth responses associated with year-to-year climatic variability. Each raw ring-width series was detrended using 60-year splines with a 50% frequency response (Cook & Kairiūkštis, 1990) using the R package DPLR (Bunn, 2008). Temporal autocorrelation was removed using first-order autoregressive modelling and a residual chronology was computed for each site using a bi-weight robust mean (Cook & Kairiūkštis, 1990). These site residual chronologies were used to evaluate the relationships between cedar growth and inter-annual climatic variability.

1.4.5 Dendroclimatic analysis

Monthly mean temperatures and total monthly precipitation were obtained for 1953–2010 at each of the 27 sampling sites using the BIOSIM 10.2 software (Régnière & Bolstad, 1994). Daily data were interpolated from the eight closest weather stations, adjusted for differences in latitude, longitude and elevation between the data sources and the site location, and averaged using a $1/d^2$ weight, where d is distance. Long-term linear trends in climatic series were linearly detrended using the time period 1953–2010 to obtain unbiased data for inter-annual climatic variations.

The relationship between climatic variability and annual growth of cedar was examined using correlation and principal component regression (PCR) analyses over the time period (Biondi & Waikul, 2004). The correlation coefficients were computed between a site residual chronology and the matrix of monthly climatic data, in order to represent the average relationship for the studied time period. PCR (also known as response function analysis) is a multiple regression technique that was used on the principal components of monthly climatic data to estimate the growth of cedar. Significance in both correlation and PCR analyses was tested using the bootstrapping technique: when the CI contains zero, the hypothesis of 'no relationship' cannot be rejected at the 95% level. The months under analysis were May of the year preceding ring formation to October of the current year of ring formation, to account for the processes of accumulation and reallocation of carbohydrate reserves from year to year (Fritts, 1976). Analyses were conducted using the R package BOOTRES (Zang & Biondi, 2009).

1.4.6 Influence of environmental conditions

The relationships between environmental conditions (e.g. site quality and associated moisture conditions) and the levels of cedar growth responses to climatic variation along the gradient were evaluated as follows. First, we selected the monthly climatic variables for which the correlation with growth residual chronologies was significant for at least 20% of sites ($n = 6$; set arbitrarily but allowed to vary in a sensitivity analysis) to focus on the main climatic drivers. Second, the correlation coefficients for these selected monthly climatic variables were used column-wise as inputs of a response matrix (Y), with the sites as rows. Third, environmental data with a significant effect on the response matrix Y were selected using a multivariate stepwise procedure and permutation tests (Blanchet *et al*., 2008; Appendix 1.2) using the R package VEGAN (Oksanen *et al*., 2013). Candidate environmental variables were mean diameter at breast height (d.b.h.) of the cored trees, total thickness of the organic layer, carbon to nitrogen ratio (C:N) in the upper 50 cm of the soil layer, and drainage (a discrete variable with two levels, hydric and mesic). We also included annual growing degree-days > 5 °C (GDD) and annual sum of precipitation from April to September (i.e. the active growing season) averaged over the period 1953–2010. The inclusion of these climatic averages was intended to disentangle the influence of specific climatic regimes on particular dendroclimatic signals (e.g. one can postulate that a correlation with drought is more probable in a warm and dry climatic regime). Finally, the effect of the environmental variables was detailed for each of the monthly correlation coefficients with a univariate multiple regression model, with each site being a replicate.

1.5 Results

1.5.1 Long-term growth and climate trajectories

The mean chronology lengths for MZ, DZ and CZ were, respectively, 280, 217 and 179 years (Fig. 1.2). The oldest tree was in MWZ, with a minimum of 422 tree rings. Low-frequency TGI chronologies shared common patterns of inter-annual to decadal variability and all the paired chronologies were significantly correlated (95%). Specifically, the MWZ and MEZ chronologies were significantly correlated [r = 0.52, 95% CI corrected for autocorrelation[4] in data (0.39; 0.61), n = 184 years]. The CZ and DZ chronologies were significantly correlated [r = 0.67, 95% CI (0.59; 0.75)]. MWZ and MEZ had lower but significant correlations with CZ chronology, respectively r = 0.48, 95% CI (0.39; 0.58) and r = 0.41, 95% CI (0.27; 0.54). DZ was the least correlated with MZ, with correlation values of r = 0.45, 95% CI (0.35; 0.54) with MWZ and r =0.35, 95% CI (0.21; 0.47) with MEZ.

The temporal trends in temperature in the meteorological time series revealed a spring (April–May) warming of 0.03 °C year^{-1} from 1953 to 2010 across the whole study area. Summer (June–August) temperatures also increased at a rate of 0.02 °C year^{-1}. Precipitation remained stable over this period. Contrary to the first hypothesis (H1.1), the recent warming did not result in a growth increase in MZ (Fig. 1.2). In fact a growth decline was observed, with an onset at *c*. 1980. This growth decrease was also observed in the raw ring width and basal area increment chronologies. That

---

[4] Computed with the software Pearson T (see calculation details in Mudelsee, 2003).

level of growth was similar to another phase of low growth observed at *c*. 1930–1950. In more southern areas, recent growth was not markedly different from past variations. Sensitivity analyses in which short tree-ring series were excluded from the computation of chronologies led to similar results and confirmed the robustness of the long-term growth trajectories (results not shown).

1.5.2 Growth–climate relationship

Inter-annual variations of growth in cedar from 1953 to 2010 were positively correlated with spring temperature (mostly May, but also March, April) across the whole study area (Fig. 1.3a). In contrast, growth was negatively correlated with warm summer (July and August) temperatures of the year preceding ring formation. This trend was significant for five DZ sites and for two CZ sites, but seemingly weakened towards northern sites (Fig. 1.3a). A negative correlation with June temperature of the current year of ring formation was also observed for most sites, except for MEZ sites. The temperature analyses thus suggested a complex response of cedar growth to monthly temperature: while high temperatures were favourable for cedars at the beginning of the growing season, they become a limiting factor during the summer in CZ, DZ and MWZ.

Radial growth was positively correlated with precipitation in June of the year preceding ring formation (Fig. 1.3b). This result was most significant in DZ. Radial growth was also positively correlated with precipitation in August of the current year in both CZ and DZ but not in MZ. In contrast, excesses of precipitation during October of the year preceding ring formation had negative correlations with growth in CZ. A negative correlation with precipitation was also observed in MZ during May of the current year. Similar results were obtained using other analytical methods, i.e. partial correlation analysis (Appendix 1.3). Therefore, while moisture was favourable for cedar during summer, too much of it from the autumn of the previous year to the beginning of ring formation limited growth in our study area.

1.5.3 Environmental conditions versus growth–climate relationships

Seven monthly climatic variables were used for this analysis (correlation coefficients significant for more than *n* = 6 sites): previous August and current May and June temperatures, and previous June, previous October, current June and current August precipitation (Fig. 1.3). According to the stepwise procedure, four environmental variables significantly explained ($P < 0.05$) the inter-site variability of these growth–climate correlation values: mean d.b.h., C:N in the upper 50 cm, annual GDD and seasonal precipitation (P). The same environmental variables were selected when the number of significant sites varied from *n* = 3 to *n* = 9 during the sensitivity analysis. Table 1.2 summarizes the effects of these environmental variables on the growth–climate relationships (correlation coefficients, *r*). The regression estimates and *P*-values associated with each environmental variable are represented in columns for the model:

$$r_i \sim \text{mean d.b.h.} + \text{C:N ratio} + \text{annual GDD}_{1953-2010} + \text{seasonal P}_{1953-2010} \quad \text{(Eq. 1.1)}$$

where r_i is the correlation coefficient of growth with one of the above-mentioned monthly climatic variables (column-wise from Fig. 1.3).

Sites where the hydrological regime was characterized by high seasonal precipitation (especially in the MEZ) had a less negative correlation with June temperature of the current year of ring formation. In sites with high mean d.b.h., growth was more negatively correlated with previous August temperature and more positively correlated with previous June and current August precipitation. Hence the hydrological regime and tree size both had an effect on the species’ response to summer thermal stress and moisture variability. Similarly, sites with a greater amount of annual GDD appeared to be slightly more sensitive to summer moisture or heat stress, with a more negative correlation with previous August temperature and a more positive correlation with August precipitation.

Regarding the influence of variables on early and late season responses, we found that the negative correlation with previous October precipitation was more pronounced in sites where annual GDD and seasonal precipitation were high (i.e. CZ). Additionally, the negative correlation with May precipitation was lower in sites with high C:N ratios. These sites also tended to have a stronger and positive correlation with May temperature. Hence there was an apparent constraint on growth as a result of water excess in the active soil layers early in the growing season, or indirectly during the autumn of the year previous to ring formation. This constraint was amplified in sites with high C:N ratios and high seasonal precipitation.

1.6 Discussion

This study investigated the effects of recent climate warming on the radial growth of cedar over a latitudinal gradient encompassing northern marginal, discontinuous and continuous distribution zones. Contrary to H_1, the recent climatic warming during the growth period was associated with a growth decrease in cedar in its northern MZ, whereas it remained stable in DZ and CZ. We will discuss a probable explanation for the growth declines that includes two different warming-induced processes affecting plant growth, the water availability constraints on photosynthesis and the higher metabolic cost of plant maintenance respiration. We will also discuss how soil hydrology and precipitation modulate plant sensitivity to climate, confirming H_2, and we consider the potential implications of our findings for characterizing the contraction or expansion of cedar populations in the context of a rapidly changing climate.

Although spring and summer temperatures rose in our study area, no growth acceleration was observed in association with a reduction in the cold constraints on growth (H_1). Instead, a growth decrease in MZ was observed after a peak around

1980. This deceleration of cedar stand growth rates during the last three decades is consistent with evidence of productivity declines in the same regions detected by remote sensing (Hicke *et al*., 2002; de Jong *et al*., 2012). These results suggest that cold is not as much of a limiting factor as previously expected at the northern margin of the species' range. This finding suggests that drought stress may limit growth despite the relatively wet environment in which cedar is growing. Indeed, another period of low growth observed in the first half of the 20th-century was synchronous with dry summers in MZ, as suggested by a fire history reconstruction (Le Goff *et al*., 2007). Moreover, a period of high growth observed at the beginning of the 19th century was synchronous with a wet period with warm springs and cool summers in the James Bay area (Wilson, 1988; Girardin *et al*., 2014). There is evidence for similar growth trends among other species found in the region. For example, the successive periods of high and low growth are synchronous with growth variations of a ring-width time series from black spruce around James Bay at latitudes of 51–53° N (Girardin *et al*., 2014).

The results of the dendroclimatic analysis allowed us to disentangle the impact of drought stress on cedar growth over our gradient and showed that temperature exerted an inconsistent effect on radial growth. Growth appeared to be positively influenced by May temperatures during the year of ring formation across the gradient. Warm springs in boreal forests are associated with earlier cambial reactivation and greater cell production, fostering growth through a longer growing period (Lupi *et al*., 2010). However, summer temperature had a negative effect on radial growth over the whole study area, indicated primarily by the negative correlation with July and August temperatures of the year preceding ring formation, especially in DZ. Elevated summer temperatures during the year preceding ring formation can cause temporary drought stress because of high evapotranspiration rates, which can lower the levels of stored carbohydrates, resulting in lower growth during the following year (Fritts, 1976; Tardif & Stevenson, 2001). The drought stress constraint on radial growth is suggested here by a positive correlation with summer precipitation (August of the current year as well as June of the previous year). The summer drought constraint on growth appeared to be greater for sites with larger trees (Table 1.2), probably reflecting the higher cost of water transportation through the stem when tree size increases (Mencuccini *et al*., 2005; Rozas *et al*., 2009).

Less clear is the physiological response behind a negative correlation with June temperature during the current year of ring formation. In our analyses, this negative effect of June temperature was not associated with a correlation to precipitation. One plausible explanation is the higher loss of carbohydrates because of maintenance respiration during warm episodes (Lavigne & Ryan, 1997). In many experiments and ecosystem models (Lavigne & Ryan, 1997; Girardin *et al*., 2014; Tang *et al*., 2014) maintenance respiration is expressed as a function of biomass and temperature and increases with the two variables. The thermal stress as a result of the elevated June temperatures that was observed for the majority of the sites could reflect this important plant growth process. However, the negative effect of June temperature was significantly lower for sites receiving more precipitation (Table 1.2), implying some compensation from the local precipitation regime for the higher metabolic costs in a warmer climate. Given that maintenance respiration is antagonistic to net primary production (Tang *et al*., 2014), maintenance respiration could be relatively less limiting for growth when precipitation allows a greater gross primary production.

We observed a negative effect of early season (May) precipitation on growth, in particular for the five sites with a negative mean annual temperature. A negative effect of late season (previous October) precipitation was also observed in CZ. These observations show that water exerts a bimodal effect on cedar, with both an excess and a lack of water constraining growth, which could be related to the edaphic conditions of the sampling sites. Negative correlations with previous October and May precipitation have also been reported in the study area for *Picea mariana* (Mill.)

BSP, another boreal species growing in similar edaphic conditions (Drobyshev *et al*., 2010). An increase in spring rain, synchronous with snow melting, could cause an elevation of the water table in swamps or a flooding episode in lakes and rivers, resulting in tree root asphyxia and growth delay. The negative effect of previous October precipitation may be related to growth limitation at the beginning of the next growing season, as a result of an overwintering effect: the wet conditions of the soils carry over to the next spring (Girardin & Wotton, 2009). This hypothesis is supported by the fact that the negative effect of previous October precipitation is significantly worse for sites receiving more precipitation (Table 1.2). The link between growth and soil hydrology is further supported by the significant effect of C:N ratio on correlations coefficients with both May temperature and precipitation (Table 1.2). Sites with a high C:N ratio could have their soils saturated with water for longer periods of time, reducing the mineralization of organic matter, thus increasing the risk of root asphyxia and limiting nitrification. Another limitation of wet sites is that the spring soil warm-up is delayed, which consequently slows initiation of growth (Fraser, 1956). This could result in a delay of soil frost thawing, which has been shown to be a growth limiting factor for *Pinus sylvestris* L. (Repo *et al*., 2005) and *Picea abies* L. Karst (Jarvis & Linder, 2000). The paradoxical shift from a water excess constraint during the spring to a drought constraint in the summer may be attributed to the shallow root system that cedar develops in hydric edaphic conditions (Musselman *et al*., 1975; Hofmeyer *et al*., 2009). During the summer lowering of the water table, the upper layer of organic soils becomes dry and the cedar's shallow roots cannot supply water. Hence, cedar growth is dependent on the seasonality of precipitation variability and on local soil hydrological conditions.

Our study is the first attempt at assessing spatial variations in the dendroclimatic signal of cedar species over a broad ecological gradient, and is thus complementary to previous cedar dendroclimatic studies. The growth–climate relationships described here for cedar populations at their northern margin in Québec are consistent with those reported by Tardif & Stevenson (2001) for the north-western distribution limit of the species in Manitoba. The Manitoba sampled cedars grew in a warmer and drier climate than those sampled in the MZ of our study (on average *c.* 510 mm $year^{-1}$ versus 909 mm $year^{-1}$; Table 1.1). The marginal population in Manitoba showed larger drought stress signals, with a negative correlation with previous June and August temperatures and a positive correlation with June and July precipitation. No negative effect of spring precipitation was detected. Two other dendroclimatic studies of cedar have taken place in the centre of the DZ of this study. Archambault & Bergeron (1992) reported a stronger summer drought stress signal with a significant positive correlation with June precipitation that we did not observe, which can be explained by the xeric rocky situation of their sampling sites. Tardif & Bergeron (1997) sampled cedars on mesic lakeshores that depicted very similar dendroclimatic signals to those reported here for sites with similar edaphic conditions (D3 and D5).

The anticipated impacts of global change on climate at the northern margins of cedar populations are now well documented and indicate significant increases in spring temperature and decreases in summer moisture availability (e.g. Bergeron *et al.*, 2010; Price *et al.*, 2013). The results of our *in situ* study suggest that these future changes will not cause growth enhancement at cedar's northern margins, as previously expected, because of probable increased drought constraints. Our results tend to support Paul *et al.*'s (2014) conclusion that cedar's northern limit in Québec is not directly linked to cold but rather to disturbance regime. Furthermore, our conclusion is counterintuitive to niche-based models that project a northward shift of cedar bioclimatic envelopes (McKenney *et al.*, 2007) without considering changes in disturbance regimes or in climatic seasonality. This is expected to cause a contraction of the rear edge of the species. Our conclusions seem to indicate that, in the case of a local extinction of northern marginal populations, one could also expect a contraction of the cedar distributional area at the northern margin. We recognize that our study was limited to the analyses of mature trees and an investigation of the dynamics of seedlings and saplings in marginal populations is necessary to evaluate the cedar’s ability to face climate change, as sexual reproduction is a determinant factor for both migration and adaptation of plant populations (Davis & Shaw, 2001). Nevertheless, our results suggest that northern marginal cedar populations will probably face hydric stress selection pressure in the future, although the impact of future global warming on cedar will be greatly modulated by the geographical variations in precipitation regime. Assessing the marginal populations’ ability to cope with this hydric stress selection pressure will be a key factor in determining the outcome for cedar distribution but will require additional research on the range of phenotypic plasticity and on cedar capacity for genetic adaptation.

1.7 Acknowledgements

We would like to thank Mélanie Desrochers, Cécile Leroy, Daniel Lesieur, XiaoJing Guo, Marc Mazerolle and Aurélie Terrier for their valuable help. We are grateful to Véronique Paul for insights on cedar ecology, Huaitong Xu for his comments on this paper, and Danielle Charron, Jam Roy, Maxime Tremblay and Albanie Leduc for their help in the field and in the laboratory. This study was conducted with the financial support of the Natural Sciences and Engineering Research Council of Canada (NSERC) through its CREATE programme in Forest Modelling Complexity and the French programme Paris Nouveau Monde of the heSam consortium (PhD grants to J.H.). This research was also funded by a NSERC strategic grant (STPGP336871) to Francine Tremblay. The research was carried out within the framework of the International Associated Laboratory (LIA France-Canada) CNRS-UM2-EPHE-UQAT-UQAM-UQAC entitled MONTABOR. We are grateful to Stephen Cavers and several anonymous referees for constructive critiques of the manuscript.

1.8 References

Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T. & Curtis-McLane, S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.

Archambault, S. & Bergeron, Y. (1992) An 802-year tree-ring chronology from the Québec boreal forest. *Canadian Journal of Forest Research*, **22**, 674–682.

Babst, F., Poulter, B., Trouet, V., Tan, K., Neuwirth, B., Wilson, R., Carrer, M., Grabner, M., Tegel, W., Levanic, T., Panayotov, M., Urbinati, C., Bouriaud, O., Ciais, P. & Frank, D. (2013) Site- and species-specific responses of forest growth to climate across the European continent. *Global Ecology and Biogeography*, **22**, 706–717.

Beaudoin, A., Bernier, P.Y., Guindon, L., Villemaire, P., Guo, X.J., Stinson, G., Bergeron, T., Magnussen, S. & Hall, R.J. (2014) Mapping attributes of Canada's forests at moderate resolution through *k*NN and MODIS imagery. *Canadian Journal of Forest Research*, **44**, 521–532.

Bergeron, Y., Cyr, D., Girardin, M.P. & Carcaillet, C. (2010) Will climate change drive 21st century burn rates in Canadian boreal forest outside of its natural variability: collating global climate model experiments with sedimentary charcoal data. *International Journal of Wildland Fire*, **19**, 1127–1139.

Biondi, F. & Waikul, K. (2004) DENDROCLIM2002: a C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers and Geosciences*, **30**, 303–311.

Blanchet, F.G., Legendre, P. & Borcard, D. (2008) Forward selection of explanatory variables. *Ecology*, **89**, 2623–2632.

Boisvenue, C. & Running, S.W. (2006) Impacts of climate change on natural forest productivity: evidence since the middle of the 20th century. *Global Change Biology*, **12**, 862–882.

Bunn, A.G. (2008) A dendrochronology program library in R (dplR). *Dendrochronologia*, **26**, 115–124.

Cook, E.R. & Kairiūkštis, L. (1990) *Methods of dendrochronology: applications in the environmental sciences*. Kluwer Academic Publishers, Dordrecht.

Cook, E.R. & Peters, K. (1997) Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene*, **7**, 361–370.

Davis, M.B. & Shaw, R.G. (2001) Range shifts and adaptive responses to quaternary climate change. *Science*, **292**, 673–679.

Drobyshev, I., Simard, M., Bergeron, Y. & Hofgaard, A. (2010) Does soil organic layer thickness affect climate–growth relationships in the black spruce boreal ecosystem? *Ecosystems*, **13**, 556–574.

Esper, J. & Schweingruber, F.H. (2004) Large-scale treeline changes recorded in Siberia. *Geophysical Research Letters*, **31**, L06202.

Fisichelli, N.A., Frelich, L.E. & Reich, P.B. (2014) Temperate tree expansion into adjacent boreal forest patches facilitated by warmer temperatures. *Ecography*, **37**, 152–161.

Fraser, D.A. (1956) Ecological studies of forest trees at Chalk River, Ontario, Canada. II. Ecological conditions and radial increment. *Ecology*, **37**, 777–789.

Fritts, H.C. (1976) *Tree rings and climate.* London, New York, San Francisco, Academic Press.

Girardin, M.P. & Wotton, B.M. (2009) Summer moisture and wildfire risks across Canada. *Journal of Applied Meteorology and Climatology*, **48**, 517–533.

Girardin, M.P., Guo, X.J., Bernier, P.Y., Raulier, F. & Gauthier, S. (2012) Changes in growth of pristine boreal North American forests from 1950 to 2005 driven by landscape demographics and species traits. *Biogeosciences Discussion*, **9**, 1021–1053.

Girardin, M.P., Guo, X.J., De Jong, R., Kinnard, C., Bernier, P. & Raulier, F. (2014) Unusual forest growth decline in boreal North America covaries with the retreat of Arctic sea ice. *Global Change Biology*, **20**, 851–866.

Grace, J., Berninger, F. & Nagy, L. (2002) Impacts of climate change on the tree line. *Annals of Botany*, **90**, 537–544.

Grissino-Mayer, H.D. (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research*, **57**, 205–221.

Hicke, J.A., Asner, G.P., Randerson, J.T., Tucker, C., Los, S., Birdsey, R., Jenkins, J.C., Field, C. & Holland, E. (2002) Satellite-derived increases in net primary productivity across North America, 1982–1998. *Geophysical Research Letters*, **29**, 69–1.

Hofmeyer, P.V., Kenefic, L.S. & Seymour, R.S. (2009) Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: a synthesis of knowledge. *Northern Journal of Applied Forestry*, **26**, 21–27.

Innes, J.L. (1991) High-altitude and high-latitude tree growth in relation to past, present and future global climate change. *The Holocene*, **1**, 168–173.

IPCC (2013) *Climate Change 2013: the physical science basis. Working Group I Contribution to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, UK, and New York.

Jarvis, P. & Linder, S. (2000) Botany: constraints to growth of boreal forests. *Nature*, **405**, 904–905.

de Jong, R., Verbesselt, J., Schaepman, M.E. & de Bruin, S. (2012) Trend changes in global greening and browning: contribution of short-term trends to longer-term change. *Global Change Biology*, **18**, 642–655.

Jump, A.S., Mátyás, C. & Peñuelas, J. (2009) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, **24**, 694–701.

Kramer, K., Leinonen, I. & Loustau, D. (2000) The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *International Journal of Biometeorology*, **44**, 67–75.

Lafontaine, G. & Payette, S. (2010) The origin and dynamics of subalpine white spruce and balsam fir stands in boreal Eastern North America. *Ecosystems*, **13**, 932–947.

Lavigne, M.B. & Ryan, M.G. (1997) Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern boreas sites. *Tree Physiology*, **17**, 543–551.

Le Goff, H., Flannigan, M.D., Bergeron, Y. & Girardin, M.P. (2007) Historical fire regime shifts related to climate teleconnections in the Waswanipi area, central Quebec, Canada. *International Journal of Wildland Fire*, **16**, 607–618.

Little, E.L.J. (1971) *Atlas of United States trees*, Vol. 1, *Conifers and important hardwoods*. Miscellaneous publication 1146. Forest Service, USDA, Washington, DC.

Lloyd, A.H., Bunn, A.G. & Berner, L. (2011) A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Global Change Biology*, **17**, 1935–1945.

Lupi, C., Morin, H., Deslauriers, A. & Rossi, S. (2010) Xylem phenology and wood production: resolving the chicken-or-egg dilemma. *Plant, Cell and Environment*, **33**, 1721–1730.

McKenney, D.W., Pedlar, J.H., Lawrence, K., Campbell, K. & Hutchinson, M.F. (2007) Potential impacts of climate change on the distribution of North American trees. *BioScience,* **57**, 939–948.

Mencuccini, M., Martínez-Vilalta, J., Vanderklein, D., Hamid, H.A., Korakaki, E., Lee, S. & Michiels, B. (2005) Size-mediated ageing reduces vigour in trees. *Ecology Letters*, **8**, 1183–1190.

Musselman, R.C., Lester, D.T. & Adams, M.S. (1975) Localized ecotypes of *Thuja occidentalis* L. in Wisconsin. *Ecology*, **56**, 647–655.

Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) *vegan: community ecology package. R package version 2.0–10*. Available at: http://CRAN.R-project.org/package=vegan.

Paul, V., Bergeron, Y. & Tremblay, F. (2014) Does climate control the northern range limit of eastern white cedar (*Thuja occidentalis* L.)? *Plant Ecology*, **215**, 181–194.

Payette, S. (2007) Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. *Ecology*, **88**, 770–780.

Pearson, R.G. & Dawson, T.P. (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? *Global Ecology and Biogeography*, **12**, 361–371.

Price, D.T., Alfaro, R.I., Brown, K.J., Flannigan, M.D., Fleming, R.A., Hogg, E.H., Girardin, M.P., Lakusta, T., Johnston, M., McKenney, D.W., Pedlar, J.H., Stratton, T., Sturrock, R.N., Thompson, I.D., Trofymow, J.A. & Venier, L.A. (2013) Anticipating the consequences of climate change for Canada's boreal forest ecosystems. *Environmental Reviews*, **21**, 322–365.

R Development Core Team (2007) *R: a language and environment for statistical computing.* R Foundation for Statistical Computing, Vienna.

Régnière, J. & Bolstad, P. (1994) Statistical simulation of daily air temperature patterns in eastern North America to forecast seasonal events in insect pest management. *Environmental Entomology*, **23**, 1368–1380.

Rehfeldt, G.E., Ying, C.C., Spittlehouse, D.L. & Hamilton, D.A., Jr (1999) Genetic responses to climate in *Pinus contorta*: niche breadth, climate change, and reforestation. *Ecological Monographs*, **69**, 375–407.

Reich, P.B. & Oleksyn, J. (2008) Climate warming will reduce growth and survival of Scots pine except in the far north. *Ecology Letters*, **11**, 588–597.

Repo, T., Kalliokoski, T., Domisch, T., Lehto, T., Mannerkoski, H., Sutinen, S. & Finér, L. (2005) Effects of timing of soil frost thawing on Scots pine. *Tree Physiology*, **25**, 1053–1062.

Richardson, A.D., Anderson, R.S., Arain, M.A. *et al*. (2012) Terrestrial biosphere models need better representation of vegetation phenology: results from the North American Carbon Program Site Synthesis. *Global Change Biology*, **18**, 566–584.

Rozas, V., DeSoto, L. & Olano, J.M. (2009) Sex-specific, age-dependent sensitivity of tree-ring growth to climate in the dioecious tree *Juniperus thurifera*. *New Phytologist*, **182**, 687–697.

SAS Institute Inc. (2011) *SAS/STAT 9.3 user's guide.* SAS Institute Inc., Cary, NC.

Sirois, L. (1997) Distribution and dynamics of balsam fir (*Abies balsamea* L. Mill.) at its northern limit in the James Bay area. *Ecoscience*, **4**, 340–352.

Soja, A.J., Tchebakova, N.M., French, N.H.F., Flannigan, M.D., Shugart, H.H., Stocks, B.J., Sukhinin, A.I., Parfenova, E.I., Chapin, F.S. & Stackhouse, P.W. (2007) Climate-induced boreal forest change: predictions versus current observations. *Global and Planetary Change*, **56**, 274–296.

Tang, J., Luyssaert, S., Richardson, A.D., Kutsch, W. & Janssens, I.A. (2014) Steeper declines in forest photosynthesis than respiration explain age-driven decreases in forest growth. *Proceedings of the National Academy of Sciences USA*, **111**, 8856–8860.

Tardif, J. & Bergeron, Y. (1997) Comparative dendroclimatological analysis of two black ash and two white cedar populations from contrasting sites in the Lake

Duparquet region, northwestern Quebec. *Canadian Journal of Forest Research,* **27**, 108–116.

Tardif, J. & Stevenson, D. (2001) Radial growth–climate association of *Thuja occidentalis* L. at the northwestern limit of its distribution, Manitoba, Canada. *Dendrochronologia*, **19**, 179–187.

Wilson, C.V. (1988) *The summer season along the east coast of Hudson Bay during the nineteenth century. III. Summer thermal and wetness indices B: the Indices, 1800 to 1900. Report 88–3.* Atmospheric Environment Service, Canadian Climate Centre, Downsview, ON.

Woodward, F.I. (1987) *Climate and plant distribution.* Cambridge University Press, Melbourne.

Xu, H., Tremblay, F., Bergeron, Y., Paul, V. & Chen, C. (2012) Genetic consequences of fragmentation in 'arbor vitae', eastern white cedar (*Thuja occidentalis* L.), toward the northern limit of its distribution range. *Ecology and Evolution*, **2**, 2506–2520.

Zang, C. & Biondi, F. (2009) *bootRes: bootstrapped response and correlation functions. R package version 0.2*. Available at: http://cran. r-project. org/web/packages/bootRes.

1.9 Tables

Table 1.1 Location of *Thuja occidentalis* study sites in western Québec, Canada, showing the main climatic, edaphic and dendrochronological features.

Sample sites are ordered by increasing annual growing degree-days > 5 °C (GDD). Spatial coordinates are presented in decimal degrees (dd). Annual climatic data were averaged over the period ad 1953–2010. C:N, carbon to nitrogen ratio; d.b.h., diameter at breast height; EPS, expressed population signal (a statistic representing the strength of the common signal in all the trees of a sampling site); MAT, mean annual temperature; P, precipitation; OLT, organic layer thickness; Topo., topography (LS, lake shore; RS, river shore; Sw, swamp; Sl, mesic slope).

Distribution zone	Site	Latitude (dd)	Longitude (dd)	MAT °C	Mean annual GDD	Mean annual P (mm)	P Apr-Sept	Topo[1]	OLT (cm)	C:N	Mean DBH (cm)	Starting year	Stand min. age	*n* trees	EPS
Marginal East (Chibougamau) MEZ	H2	49.876	-74.393	-0.49	1 128	965	567	Sw	50	45.2	28.7	1715	295	29	0.96
	H4	49.953	-74.229	-0.42	1 147	959	563	Sw	350	41.2	23.5	1786	224	30	0.94
	H3	49.909	-74.322	-0.27	1 174	962	565	LS	100	32.5	27.0	1714	296	30	0.97
	H5	49.642	-74.334	0.02	1 207	966	566	Sw	100	26.6	24.8	1703	307	12	0.57
Marginal West (James Bay) MWZ	M5	49.856	-78.645	-0.08	1 214	855	523	RS	3	26.1	32.8	1735	275	17	0.83
	M4	49.883	-78.646	-0.02	1 216	855	523	LS	200	34.0	26.2	1718	292	28	0.92
	M3	49.858	-78.606	0.03	1 220	857	524	LS	23	39.3	29.9	1586	424	31	0.92
	M2	49.423	-79.211	0.20	1 245	866	528	Sw	350	28.3	24.3	1792	218	9	0.81
	M1	48.928	-78.886	0.76	1 310	886	541	LS	150	34.2	31.8	1825	185	11	0.8
Discontinuous (Abitibi) DZ	D1	48.540	-78.642	0.90	1 322	944	563	Sw	100	27.8	26.8	1788	222	29	0.94
	D5	48.500	-79.411	1.32	1 383	884	524	LS	7	17.2	31.5	1832	178	30	0.97
	D3	48.500	-79.422	1.33	1 385	884	524	LS	6	17.2	30.3	1818	192	28	0.96
	D6	48.432	-79.402	1.40	1 394	878	520	Sw	45	23.5	24.7	1764	246	29	0.96
	D8	48.431	-79.384	1.41	1 397	880	521	Sw	90	31.1	29.6	1676	334	30	0.96
	D2	48.470	-79.452	1.42	1 401	879	520	Sw	50	31.2	27.7	1794	216	30	0.95
	D7	48.263	-78.575	1.50	1 401	880	518	Sw	350	27.6	30.3	1814	196	30	0.97
	D4	48.480	-79.437	1.48	1 412	882	521	Sl	13	17.3	27.1	1834	176	23	0.96
	D9	48.201	-79.419	1.75	1 448	856	502	Sl	35	20.1	36.4	1819	191	31	0.97
Continuous (Temiscamingue) CZ	C8	47.419	-78.678	2.09	1 461	974	552	Sw	350	31.1	26.4	1852	158	29	0.95
	C1	47.429	-78.678	2.12	1 464	969	550	Sl	12	20.7	30.6	1829	181	29	0.95
	C2	47.417	-78.682	2.26	1 482	960	545	LS	29	25.8	29.0	1808	202	30	0.93
	C3	47.396	-78.731	2.27	1 483	965	547	Sl	10	16.6	33.1	1866	144	29	0.92
	C9	47.416	-78.712	2.38	1 498	947	539	Sw	350	32.8	30.3	1804	206	29	0.95
	C7	47.454	-78.587	2.46	1 508	922	530	Sw	300	31.3	24.6	1834	176	30	0.93
	C6	47.311	-78.515	2.48	1 510	952	541	Sw	350	44.0	26.3	1794	216	30	0.96
	C4	47.317	-78.954	2.72	1 546	908	520	Sw	50	37.5	27.6	1834	176	30	0.96
	C5	47.345	-79.393	3.14	1 626	804	470	Sw	350	30.4	22.2	1864	146	30	0.98

Table 1.2 Effect of environmental variables on the main *Thuja occidentalis* growth–climate correlation coefficients for monthly temperature (T) and precipitation (P) at sites in western Québec, Canada.

Slopes and P-values were computed for monthly correlation coefficients against each environmental variable using Eq. 1.1. Slopes with a $P < 0.10$ value are shown in bold. Months in capital letters represent the current year of ring formation, months in lower case represent climate conditions during the year preceding ring formation. The adjusted R^2 is indicated in the last row, representing the percentage of inter-site variability explained by the model for each dependent variable. The significance level of the explanatory variables is coded as follow: “ *** ” for a $P < 0.001$, “ ** ”for a $P < 0.01$, “ * ” for a $P < 0.05$ and “.” for a $P < 0.1$.

	T aug	T MAY	T JUN	P jun	P oct	P MAY	P AUG
Annual GDD	**–0.04** $P = 0.07$	0.01 $P = 0.759$	0.03 $P = 0.368$	0 $P = 0.907$	**–0.11** $P = 0$***	0 $P = 0.967$	**0.05** $P = 0.097$
P Apr–Sept	0.02 $P = 0.278$	0.02 $P = 0.265$	**0.09** $P = 0.004$**	–0.03 $P = 0.143$	**–0.04** $P = 0.026$*	**–0.05** $P = 0.079$	–0.02 $P = 0.446$
Mean d.b.h.	**–0.06** $P = 0.004$**	0.02 $P = 0.295$	–0.04 $P = 0.149$	**0.03** $P = 0.091$	–0.02 $P = 0.256$	–0.02 $P = 0.488$	**0.06** $P = 0.026$*
C:N	**0.04** $P = 0.029$*	**0.06** $P = 0.008$**	0.04 $P = 0.12$	–0.02 $P = 0.285$	–0.01 $P = 0.364$	**–0.08** $P = 0.008$**	–0.04 $P = 0.132$
Adjusted R^2	0.599	0.243	0.408	0.236	0.621	0.348	0.435

C:N, carbon to nitrogen ratio; d.b.h., diameter at breast height; P, precipitation.

$$r_i \sim \text{mean d.b.h.} + C\text{:N ratio} + \text{annual GDD}_{1953-2010} + \text{seasonal P}_{1953-2010} \text{(Eq. 1.1)}$$

1.10 Figures

Figure 1.1 Location of *Thuja occidentalis'* sampling sites and distribution area

(a) Location of *Thuja occidentalis* sample sites in western Québec, Canada (black squares). The base map represents the *T. occidentalis* biomass in tonnes ha^{-1} (Beaudoin *et al.*, 2014). Sampling was stratified between the continuous zone of distribution (CZ), the discontinuous zone (DZ) and the marginal zone (MZ). In some analyses, the western and eastern parts of MZ were distinguished, as MWZ and MEZ, respectively. (b) The study area (black box) in the northern part of the species' range (hatched area; Little, 1971). Projection: North American Datum (1983) Québec Lambert. Author: Center for Forest Research (2014).

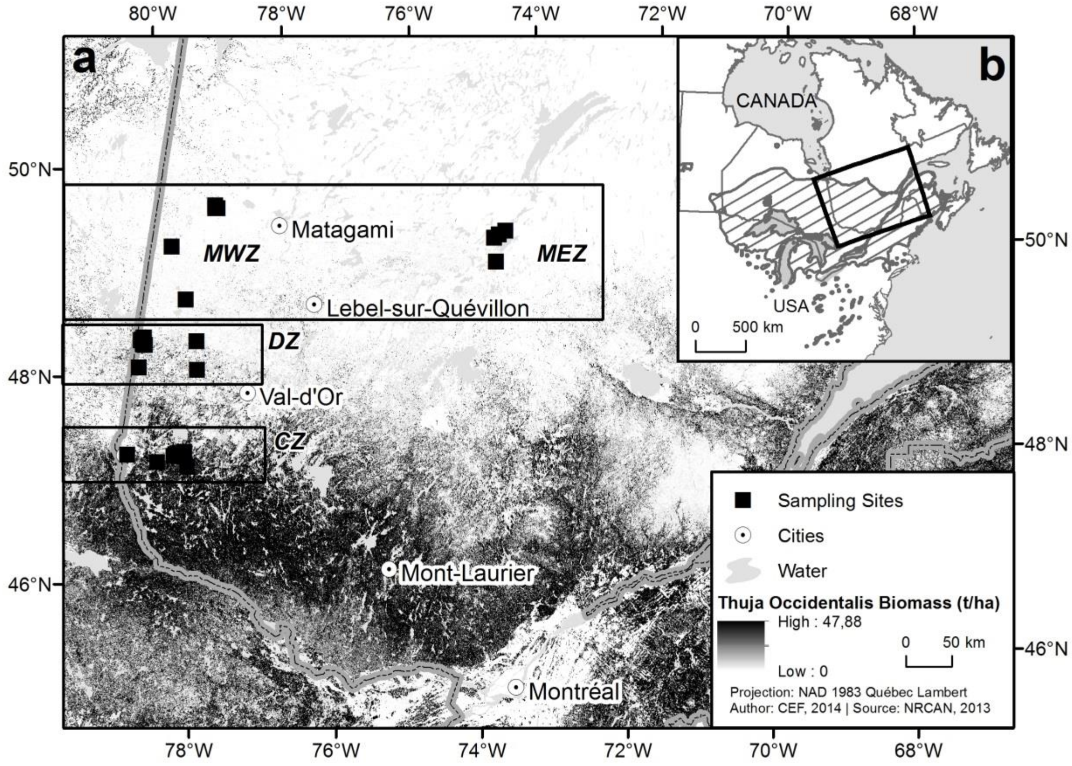


Figure 1.2 Low-frequency growth variations for *Thuja occidentalis* from sites in western Québec, Canada.

An annual *T. occidentalis* tree growth index (TGI) chronology was compiled for each distributional zones (CZ, continuous zone; DZ, discontinuous zone; MWZ, marginal west zone; MEZ, marginal east zone) from the mean of all single tree detrended tree-ring width measurement series (blue line). The grey area depicts the 90% confidence interval (CI) for the mean of sampled trees during a given year; non-overlapping CI between two years suggests a significant difference ($P < 0.05$) in mean TGI and vice versa. A 32-year second-order spline smoothing of the TGI data is shown by the red line. The black dashed lines represent the sample depth, corresponding to the tree numbers.

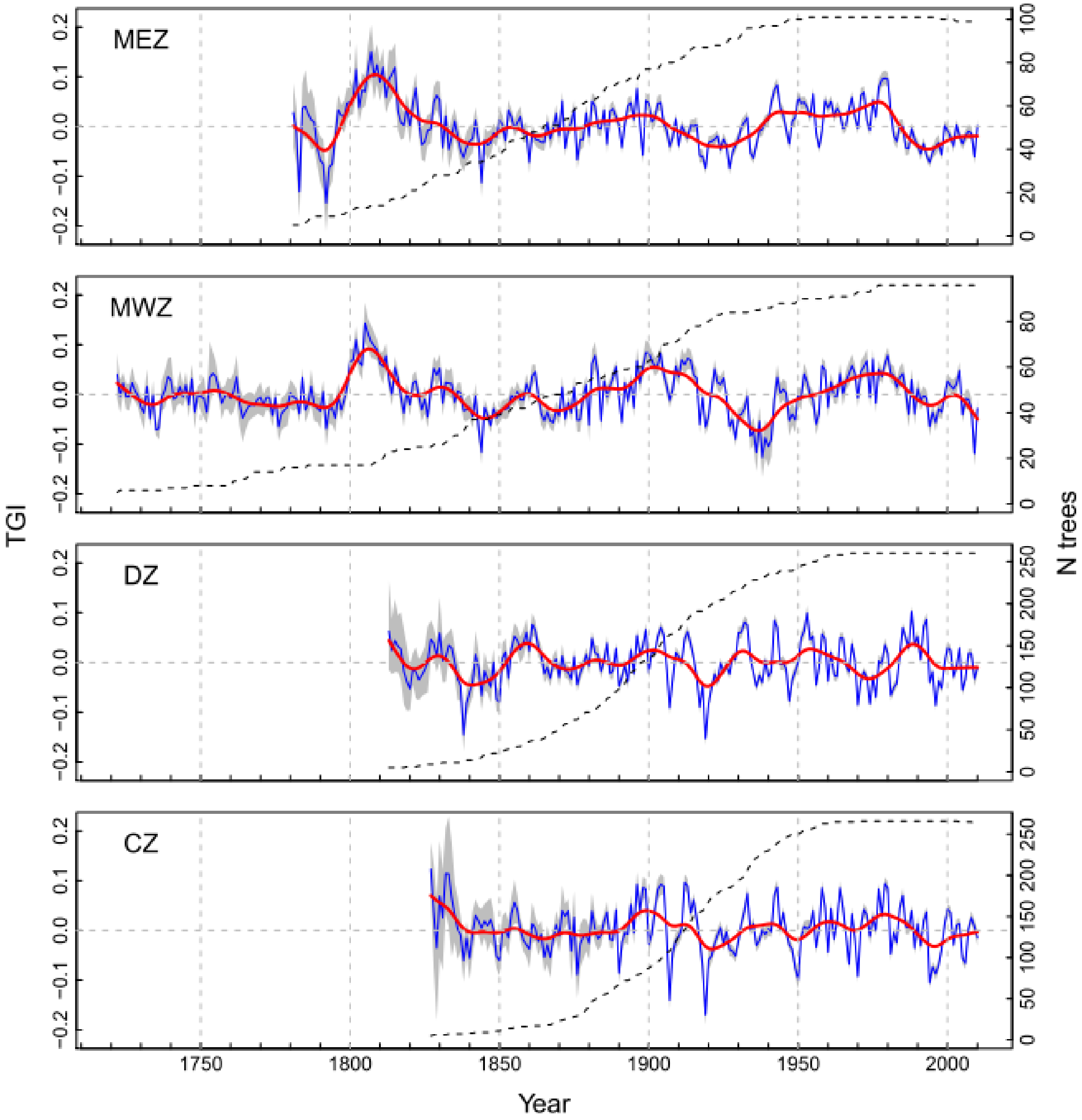
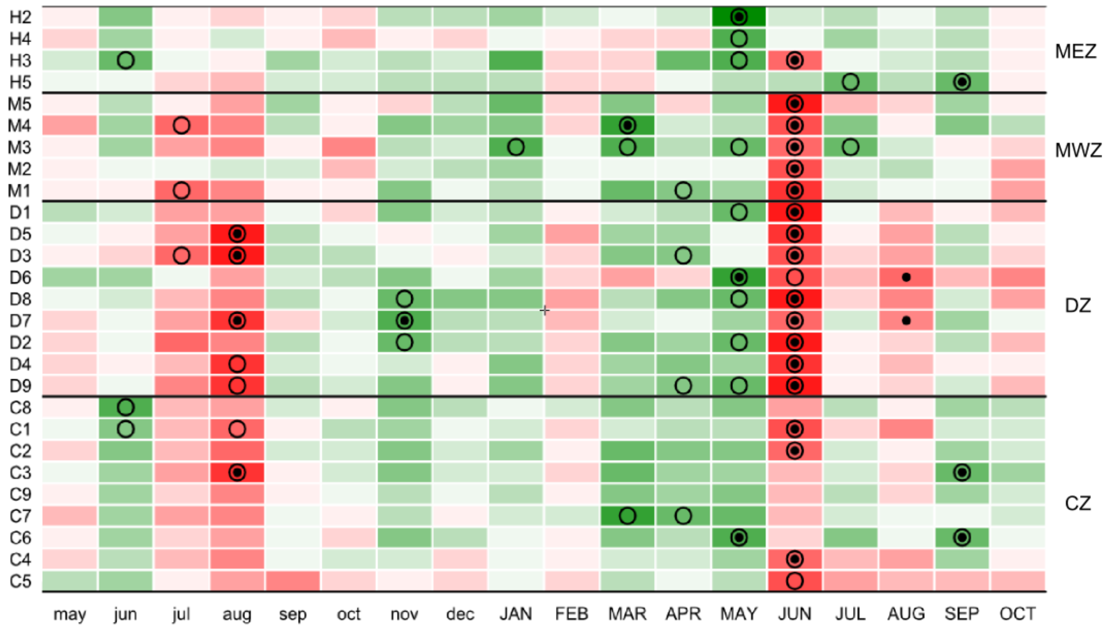

MEZ
MWZ
DZ
CZ
TGI
N trees
Year
−0.2
−0.1
0.0
0.1
0.2
0
20
40
60
80
100
50
100
150
200
250
1750
1800
1850
1900
1950
2000

Figure 1.3 Bootstrapped correlation coefficients computed between *Thuja occidentalis* residual chronology and the detrended monthly temperature and precipitation.

Bootstrapped correlation coefficients computed between *Thuja occidentalis* residual chronology and the detrended monthly mean temperature (a) and the monthly total precipitation (b) for sites from western Québec, Canada (see Table 1.1 for site codes). Months in capital letters represent the current year of ring formation, months in lower case represent climate variables during the year preceding ring formation. Significant correlations are represented by dots for the bootstrapped response function method and by circles for the bootstrapped correlation function. Sites are sorted by increasing number of mean annual growing degree-days > 5 °C over the period AD 1953–2010. Horizontal black lines indicate the separation between the distributional zones (CZ, continuous zone; DZ, discontinuous zone; MWZ, marginal west zone; MEZ, marginal east zone).

(a) Correlations of radial growth with mean temperature



(b) Correlations of radial growth with monthly total precipitation

1.11 Supporting Information

Appendix 1.1 Tree species composition of the sampling sites.

Appendix 1.2 Method for selecting environmental variables.

Appendix 1.3 Partial correlation for May temperature and precipitation.

Appendix 1.1 Tree species composition (as a percentage of the total basal area) and total basal area of the sampling sites. Data were obtained from 400-m² sampling plots at each site, superimposed with our dendrochronological sampling sites. Sites are ordered by increasing annual growing degree-days above 5 °Celsius. Horizontal black lines indicate the separation between the distributional zones (CZ, continuous zone; DZ, discontinuous zone; MWZ, marginal west zone; MEZ, marginal east zone).

Site	Yellow birch (%)[1]	White birch (%)[2]	White spruce (%)[3]	Black spruce (%)[4]	American larch (%)[5]	Balsam fir (%)[6]	Willow (%)[7]	Eastern white cedar (%)[8]	Total basal area (m² ha^{-1})	Mean % cedar per zone
H2				10		1		89	39.3	
H4				10				90	35.7	MEZ
H3		1	8	6		3		82	77.2	88
H5				8		3		89	33.3	
M5		3	30	5		11		51	116.1	
M4			3	2		17		78	53.4	MWZ
M3			1	16		20		63	95.7	66
M2				18	21	2		60	15.5	
M1		1	2	14		5		78	67.7	
D1				13		0	1	86	61.8	
D5		7	10			3		81	69.2	
D3			9					91	36.2	
D6		1	10		4			84	44.2	DZ
D8				5		2	2	91	56.1	85
D7				2	6			92	58.8	
D2				6		2	1	90	50.8	
D4		21	6	6		2		64	49.2	
D9			8			6		86	102.0	
C8		2		10	9	2		77	42.8	
C1		7	8					85	45.3	
C2		3	2	2		3		91	76.8	
C3	36		1			2		62	59.5	CZ
C9				1	1			97	32.3	86
C7				5				95	62.8	
C6				1				99	26.0	
C4		1				5		94	67.0	
C5				23		6		70	48.5	

(1) *Betula alleghaniensis* Britton; (2) *Betula papyrifera* Marsh.; (3) *Picea glauca* (Moench) Voss; (4) *Picea mariana* (Mill.) BSP; (5) *Larix laricina* (Du Roi) Koch; (6) *Abies balsamea* (Linné) Miller; (7) *Salix* pp.; (8) *Thuja occidentalis* Linné.

Appendix 1.2 Method and output of the redundancy analysis (rda) stepwise procedure used to select environmental variables affecting inter-site variability in the growth–climate relationships. Environmental variables affecting the dendroclimatic responses of cedar along its distributional gradient were evaluated using a multivariate stepwise procedure. The monthly bootstrapped correlation coefficients derived from the dendroclimatic analysis were used column-wise as inputs of a response matrix (Y), with the sites as rows. All the columns of Y were centred. The environmental data that had a significant effect on the response matrix Y were selected using the 'ordistep' function in the R package VEGAN (Oksanen *et al.*, 2013[5]). *P*-values were calculated with 1000 permutation tests. Candidate environmental variables were mean diameter at breast height (d.b.h.) of the cored trees, total thickness of the organic layer, carbon to nitrogen (C:N) ratio in the upper 50 cm of the soil layer and drainage (a discrete variable with two levels, hydric and mesic). We also included annual growing degree-days > 5 °C (GDD) and annual sum of precipitation from April to September (i.e. during the active vegetation stage) averaged over the period AD 1953–2010. The climatological averages were included in order to disentangle the influence of specific climatic regimes on particular dendroclimatic signals (e.g. one can postulate that a correlation to drought is more probable in a warm and dry climatic regime). Discrete variables were transformed into dummy variables and all the environmental variables were centred and scaled. The model including all the variables was significant, which is a prerequisite to performing forward selection of variables (Blanchet *et al.*, 2008[6]). The low variance inflation factor (VIF) of the model ensured that collinearity did not affect the robustness of further analysis (VIF < 1.4).

---

[5] Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, B., Simpson, G.L., Solymos, P., Stevens, M.H.H. & Wagner, H. (2013) *vegan: community ecology package. R package version 2.0–10*. Available at: http://CRAN.R-project.org/package=vegan.

[6] Blanchet, F.G., Legendre, P. & Borcard, D. (2008) Forward selection of explanatory variables. Ecology, 89, 2623–2632.

```
> mod0 <- rda(Y ~ 1, X.all)
> mod1 <- rda(Y ~ ., X.all)

> anova(mod1)

Permutation test for rda under reduced model
Model: rda(formula = Y ~ Drainage + meanDBH.Mature + MeanAnnualGDD +
AnnualP_AprToSept + ep_OM_total + C.N_50cm, data = X.all)
         Df      Var      F N.Perm Pr(>F)
Model     6 0.066345 4.0308    199  0.005 **
Residual 20 0.054865
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


> ordistep.env <- ordistep(mod0, scope = formula(mod1),
direction="both", Pin = 0.05, Pout= 0.1, perm.max = 1000)


Start: Y ~ 1

DfAIC F N.Perm Pr(>F)
+ C.N_50cm 1 -61.790 8.3666199  0.005 **
+ MeanAnnualGDD 1 -59.041 5.1367199  0.010 **
+ AnnualP_AprToSept  1 -59.281 5.4062199  0.015 *
+ meanDBH.Mature1 -58.284 4.3041199  0.015 *
+ ep_OM_total   1 -56.357 2.2853499  0.086 .
+ DrainageLow   1 -56.151 2.0782299  0.100 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


Step: Y ~ C.N_50cm

 DfAIC F N.Perm Pr(>F)
- C.N_50cm  1 -55.995 8.366699   0.01 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

DfAIC F N.Perm Pr(>F)
+ AnnualP_AprToSept  1 -63.592 3.6301199 0.0150 *
+ MeanAnnualGDD 1 -63.702 3.7427399 0.0175 *
+ meanDBH.Mature1 -62.270 2.3090999 0.0580 .
+ DrainageLow   1 -60.600 0.731799 0.5200
+ ep_OM_total   1 -60.654 0.780699 0.5800
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


Step: Y ~ C.N_50cm + AnnualP_AprToSept

DfAIC F N.Perm Pr(>F)
- AnnualP_AprToSept  1 -61.790 3.630199   0.01 **
- C.N_50cm 1 -59.281 6.320199   0.01 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

  DfAIC F N.Perm Pr(>F)
+ MeanAnnualGDD   1 -65.515 3.5963199  0.005 **
```

```
+ meanDBH.Mature  1 -64.645 2.7525299  0.020 *
+ ep_OM_total1 -62.912 1.152299  0.380
+ DrainageLow1 -62.536 0.817699  0.550
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Step: Y ~ C.N_50cm + AnnualP_AprToSept + MeanAnnualGDD

DfAIC F N.Perm Pr(>F)
- AnnualP_AprToSept  1 -63.702 3.488399   0.02 *
- MeanAnnualGDD 1 -63.592 3.596399   0.02 *
- C.N_50cm 1 -60.946 6.335599   0.01 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

  DfAIC F N.Perm  Pr(>F)
+ meanDBH.Mature  1 -67.266 3.2791299 0.01667 *
+ ep_OM_total1 -65.455 1.6391299 0.10000 .
+ DrainageLow1 -64.672 0.963599 0.48000
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1


Step: Y ~ C.N_50cm + AnnualP_AprToSept + MeanAnnualGDD +
meanDBH.Mature

DfAIC F N.Perm Pr(>F)
- meanDBH.Mature1 -65.515 3.2791199   0.03 *
- AnnualP_AprToSept  1 -64.904 3.8575199   0.03 *
- MeanAnnualGDD 1 -64.645 4.107499   0.01 **
- C.N_50cm 1 -64.248 4.493799   0.01 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

DfAIC F N.Perm Pr(>F)
+ ep_OM_total  1 -66.069 0.633499   0.68
+ DrainageLow  1 -65.904 0.501599   0.77


Anova of the final model:
> anova(ordistep.env)

Permutation test for rda under reduced model
Model: rda(formula = Y ~ C.N_50cm + AnnualP_AprToSept +
MeanAnnualGDD + meanDBH.Mature, data = X.all)
         Df      Var      F N.Perm Pr(>F)
Model     4 0.061841 5.7289    199  0.005 **
Residual 22 0.059370
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

> vif.cca(ordistep.env)
 C.N_50cm AnnualP_AprToSeptMeanAnnualGDDmeanDBH.Mature
 1.2920711.3602851.3987901.172402
```

Appendix 1.3 Correlation between May temperature (T) and May precipitation (P) for each site and partial correlation of May temperature (primary variable) and May precipitation (secondary variable). Sites with a significant partial correlation with May precipitation appear in bold. Sites are ordered by increasing annual growing degree-days above 5 °C.

Site	Cor. between May P and May T	Primary variable (May T)		Secondary variable (May P)	
		Correlation	Significant	Correlation	Significant
H2	**–0.29**	**0.45**	**True**	**–0.27**	**True**
H4	**–0.30**	**0.33**	**True**	**–0.26**	**True**
H3	**–0.29**	**0.32**	**True**	**–0.24**	**True**
H5	–0.31	0.13	False	–0.05	False
M5	–0.06	0.17	False	–0.24	False
M4	**–0.06**	**0.12**	**False**	**–0.32**	**True**
M3	–0.07	0.29	True	–0.07	False
M2	–0.06	0.04	False	–0.04	False
M1	–0.11	0.19	False	–0.04	False
D1	–0.12	0.28	False	0.03	False
D5	–0.02	0.03	False	0.15	False
D3	–0.02	0.01	False	0.03	False
D6	–0.04	0.39	True	0.17	False
D8	–0.04	0.27	True	0.00	False
D7	–0.16	0.17	False	0.02	False
D2	–0.03	0.28	False	–0.07	False
D4	**–0.03**	**0.17**	**False**	**0.13**	**True**
D9	–0.12	0.29	True	0.04	False
C8	–0.25	0.20	False	–0.10	False
C1	–0.26	0.11	False	–0.22	False
C2	–0.25	0.23	True	–0.19	False
C3	–0.25	0.19	False	–0.12	False
C9	–0.25	0.23	True	–0.03	False
C7	–0.27	0.26	True	–0.09	False
C6	**–0.27**	**0.33**	**True**	**–0.11**	**True**
C4	–0.28	0.19	True	–0.15	False
C5	–0.27	0.10	False	–0.04	False

CHAPITRE II

CLIMATIC CONTROL ON RADIAL GROWTH OF *THUJA OCCIDENTALIS* MODULATED BY ITS GENETIC STRUCTURE

(INFLUENCE DU CLIMAT SUR LA CROISSANCE DU *THUJA OCCIDENTALIS* MODULEE PAR SA STRUCTURE GÉNÉTIQUE)

Johann M. Housset[1,2,3,4*], Martin P. Girardin[2,5], Huaitong Xu[1,2], Francine Tremblay[1,2], Christopher Carcaillet[3,4], Yves Bergeron[1,2]

[1]Natural Sciences and Engineering Research Council of Canada Industrial Chair in Sustainable Forest Management, Forest Research Institute, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, QC, J9X 5E4, Canada, [2]Centre d'étude de la forêt, Université du Québec à Montréal, C.P. 8888, Montréal, QC, H3C 3P8, Canada, [3]École Pratique des Hautes Etudes (EPHE), 4-14 rue Ferrus, F-75014 Paris, France, [4]LEHNA (UMR5023, CNRS), Université Lyon 1, F-69622 Villeurbanne, France, [5]Natural Resources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S, PO Box 10380, Stn. Sainte-Foy, Quebec, QC, G1V 4C7, Canada

*Auteur correspondant: Johann Housset, Centre d'Étude de la Forêt, CP 8888, Montréal, QC, H3C 3P8, Canada. E-mail: housset.johann@courrier.uqam.ca

Manuscrit soumis et en cours de révision au moment de la fin de la thèse..

2.1 Abstract

Climate change effects are expected to be most visible at species' margins, where populations are farther from their climatic optimum. Due to their isolation, peripheral populations have, in theory, a reduced genetic diversity and higher inbreeding rates. Those characteristics could hinder their ability to adapt to their new climatic conditions. In the present study, we assessed the adaptability of northern peripheral populations of *Thuja occidentalis* in the Canadian boreal forest. We focused on tree radial growth and tested the hypothesis that variability in sensitivity to climate among site (dendroclimatic signal) was explained by the species' genetic structure. The link between radial growth intrapopulation phenotypic variability and intrapopulation genetic diversity was also tested. Our results suggest that, although intersite variability in sensitivity to climate was mostly explained by environmental variables, the genetic structure significantly modulated the relation between growth and June precipitation in the year prior to ring formation, and May temperature in the current ring formation year. This finding suggests that there might be a genetic control of drought stress resistance and of temperature sensitivity to resume dormancy. Intrapopulation growth variability was explained by both the precipitation regime and the diversity of alleles in the population. Our result suggest that there is an adaptation potential of radial growth to climate warming, but this adaptability is dependent on intrapopulation genetic diversity.

Keywords: Adaptation, boreal forest, climate change, dendroclimatology, genetic structure, peripheral populations, tree growth.

2.2 Résumé

Les effets du changement climatique seront en théorie plus visibles aux marges de distributions des espèces, où les populations sont le plus loin de leur optimum climatique. En raison de leur isolement, de leurs petites tailles et de leur marginalité, les populations périphériques ont en théorie une diversité génétique réduite et les taux plus élevés de consanguinité. Ces caractéristiques pourraient nuire à leur capacité d’adaptation génétique envers leurs nouvelles conditions climatiques. Cette étude a pour objectif d’évaluer la capacité d'adaptation des populations marginales nordiques de *Thuja occidentalis* L. dans la forêt boréale canadienne, en se concentrant sur les traits liés à la croissance radiale. Notre hypothèse est que la variabilité inter-sites de la sensibilité au climat est expliquée par la structure génétique des espèces. Le lien entre la variabilité de croissance intra-population (synchronisme entre les arbres) et la diversité génétique intra-population a également été testé. Les résultats suggèrent que, bien que la variabilité de la sensibilité au climat a été principalement expliquée par les variables environnementales, la structure génétique module significativement les valeurs de corrélation entre la croissance radiale et les température de mai d’une part, et les précipitation de juin de l’année précédant la formation du cerne d’autre part. Ce résultat suggère qu'il pourrait y avoir un contrôle génétique de la sensibilité à la température printanière pour la sortie de dormance, ainsi que de la résistance au stress hydrique. La variabilité de croissance intra-population était expliqué à la fois par le régime de précipitation et par la diversité des allèles dans la population. Nos résultats suggèrent qu'il existe un potentiel d'adaptation de la croissance radiale au réchauffement climatique, mais cette adaptation dépendra de la diversité génétique intra-population disponible pour la sélection naturelle.

Mots-clés : Adaptation, forêt boréale, changements climatiques, dendroclimatologie, structure génétique, populations périphériques, croissance des arbres.

2.3 Introduction

Increasing atmospheric greenhouse gas emissions over the next century will alter climatic gradients, notably via pole-ward shifts of isotherms and locally-dependent changes of precipitation patterns (IPCC, 2013). These modifications will result in changes in the patterns of selection pressures acting on plant distribution, such as temperature and dryness (Chapin *et al.*, 2011 ; Polechová *et al.*, 2009). For instance, boreal forests are projected to experience rises in mean annual temperature over the 21st century ranging from 1.5 to 4.5°C at their southern edges and from 2.0 to 5.5°C at their northern ones (IPCC, 2013). Even though precipitation is projected to increase in the summer and winter over the boreal zone, recent forest growth reductions reported from remote sensing and dendrochronological analyses lead authors to question trees' capacity to cope with the rapid climate change (Beck *et al.*, 2011 ; Berner *et al.*, 2011 ; Girardin *et al.*, 2014 ; Porter et Pisaric, 2011).

To survive a rapidly changing climate, species have three alternatives: acclimatation, migration, or adaption (Aitken *et al.*, 2008 ; Jump et Peñuelas, 2005). The impacts of climatic changes should be most visible on the margins of a species' distribution, far from the species' fitness optimum (Guo *et al.*, 2005 ; Sexton *et al.*, 2009). Peripheral populations could therefore play a key role in the expected range expansions and adaptation, depending on their capacity to deal with the new local climatic conditions (Sexton *et al.*, 2009). Nevertheless, the isolation and reduced demographic size of peripheral populations theoretically hinder their adaptive capacity (Eckert *et al.*, 2008 ; Lesica et Allendorf, 1995). According to the "abundant centre" hypothesis, the decreased number of individuals towards margins causes the net gene flow to occur predominantly from the centre to the margin (central-marginal model), which brings maladapted genes to peripheral populations (Bridle *et al.*, 2010 ; Sexton *et al.*, 2009). The intrapopulation genetic diversity of small populations is likely to be reduced by the additive effects of genetic drift, inbreeding and past demographic events such as founder effects or genetic bottlenecks. As a consequence, we can expect that marginal populations will have a lower response capacity to the selection pressure caused by the new climatic conditions.

A population's ability to adapt on a certain trait in response to selection pressure requires two conditions: (1) a genetic control on the trait, and (2) the existence of intrapopulation genetic variability. Although a lot of modelling efforts have been put in studying evolutionary dynamics at range limits (see review in Sexton *et al.*, 2009), the predictive power of models of adaptation rates is limited by a lack of empirical knowledge on species' genetic architecture and response to selection (Polechová *et al.*, 2009 ; Sexton *et al.*, 2009 ; Shaw et Etterson, 2012). *In situ* studies documenting both the genetic structure and plant traits over broad ecological gradients including range limits are needed to calibrate models of adaptation through space and time (Aitken *et al.*, 2008 ; Sexton *et al.*, 2009).

Here, we tested the adaptive response capacity of a boreal tree species, *Thuja occidentalis* L. (hereafter called cedar), to warming-induced selection pressure on traits that are relative to stem annual radial growth (i.e. annual xylem production), from the centre to the northern leading edge of the species' distribution. This assessment was carried out using an innovative approach testing the link between *in situ* genetic structure and responses of stem radial growth to interannual climatic variability over multiple sites. Cedar is an evergreen long-lived and shade-tolerant species native to North America (Hofmeyer *et al.*, 2009), with a latitudinal distribution (Fig. 2.1b) ranging from James Bay, Canada, in the north, to New York, Ohio and Michigan, USA, in the south (Little, 1971).

A previous study of stem annual growth carried out at the cedar's northern margin in Québec concluded that warming should cause an increasing summer drought growth constraint that could induce a selection pressure on the species at its leading edge in James Bay (Housset *et al.*, 2015). Also, a study of cedar genetic structure conducted in the same study area revealed an elevated inbreeding rate at the northern margin of the species that could affect its adaptive response (Xu *et al.*, 2012). Building on these two studies, we formulated the following hypotheses:

H2.1: Stem radial growth response to climate variability is influenced by genetic structure in cedar. The existence of genetic control on the observed phenotype is a prerequisite condition for natural selection to operate. The alternative hypothesis is that variability in climate response among sites is due to environmental conditions only (i.e. no effects from genetic structure).

H2.2: Intrapopulation phenotypic variability in traits related to radial growth and intrapopulation genetic diversity are lower for marginal populations, following the central-marginal model.

H2.3: Radial growth synchronicity between trees of a single site decreases with intrapopulation genetic diversity. An alternative hypothesis is that growth synchronicity is more related to climatic conditions; by placing a common growth constraint on all trees of a site, a more stressful local climate could theoretically lead to a greater synchronicity (Schweingruber, 1996).

2.4 Material and method

2.4.1 Study area

The study area is located in western Quebec (Abitibi, Témiscamingue, Jamésie and Chibougamau), from the centre to the northern leading edge of cedar distribution (Fig. 2.1b). A latitudinal transect was established from 47.3ºN to 50ºN and divided into three zones based on the cedar abundance: the continuous zone (CZ), where cedars are common, the discontinuous zone (DZ), which marks the northern edge of the continuous distribution and where cedars become less common in the forest matrix, and the marginal zone (MZ) where only a few isolated patches of cedars are found (Fig. 2.1a.). The relative abundance of cedars in the continuous, discontinuous, and marginal zones was estimated at 55%, 9%, and 3%, respectively (Beaudoin *et al.*, 2014 ; Fig. 2.1b; Xu *et al.*, 2012). A total of 24 cedar stands were sampled along this gradient, with 8 sites in the CZ, 7 in the DZ, and 9 in the MZ. Cedar shows very plastic tolerance to moisture edaphic conditions, occupying both poorly drained lowland sites and xeric or rocky sites (Burns et Honkala, 1990 ; Denneler *et al.*, 2008 ; Hofmeyer *et al.*, 2009). All cedar stands in the MZ were found in forest swamps or along lake and river shores. Then, the same edaphic situations were sampled in the CZ and DZ to sample trees growing in similar environments and to limit sampling bias (Paul *et al.*, 2014). Over the 1953-2010 period, climate was colder in the MZ, with a mean annual temperature (MAT) of -0.03 °C (SD=0.37), than in the DZ and CZ, which had a MAT of 1.40 ± 0.25 °C and 2.40 ± 0.33 °C respectively (Table 2.1). Annual sum of precipitation was on average (±SD) 908 ±53 mm.year^{-1} in the MZ, 886 ±27 mm.year^{-1} in the DZ and 937 ±56 mm.year^{-1} in the CZ (Table 2.1).

2.4.2 Growth-climate correlation matrix

In this study, we focused on the variability in growth sensitivity to climate among sites, but not on the growth itself. As response variables, we used the correlation matrix between climate and cedar growth relationships described in Housset et al. (2015). This matrix was built from a detailed analysis of the correlation between monthly climatic variability and annual radial growth increments of white cedar from 27 sites, including the 24 sites of this study. Annual radial growth increments were obtained and analytical approaches were conducted using classical procedures in dendroclimatology. This section summarizes the methodological approaches employed by Housset et al. (2015) to derive the correlation matrix, and the main variables retained for this work.

During summer 2010, up to 30 dominant and codominant cedars were sampled in each site for dendroclimatic analysis (Housset *et al.*, 2015). Two cores per tree were collected at 1.3 m above ground, sanded, measured, and crossdated. To maximise the high-frequency growth responses associated with year-to-year climatic variability, each raw ring-width time series was detrended using 60-year splines with a 50% frequency response (E. Cook et Kairiūkštis, 1990 ; E. R. Cook et Peters, 1981). After removing the first order autocorrelation, a mean Tree Growth Index (TGI) chronology was computed for each site. These residual chronologies were statistically tested against climatic time-series using bootstrapped correlation analyses over the 1953-2010 period covered by meteorological observations (Biondi et Waikul, 2004 ; see details in Housset *et al.*, 2015). Climatic time-series included in the analysis of Housset et al. (2015) were monthly mean temperatures and total monthly precipitation interpolated at each of the sampling sites using the BioSIM software (Régnière et Bolstad, 1994). This analysis revealed that cedar interannual growth variability was positively correlated with May temperature but negatively correlated with June temperatures of the current year and August temperatures of the year preceding ring formation. Climatic conditions of the previous year can affect tree growth, for instance through the process of carbohydrates reserve accumulation (Fritts, 1976). Precipitation also influenced annual radial growth, with a negative correlation with previous October and current-year May precipitation, and a positive correlation with previous June and current-year August precipitation. Figure 2.2 sums up the correlation scores of cedar radial growth with those seven monthly climatic variables, which will be the plant traits under study in the following section.

2.4.3 Genetic structure vs growth-climate correlation variability among site

We used model selection to test the hypothesis that genetic structure modulates the growth−climate correlation coefficients of the matrix described above. The alternative hypothesis is that the environmental conditions of each site explain the among-sites variability in the growth−climate relationships. In the model selection approach, each hypothesis is associated with a model that can be compared with other model hypotheses through the corrected Akaike Information Criteria (AICc) statistic (Burnham et Anderson, 2010). The model with the lowest AICc corresponds to the model with the highest likelihood and greatest parsimony (lower parameter K). This method selects the hypothesis with the greatest likelihood to fit the observed data while avoiding the risk of overfitting them. Models with a difference in AICc greater than two with the best model can be rejected.

Therefore, we included in the analysis a model with variables describing the genetic structure of each site and a model with the environmental variable having an effect on sensitivity to climate. A model including both the genetic structure and the environmental variables was also included in the model selection. Genetic structure variables are from Xu et al. (2012) who analysed cedar genetic structure at the same 24 sites as for dendrochronology. For each site, 15 to 30 trees were randomly selected and used for microsatellite genotyping. The genetic structure of cedar was determined by conducting a clustering analysis on the genotypes at four polymorphic microsatellite loci (TP9, TP10, TP11, and TP12) using the STRUCTURE v. 2.3.2 software (Pritchard *et al.*, 2000). This procedure identified three clusters, representing groups of trees with similar genotypes, hereafter depicted using the following three colours: orange, yellow, and blue (Table 2.1). Tree percentage in each cluster is used as explanatory variables in the analysis to test for the influence of the genetic cluster. Four environmental variables having an effect on among-site variability of the above-mentioned growth−climate correlation values were identified in a previous study of cedar dendroclimatic response (Housset *et al.*, 2015) and were included in the environment model Those four variables were: mean diameter at breast height (DBH) of the cored trees, carbon to nitrogen ratio (C:N) in the upper 50 cm, annual growing degree days (GDD, >5°C) and seasonal precipitation (annual sum of precipitation from April to September, i.e. the actual vegetation period) averaged over the 1953-2010 period.

To sum up, the three following models were compared:

$$(\text{Eq. } 2.1)\ \text{genetic model: } r_i \sim \%_{\text{blue}} + \%_{\text{yellow}} + \%_{\text{orange}}\ ;$$

$$(\text{Eq. } 2.2)\ \text{environmental model: } r_i \sim mean\ DBH + C\!:\!N\ ratio + annual\ GDD_{1953-2010} + Seasonal\ P_{1953-2010}\ ;$$

$$(\text{Eq. } 2.3)\ \text{complete model: } r_i \sim mean\ DBH + C\!:\!N\ ratio + annual\ GDD_{1953-2010} + Seasonal\ P_{1953-2010} + \%_{\text{blue}} + \%_{\text{yellow}} + \%_{\text{orange}}\ ;$$

where r_i is the correlation coefficient of growth with one of the above-mentioned monthly climatic variables (column-wise from Fig. 2.2).

Additionally, for each of the monthly correlation coefficients, a variance partitioning was computed between the three models to assess the amount of variability (adjusted R^2) explained by each group of variables. The overall effect of environmental *versus* genetic structure variables was assessed through the calculation of a multivariate variance partitioning on the seven monthly climatic variables using the R package “vegan” (Oksanen *et al.*, 2013), following the method of Legendre and Legendre (2012).

2.4.4 Intra-population variability analysis

To assess intrapopulation phenotypic variability, growth synchronicity was evaluated between trees per site. A mean chronology was computed for each tree from the spline-detrended chronologies of all its cores. The average pairwise correlation between single-tree chronologies within site (r_{bt}) was calculated (E. Cook et Kairiūkštis, 1990). This statistic, representing the average correlation between trees, was used as an indicator of growth synchronicity in our analysis. To remove biases due to population size differences, we resampled eight trees in each site and estimated this parameter by averaging it over 1000 repetitions. For each resampling, the r_{bt} statistic was computed using the R package dplR (Bunn, 2008). Growth synchronicity between trees could be influenced by various factors such as differences in DBH or by intrapopulation genetic variability. Variability in DBH was estimated using the standard deviation of tree DBH for each sampling site (sd_{DBH}). Three complementary proxies of intrapopulation genetic diversity were used: Allelic Richness (AR), expected heterozygoty (H_e), and average within-population pairwise relatedness between each pair of trees in a site ($Gen_{relatedness}$). H_e and $Gen_{relatedness}$ statistics were computed with the software Genalex 6.5 (Peakall et Smouse, 2012) on the same microsatellites used for the genetic structure analysis (see above). The AR parameter, representing the number of alleles corrected for sampled population size effect, was calculated using the software FSTAT2.9.3. H_e indicates gene diversity, with values ranging from 0 for low diversity to 1 for high diversity (Eckert *et al.*, 2008). We also included the inbreeding coefficient (F_{is}) in the model selection, which was calculated for each population using the software FSTAT2.9.3. The effect of climate on growth synchronicity (alternative hypothesis) was assessed through annual growing degree days (GDD, >5°C) and the annual sum of precipitation from April to September (i.e. during the active vegetation stage) averaged over the 1953-2010 period. To determine which variable best explained growing variability in our data, we used model selection based on AICc, with the same method as the one described above. Each model had growing variability (r_{bt}) as dependant variable and one of the following independent variables: sd_{DBH}, AR, H_e, $Gen_{relatedness}$, F_{is}, $annual\ GDD_{1953-2010}$ or $Seasonal\ P_{1953-2010}$.

2.5 Results

2.5.1 Variability among site

Model selection revealed that hypothesis H2.1 (unequal radial growth responses to climate variability for all genetic clusters) was rejected for the correlation with five monthly climatic variables: the model including environmental variables best explained variability among sites in the correlation with previous August and current June temperatures, and with previous October, current May, current August precipitation (Table 2.2). According to variance partitioning, environmental variables captured most of the explained variance for those monthly climatic variables (Fig. 2.4a). Nevertheless, hypothesis H2.1 was validated for the correlation with current May temperature and previous June precipitation. The genetic model (Eq. 2.2) better explained the variability among sites for the correlation coefficient with those two climatic variables (Table 2.2). Although this model was more parsimonious (K=4) than the environment one (K=6), the Δ AICc (5.2 and 5.4 respectively) largely exceeded the difference in K. Sites with a greater percentage of trees assigned to the blue cluster were significantly ($p = 0.019$) less positively correlated with May temperature (Fig. 2.3a; Appendix 2.1a). A greater percentage of “blue” trees in the site was also significantly ($p = 0.012$) linked to a more positive correlation with previous June precipitation (Fig. 2.3b; Appendix 2.1b). The genetic structure accounted for the most important part of the explained variance for those two dependent variables (Fig. 2.4a) with an adjusted R^2 of 0.17 for the correlation with

May temperature and of 0.21 for previous June precipitation. The complete model with both the environmental and genetic cluster variables had the worst AICc for all the monthly climatic correlation coefficients included in the analysis (Table 2.2) although the adjusted R^2 was greater (Fig. 2.4a). Overall, multivariate variance partitioning computed on the seven dependent variables (growth correlation with climate variables) revealed that environmental variables only explained 24% of the variance while genetic structure only explained 5%. The part of variance that was jointly explained by both environmental and genetic data accounted for 13% of the total variance, while 57% of it remained unexplained by our data.

2.5.2 Intra-site genetic and phenotypic variability

Figure 2.5a shows that growth synchronicity between the trees of a given site (r_{bt}) was smaller in the MZ than in the DZ (p = 0.025). No statistical differences in r_{bt} were observed between the CZ and DZ, nor between the CZ and MZ. Genetic pairwise relatedness was smaller in the MZ than in the CZ (p = 0.049) (Fig. 2.5b). Based on model selection (Table 2.3), hypothesis H2.2 was rejected. The best model to explain growth synchronicity between the trees of a site is the one with $Seasonal\ P_{1953-2010}$ as explanatory variable. Sites receiving more precipitation had a lower synchronicity. Nevertheless, this relation was barely significant (p = 0.053) and poorly explains the intrapopulation growth variability (adjusted R^2 = 0.122). Four other models had a difference in AICc (Δ AICc) lower than two, with the following explanatory variables: H_e, $annual\ GDD_{1953-2010}$ (Δ AICc=0.56), AR (1.39) and $Gen_{relatedness}$ (1.68). None of those models had a significant relation with r_{bt}. The major part of growth variability between trees was not captured by our variables.

2.6 Discussion

Our study on the connection between genetic structure and the dendroclimatic response of cedar (*Thuja occidentalis*) indicates that variation in the growth−climate correlation coefficient among sites is mainly explained by environmental variables. Nevertheless, sensitivity to current-year May temperature and to previous June precipitation was modulated by genetic structure. In the following sections, we discuss the likely mechanisms of genetic influence on growth sensitivity to spring temperature and summer precipitation, intrapopulation phenotypic and genetic variability and, finally, the implications for cedar margins adaptability to warming.

2.6.1 Growth sensitivity to climate is largely influenced by the environment

Our results confirm the key impact of environmental conditions on growth sensitivity to climate for the correlation with summer temperatures (August of the previous year and June of the current year), October precipitation of the previous year, and May and August precipitation of the current year. Housset et al. (2015) depict more thoroughly the relationships between environmental variables and growth sensitivity to climate. Although some common garden experiments showed that height growth differed significantly among cedar provenances (Jokela *et al.*, 1977 ; but see also Russell *et al.*, 2003 for *Thuja plicata*), no experiment has tested the effect of genetics on cedar interannual growth variations. However, our results are consistent with the findings of studies conducted on other boreal coniferous species. For instance, a study of the dendroclimatological response of different provenances of *Pinus banksiana* Lamb. in a common garden experiment in Canada concluded that there was no difference between provenances in growth−climate relationships (Savva *et al.*, 2008). In another common garden experiment of *Pinus sylvestris* L. in Siberia, Savva et al. (2002) showed that provenances accounted for only 15% of the variation in the dendroclimatic signal, while 85% was due to the environment. The authors of this study point out that the variability between trees within a provenance was one to four times higher than the variability observed among provenances. We stress the need for specific research testing the genetic effect on growth sensitivity to climate at the tree scale which could be more powerful than investigating average values at the population scale. According to Xu et al. (2012), intrapopulation variability of cedar accounted for 95% of the genetic variability whereas only 5% of variability was observed among populations and the genetic effect may be stronger at the tree scale. An analysis of the link between potentially adaptive genetic variation and the dendroclimatic signal could also lead to potentially stronger and more meaningful correlations than our first analysis with neutral genetic markers.

2.6.2 Genetic structure versus correlation with May temperature

The correlation with May temperature significantly varied with genetic structure, which could be explained by a genetic control on the date of cambium reactivation. The blue genetic cluster is less positively correlated with May temperature, and we can hypothesize that cambial activity starts earlier in trees of this type. The processes governing cambium phenology are still unknown for cedar. Nevertheless, studies on other coniferous species show that cambium reactivation is linked to spring temperature (Belyea *et al.*, 1951 ; Deslauriers *et al.*, 2003 ; Duchesne *et al.*, 2012 ; Fraser, 1952), and experiments of artificial stem heating during late winter caused a locally anticipated cambium activity resumption in evergreen conifers (Gričar *et al.*, 2006 ; Oribe *et al.*, 2001 ; Oribe et Kubo, 1997). Those mechanisms are consistent with studies on cedar radial growth using dendrometers in our study area (Denneler *et al.*, 2010 ; Jacques Tardif *et al.*, 2001). The effect of genetic structure on observed sensitivity to spring temperature suggests that all cedar genotypes are not equal in their thermal requirements to cease dormancy. A common garden experiment on the conifer *Pseudotsuga menziesii* (Mirb.) Franco revealed that the date of radial growth initiation differed among the provenances (Li et Adams, 1994). Moreover, it is generally accepted that dormancy phenology has a stronger genetic control than growth itself (Alberto *et al.*, 2013 ; Howe *et al.*, 2003). Research on spruce showed a link between the time of initiation of radial growth and spring frost hardiness (Nienstaedt, 1974). The timing of growth initiation bears an important evolutionary signification, since there is a trade-off between decreasing the risk of frost damage and maximizing the length of the growth period (Chuine, 2010). Natural selection could operate on this trait by promoting the genetic types showing the best trade-off under the new climatic conditions.

2.6.3 Genetic structure vs correlation with previous June precipitation

Our data show that annual growth increment sensitivity to June precipitation in the year previous to ring formation is also modulated by genetic structure. Many common garden and growth chamber experiments have already shown that genetic variations exist for the traits relative to drought resistance, such as hydraulic conductivity, stomatal number, stomatal density, and belowground/aboveground biomass ratio (Alberto *et al.*, 2013 ; Benito Garzón *et al.*, 2011 ; Raj *et al.*, 2011 ; Richter *et al.*, 2012). Common garden experiments revealed an adaptation to precipitation condition for western red cedar (*Thuja plicata* Donn ex D. Don), as both height increments and transpiration efficiency differed significantly with the precipitation regime in the site of origin of the provenances (Fan *et al.*, 2008). A study of the shrub *Ulex parviflorus* Pourr. showed that plant bulk density (i.e. plant dry biomass per volume; g.cm^{-3}) had a genetic component (Moreira *et al.*, 2014). Even the physiological response to hydric stress has a genetic control involving a cascade of gene expression, from the detection of changes in environmental conditions to the plant's response to stress (Yamaguchi-Shinozaki et Shinozaki, 2006). We can hypothesize that the genetic clusters that use water more efficiently would be less affected by hydric stress the year before ring formation, allowing them to store more carbohydrate reserves for the next year's growth. It remains unclear why only growth sensitivity to previous June precipitation is linked to genetic structure and not the other climatic variables related to summer hydric stress (previous August and June temperatures, August precipitation). On the one hand, the negative effects of summer temperature on growth could be more related to physiological processes such as a relative loss of net primary productivity due to an increased rate of maintenance respiration (Chapin *et al.*, 2011 ; Lavigne et Ryan, 1997). Furthermore, the positive effect of August precipitation coincides with a growth phase of cell enlargement that is dependent on the water supply (Denneler *et al.*, 2010 ; Wang *et al.*, 2012). Nevertheless, the significant influence of genetic structure on sensitivity to previous June precipitation suggests that adaptation to hydric stress selection pressure is possible.

2.6.4 Intrapopulation variability

At the intrapopulation level, growth synchronicity between trees (r_{bt}) was lower in the MZ, meaning that the growth patterns were more variable from one tree to another. Based on the model selection, this result was neither due to a greater spatial variability between the trees nor to size heterogeneity. Contrary to our hypothesis H2.3, growth synchronicity was mostly influenced by seasonal precipitation (best model), a drier climate being associated with an increase in synchronicity. Other studies showed that growth synchronicity was stronger under the most stressful climatic conditions (Ettinger *et al.*, 2011 ; King *et al.*, 2013). However, growth synchronicity between trees can be affected by stochastic processes such as competition or injuries, which could not be controlled in our study set and are thus accounted for as "noise". This could explain the low R^2 value (adjusted R^2=0.122) and the low p value (0.053) of the relation between r_{bt} and $Seasonal\ P_{1953-2010}$. The model with the expected heterozygoty (H_e) had an AICc score very close to the one with $Seasonal\ P_{1953-2010}$ (Δ AICc=0.07). Both the p value (0.055) and R^2 value (0.119) were also close to those of the first model. A higher H_e, meaning a higher quantity of alleles in the population, seems to decrease the growth correlation between trees (r_{bt}). Two other models including genetic diversity variables (AR and $Gen_{relatedness}$) had Δ AICc lower than two; thus, they potentially influenced secondarily synchronicity. A higher level of intrapopulation AR and a lower $Gen_{relatedness}$ (meaning more genetic difference between trees) were associated with lower synchronicity between trees. Although these relations were not significant, the small number of replicates in our data (n=24) implies a high risk of not detecting an effect (type 1 error). Genetic difference in growth traits may only be expressed when climate is favourable so climate may explain synchronicity better than genetic diversity. Disentangling the effect of climate and genetics on growth synchronicity would require additional research, with particular focus put on the tree scale. It remains that the amount of seasonal precipitation appears to primarily drive growth synchronicity, which confirms that hydric stress exerts a selection pressure on cedar growth in our study area.

2.6.5 Implications for cedar adaptation capacity to future climate

As mentioned above, our results show that genetic structure modulates growth sensitivity to spring temperatures and to hydric stress in June of the year before ring formation. In the context of climate change, natural selection could therefore act on cedar population to select individuals having the best fitness with the new local temperatures and precipitation regimes. Natural selection acts primarily on the pre-existing genetic variability (Kelly *et al.*, 2003 ; Savolainen *et al.*, 2007).

Microsatellites genotyping revealed that our sampled sites had a higher allelic richness (Appendix 2.2a) and a lower pairwise genetic relatedness (Fig. 2.5b) in the MZ than in the CZ. Cedar's northern margin did not suffer genetic diversity loss as we could theoretically expect according to the central-marginal model, meaning that genetic variation is readily available for selection. In a longer-term perspective, adaptation will be dependent on the acquisition of new genetic combinations through sexual reproduction, gene migration from other populations, or mutation (Antoine Kremer *et al.*, 2012 ; Savolainen *et al.*, 2007). The high current inbreeding rate suggests that the gene flow reaching marginal populations is not very high. However, Kremer and Le Corre (2012) suggest that the large pre-existing intrapopulation genetic variability in tree populations can lead to a rapid appearance of new allelic associations in response to selection pressure, without inducing a strong change in population allelic frequencies. Paul et al. (2014) showed that the seed production and germination did not decrease toward cedar's northern margin in Québec. They observed a lower seedling recruitment compensated by a higher rate of vegetative layering, Although cedar's northern margin may have sufficient genetic variation to adapt to warming, its long-term fate will highly depend on the effective gene flow (recruited seedlings) from more drought-tolerant populations. To facilitate this, forest management practices aiming to limit cedar distribution fragmentation and maintain marginal populations would be suitable.

2.7 Acknowledgements

We would like to thank Aurélie Terrier for her useful comments on a preliminary version of this manuscript, but also Cécile Leroy, Mélanie Desrochers, Danielle Charron and Daniel Lesieur for their valuable help. This study was conducted with the financial support of the Natural Sciences and Engineering Research Council of Canada (NSERC) through its CREATE programme in Forest

Modelling Complexity and the French programme Paris Nouveau Monde of the heSam consortium (PhD grants to J.H.). This research was also funded by a NSERC strategic grant (STPGP336871) to Francine Tremblay. The research was carried out within the framework of the International Associated Laboratory (LIA France-Canada) CNRS-UM2-EPHE-UQAT-UQAM-UQAC entitled MONTABOR.

2.8 References

Aitken, S. N. et al. 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. - Evolutionary Applications 1: 95–111.

Alberto, F. J. et al. 2013. Potential for evolutionary responses to climate change – evidence from tree populations. - Global Change Biology 19: 1645–1661.

Beaudoin, A. et al. 2014. Mapping attributes of Canada's forests at moderate resolution through *k*NN and MODIS imagery. - Can. J. For. Res. 44: 521–532.

Beck, P. S. A. et al. 2011. Changes in forest productivity across Alaska consistent with biome shift. - Ecology Letters 14: 373–379.

Belyea, R. M. et al. 1951. Seasonal growth of some trees in Ontario. - The Forestry Chronicle 27: 300–305.

Benito Garzón, M. et al. 2011. Intra-specific variability and plasticity influence potential tree species distributions under climate change. - Global Ecology and Biogeography 20: 766–778.

Berner, L. T. et al. 2011. High-latitude tree growth and satellite vegetation indices: Correlations and trends in Russia and Canada (1982–2008). - J. Geophys. Res. 116: G01015.

Biondi, F. and Waikul, K. 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. - Computers & Geosciences 30: 303–311.

Bridle, J. R. et al. 2010. Why is adaptation prevented at ecological margins? New insights from individual-based simulations. - Ecology Letters 13: 485–494.

Bunn, A. G. 2008. A dendrochronology program library in R (dplR). - Dendrochronologia 26: 115–124.

Burnham, K. P. and Anderson, D. R. 2010. Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach. - Springer.

Burns, R. M. and Honkala, B. H. 1990. Silvics of North America. - In: Agriculture Handbook. USDA Forest Service, in press.

Chapin, F. S. I. et al. 2011. Principles of Terrestrial Ecosystem Ecology. - Springer.

Chuine, I. 2010. Why does phenology drive species distribution? - Phil. Trans. R. Soc. B 365: 3149–3160.

Cook, E. R. and Peters, K. 1981. The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. - Tree-Ring Bulletin 41: 45–53.

Cook, E. and Kairiūkštis, L. 1990. Methods of dendrochronology: applications in the environmental sciences. - Kluwer Academic Publishers.

Denneler, B. et al. 2008. Growth responses of riparian *Thuja occidentalis* to the damming of a large boreal lake. - Botany 86: 53–62.

Denneler, B. et al. 2010. Flooding effects on tree-ring formation of riparian eastern white-cedar (*Thuja occidentalis* L.), northwestern Quebec, Canada. - Tree-Ring Research 66: 3–17.

Deslauriers, A. et al. 2003. Daily weather response of balsam fir (Abies balsamea (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). - Trees 17: 477–484.

Duchesne, L. et al. 2012. Influence of climate on seasonal patterns of stem increment of balsam fir in a boreal forest of Québec, Canada. - Agricultural and Forest Meteorology 162–163: 108–114.

Eckert, C. G. et al. 2008. Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. - Molecular Ecology 17: 1170–1188.

Ettinger, A. K. et al. 2011. Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. - Ecology 92: 1323–1331.

Fan, S. et al. 2008. Morphological and physiological variation in western redcedar (Thuja plicata) populations under contrasting soil water conditions. - Trees 22: 671–683.

Fraser, D. A. 1952. Initiation of Cambial Activity in Some Forest Trees in Ontario. - Ecology 33: 259–273.

Fritts, H. C. 1976. Tree rings and climate. - London, New York, San Francisco. Academic Press.

Girardin, M. P. et al. 2014. Unusual forest growth decline in boreal North America covaries with the retreat of Arctic sea ice. - Global Change Biology 20: 851–866.

Gričar, J. et al. 2006. Effect of local heating and cooling on cambial activity and cell differentiation in the stem of Norway spruce (*Picea abies*). - Annals of Botany 97: 943–951.

Guo, Q. et al. 2005. Spatial-temporal population dynamics across species range: from centre to margin. - Oikos 108: 47–57.

Hofmeyer, P. V. et al. 2009. Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: a synthesis of knowledge. - Northern Journal of Applied Forestry 26: 21–27.

Howe, G. T. et al. 2003. From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. - Canadian Journal of Botany 81: 1247–1266.

IPCC 2013. Climate Change 2013: The Physical Science Basis. Contribution of the Working Group I to the Fifth Assessment Report of the IPCC.: 1535.

Jokela, J. J. et al. 1977. Performance of northern white-cedar in central Illinois. - Proceedings, Thirteenth Lake States Forest Tree Improvement Conference: 100–106.

Jump, A. S. and Peñuelas, J. 2005. Running to stand still: adaptation and the response of plants to rapid climate change. - Ecology Letters 8: 1010–1020.

Kelly, C. K. et al. 2003. Temperature-based population segregation in birch. - Ecology Letters 6: 87–89.

King, G. M. et al. 2013. Tree growth response along an elevational gradient: climate or genetics? - Oecologia 173: 1587–1600.

Kremer, A. and Le Corre, V. 2012. Decoupling of differentiation between traits and their underlying genes in response to divergent selection. - Heredity 108: 375–385.

Kremer, A. et al. 2012. Long-distance gene flow and adaptation of forest trees to rapid climate change. - Ecology Letters 15: 378–392.

Lavigne, M. B. and Ryan, M. G. 1997. Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. - Tree Physiol 17: 543–551.

Legendre, P. and Legendre, L. F. J. 2012. Numerical Ecology. - Elsevier.

Lesica, P. and Allendorf, F. W. 1995. When Are Peripheral Populations Valuable for Conservation? - Conservation Biology 9: 753–760.

Li, P. and Adams, W. T. 1994. Genetic variation in cambial phenology of coastal Douglas-fir. - Can. J. For. Res. 24: 1864–1870.

Little, E. L. J. 1971. Atlas of United States trees. Volume 1. Conifers and important hardwoods. - In: Miscellaneous publication 1146. USDA, Forest Service, in press.

Moreira, B. et al. 2014. Genetic component of flammability variation in a Mediterranean shrub. - Mol Ecol 23: 1213–1223.

Nienstaedt, H. 1974. Genetic Variation in Some Phenological Characteristics of Forest Trees. - In: Lieth, H. (ed), Phenology and Seasonality Modeling. Ecological Studies. Springer Berlin Heidelberg, pp. 389–400.

Oksanen, J. et al. 2013. vegan: Community Ecology Package. - R package version 2.0-10.

Oribe, Y. and Kubo, T. 1997. Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. - Tree Physiology 17: 81–87.

Oribe, Y. et al. 2001. Cambial reactivation in locally heated stems of the evergreen conifer Abies sachalinensis (Schmidt) Masters. - Planta 212: 684–691.

Paul, V. et al. 2014. Does climate control the northern range limit of eastern white cedar (*Thuja occidentalis* L.)? - Plant Ecol 215: 181–194.

Peakall, R. and Smouse, P. E. 2012. GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. - Bioinformatics 28: 2537–2539.

Polechová, J. et al. 2009. Species' Range: Adaptation in Space and Time. - The American Naturalist 174: E186–E204.

Porter, T. J. and Pisaric, M. F. J. 2011. Temperature-growth divergence in white spruce forests of Old Crow Flats, Yukon Territory, and adjacent regions of northwestern North America. - Global Change Biology 17: 3418–3430.

Pritchard, J. K. et al. 2000. Inference of Population Structure Using Multilocus Genotype Data. - Genetics 155: 945–959.

Raj, S. et al. 2011. Clone history shapes Populus drought responses. - PNAS 108: 12521–12526.

Régnière, J. and Bolstad, P. 1994. Statistical simulation of daily air temperature patterns in Eastern North America to forecast seasonal events in insect pest management. - Environmental Entomology 23: 1368–1380.

Richter, S. et al. 2012. Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. - Oecologia 169: 269–279.

Russell, J. H. et al. 2003. Inbreeding depression and variance structures for height and adaptation in self-and outcross Thuja plicata families in varying environments. - Forest Genetics 10: 171–184.

Savolainen, O. et al. 2007. Gene Flow and Local Adaptation in Trees. - Annual Review of Ecology, Evolution, and Systematics 38: 595–619.

Savva, Y. et al. 2002. Genetic and environmental signals in tree rings from different provenances of Pinus sylvestris L. planted in the southern taiga, central Siberia. - Trees - Structure and Function 16: 313–324.

Savva, Y. et al. 2008. Effect of interannual climate variations on radial growth of jack pine provenances in Petawawa, Ontario. - Canadian Journal of Forest Research 38: 619–630.

Schweingruber, F. H. 1996. Tree rings and environment. Dendroecology. - Paul Haupt AG Bern.

Sexton, J. P. et al. 2009. Evolution and Ecology of Species Range Limits. - Annual Review of Ecology, Evolution, and Systematics 40: 415–436.

Shaw, R. G. and Etterson, J. R. 2012. Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. - New Phytologist 195: 752–765.

Tardif, J. et al. 2001. An Analysis of the Daily Radial Activity of 7 Boreal Tree Species, Northwestern Quebec. - Environ Monit Assess 67: 141–160.

Wang, Z. et al. 2012. Research progress in monitoring and simulating stem radius growth: an overview. - Sciences in Cold and Arid Regions 4: 0175–0183.

Xu, H. et al. 2012. Genetic consequences of fragmentation in “arbor vitae,” eastern white cedar (*Thuja occidentalis* L.), toward the northern limit of its distribution range. - Ecology and Evolution 2: 2506–2520.

Yamaguchi-Shinozaki, K. and Shinozaki, K. 2006. Transcriptional Regulatory Networks in Cellular Responses and Tolerance to Dehydration and Cold Stresses. - Annual Review of Plant Biology 57: 781–803.

2.9 Tables

Table 2.1 Geographic, climatic, and neutral genetic features of the *Thuja occidentalis* sampling sites.

Sites are ordered by decreasing annual growing degree days >5ºC (GDD). Annual climatic data were averaged over the 1953-2010 period. MAT = mean annual temperatures, P = precipitation, AR = allelic richness, Fis = inbreeding coefficient. Colour bars represent the percentage of the three clusters (coded by a single colour) determined by STRUCTURE v. 2.3.2 software (Pritchard *et al.*, 2000). Length of the genetic structure colour bar is proportional to the number of sampled trees in each site.

Distribution zone	Site	Latitude (dd)	Longitude (dd)	MAT °C	Mean annual P (mm)	Genetic data (from Xu et al. 2012)			
						AR	Fis	Corresponding site	Genetic structure cluster
Marginal East	H2	49.876	-74.393	-0.49	965	6.1	0.16	MZ1	
(Chibougamau)	H4	49.953	-74.229	-0.42	959	6.6	0.46	MZ3	
MEZ	H3	49.909	-74.322	-0.27	962	6.4	0.13	MZ2	
	H5	49.642	-74.334	0.02	966	6.9	0.27	MZ4	
Marginal West	M5	49.856	-78.645	-0.08	855	6.1	0.08	MZ9	
(Jamesie)	M4	49.883	-78.646	-0.02	855	6.7	0.17	MZ8	
MWZ	M3	49.858	-78.606	0.03	857	6.3	0.22	MZ7	
	M2	49.423	-79.211	0.20	866	5.3	-0.03	MZ6	
	M1	48.928	-78.886	0.76	886	6.6	0.21	MZ5	
Discontinuous	D1	48.540	-78.642	0.90	944	6.0	0.15	DZ1	
(Abitibi)	D6	48.432	-79.402	1.40	878	5.4	0.00	DZ4	
DZ	D8	48.431	-79.384	1.41	880	6.4	0.24	DZ6	
	D2	48.470	-79.452	1.42	879	6.1	0.23	DZ2	
	D7	48.263	-78.575	1.50	880	6.0	0.20	DZ5	
	D4	48.480	-79.437	1.48	882	5.4	0.07	DZ3	
	D9	48.201	-79.419	1.75	856	5.2	-0.19	DZ7	
Continuous	C8	47.419	-78.678	2.09	974	6.9	0.06	CZ7	
(Temiscamingue)	C1	47.429	-78.678	2.12	969	5.6	-0.07	CZ1	
CZ	C2	47.417	-78.682	2.26	960	5.2	-0.10	CZ2	
	C3	47.396	-78.731	2.27	965	4.6	-0.14	CZ3	
	C9	47.416	-78.712	2.38	947	6.1	0.03	CZ8	
	C7	47.454	-78.587	2.46	922	6.2	-0.09	CZ6	
	C6	47.311	-78.515	2.48	952	5.5	-0.15	CZ5	
	C5	47.345	-79.393	3.14	804	4.6	-0.15	CZ4	

Table 2.2 Results of the model selection explaining the variability in growth-climate correlation coefficients among site for each of the main climatic variables (column from figure 2.2).

Values represent differences in the corrected Akaike Information Criteria (Δ AICc) between a given model and the best model. Capital letters represent climate conditions prevailing during the current year of ring formation; small letters represent climate conditions prevailing during the year preceding ring formation. For each climatic variable, the best model (Δ AICc null) is highlighted in grey.

	K	T aug	T MAY	T JUN	P jun	P oct	P MAY	P AUG
Genetic Model (Eq. 2.1)	4	6.43	0.00	1.28	0.00	17.16	1.13	1.72
Environment Model (Eq. 2.2)	6	0.00	5.20	0.00	5.43	0.00	0.00	0.00
Complete Model (Eq. 2.3)	8	7.10	7.48	5.18	10.41	8.14	1.42	2.17

Table 2.3 Results of the linear model selection explaining the radial growth synchronicity between trees of a given site ($\bar{r}_{bt}$).

All models had the same number of replicates, i.e. 24 sites. Each model had one of the following explanatory variables: DBH standard deviation (sd_{DBH}), allelic richness (AR), mean pairwise genetic relatedness ($Gen_{relatedness}$), inbreeding coefficient (F_{is}), $annual\ GDD_{1953-2010}$ and $Seasonal\ P_{1953-2010}$. Models are sorted by increasing AICc, the best model being at the top.

Model	K	Δ AICc	AICc	LL
$\bar{r}_{bt} \sim Seasonal\ P_{1953-2010}$	3	0	-36.27	21.73
$\bar{r}_{bt} \sim H_e$	3	0.07	-36.20	21.70
$\bar{r}_{bt} \sim annual\ GDD_{1953-2010}$	3	0.56	-35.71	21.46
$\bar{r}_{bt}$ ~ AR	3	1.39	-34.87	21.04
$\bar{r}_{bt} \sim Gen_{relatedness}$	3	1.94	-34.33	20.77
$\bar{r}_{bt} \sim sd_{DBH}$	3	2.23	-34.03	20.62
$\bar{r}_{bt} \sim F_{is}$	3	3.05	-33.22	20.21

2.10 Figures

Figure 2.1 Location of the *Thuja occidentalis* sampling sites and distribution area.

(a) Location of the *Thuja occidentalis* sampling sites (black squares). The background shading illustrates *Thuja occidentalis* biomass in t.ha^{-1} (Beaudoin et al. 2014). Sampling was stratified between the continuous zone of distribution (CZ), the discontinuous zone (DZ) and the marginal zone (MZ). The western part and the eastern part of the marginal zone (MW and ME respectively) were distinguished in our analyses. (b) Localisation of the study area (outlined area) relative to the species' range (hatch area, Little 1971).

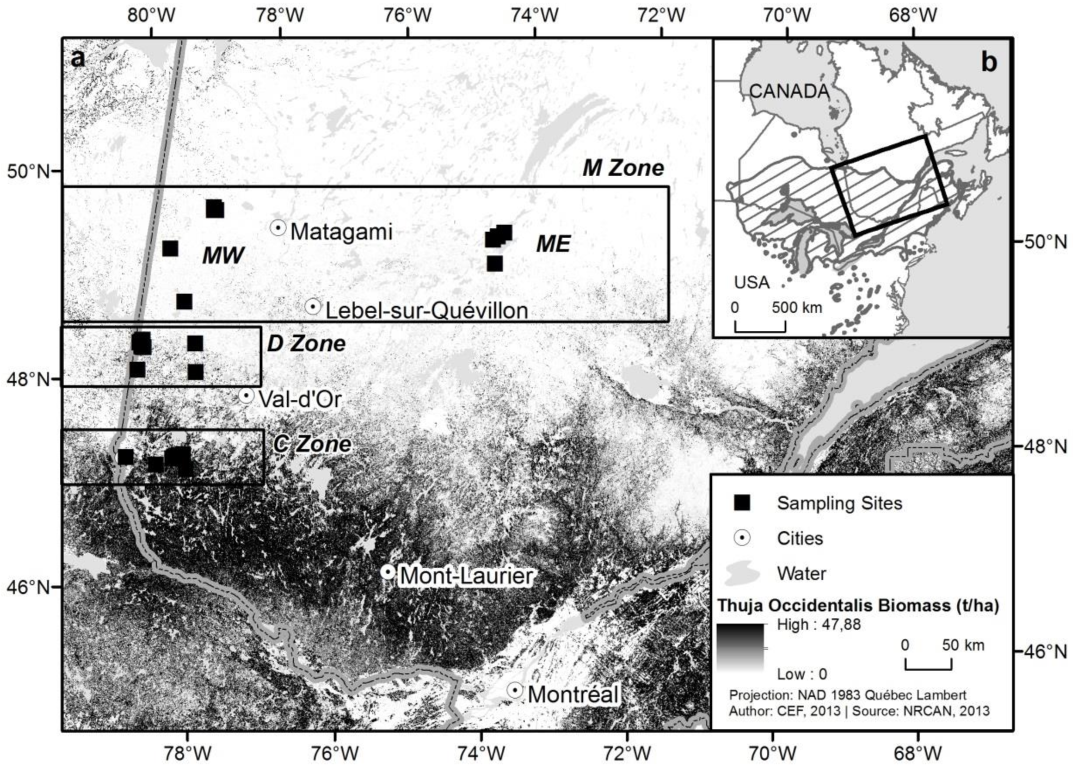


Figure 2.2 Growth-climate correlation matrix for *Thuja occidentalis*.

Growth−climate correlation matrix for the seven main monthly climatic drivers of radial growth interannual variations (columns) and the 24 sites (rows). Colours represent the value of the correlation coefficients computed between *Thuja occidentalis* residual tree-ring index chronologies and monthly mean temperature (August of the previous year, May and June of the current year) and the monthly precipitations (June and October of the previous year, May and August of the current year). Significant correlations are represented by dots for the bootstrapped response function method and by circles for the correlation function. Sites are sorted by increasing amount of mean annual growing degree days over the 1953-2010 period, the coldest sites being at the top.

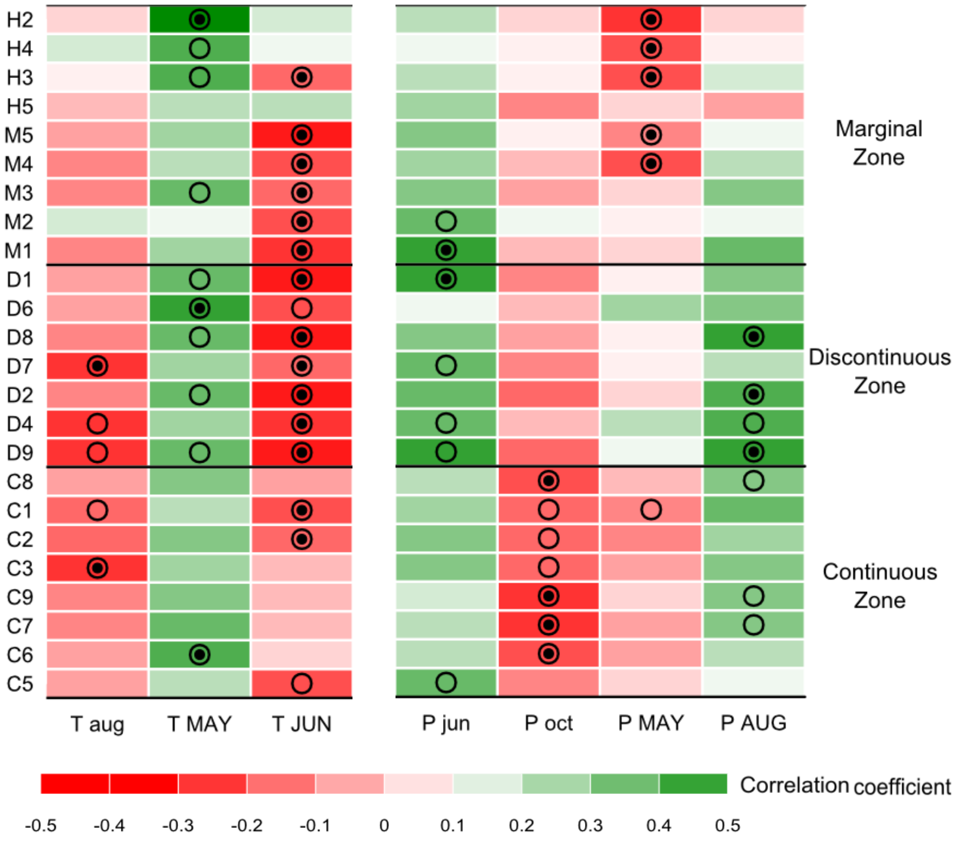
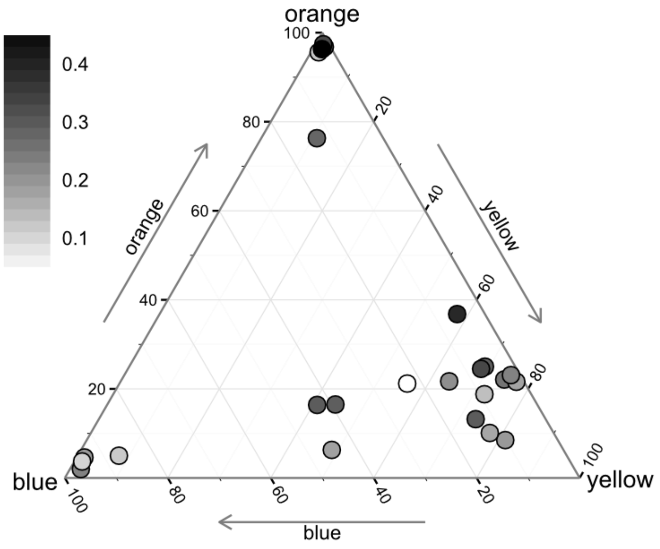


Figure 2.3 Variations in the growth-climate correlation coefficients with the genetic structure.

Variations in the growth-climate correlation coefficients with the genetic clusters (orange, blue and yellow) for (a) May temperature and (b) June precipitation of the year prior to ring formation.Each point represents one of the 24 sampling sites.

a. Correlation coefficient with May temperature



b. Correlation coefficient with previous June precipitation

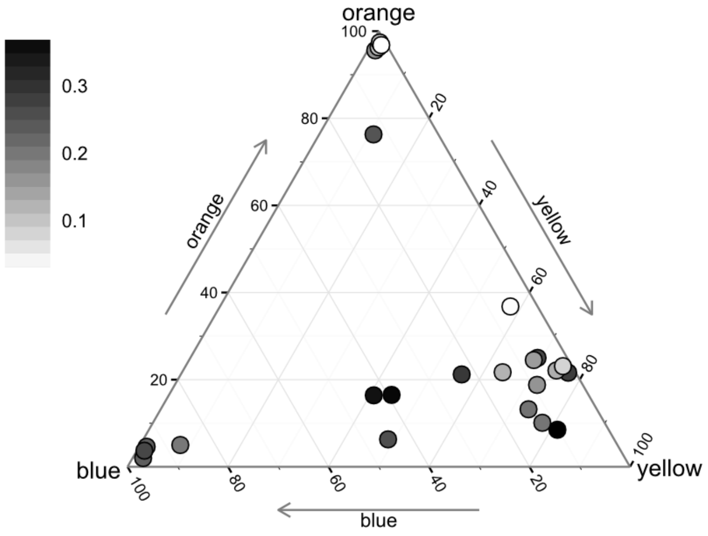


Figure 2.4 Variance partitioning between environment and genetic variables.

Variance partitioning between environment variables (Eq. 2.1) and genetic structure variables (Eq. 2.2) to explain variability in growth−climate correlation coefficient among sites for (a) each monthly climatic variable and (b) all of them. Black bars represent the percentage of variance explained by genetic structure variables only, dark grey bars represent the variance explained jointly by environmental data and genetic structure data, and pale grey bars represent the variance explained by environmental variables only. The sum of the three represents the total variance explained by all the variables (Eq. 2.3).

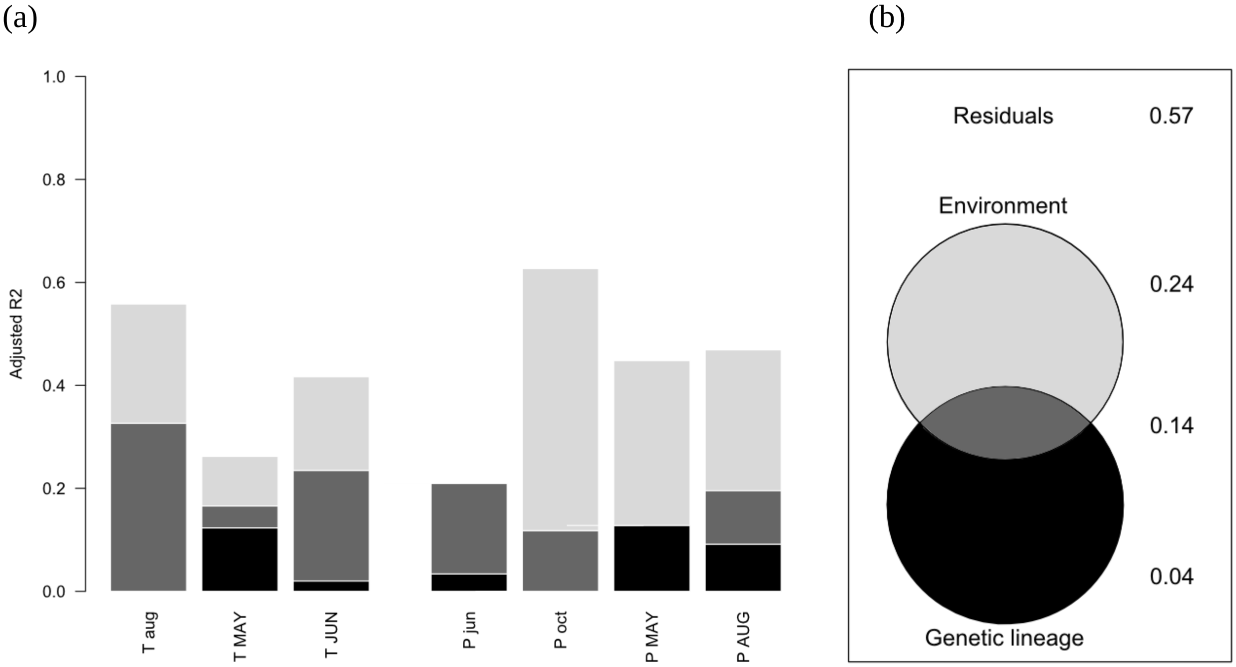
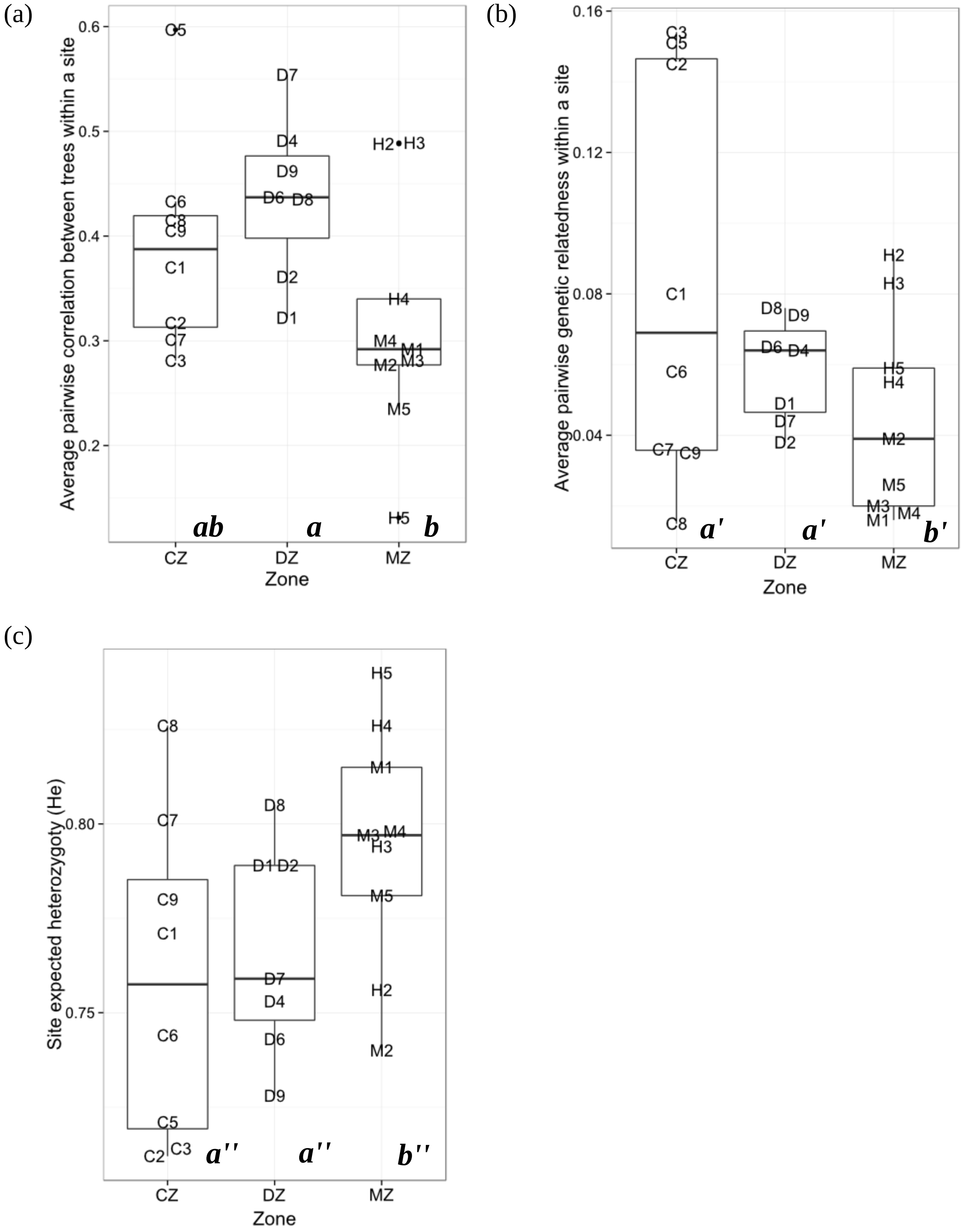


Figure 2.5 (a) Average pairwise growth correlation between trees within each site, (b) average pairwise genetic relatedness, and (c) expected heterozygoty (H_e).

CZ= continuous zone, DZ= discontinuous zone and MZ= marginal zone. Different letters indicate a pairwise significant difference in the mean value between two groups (p < 0.05).



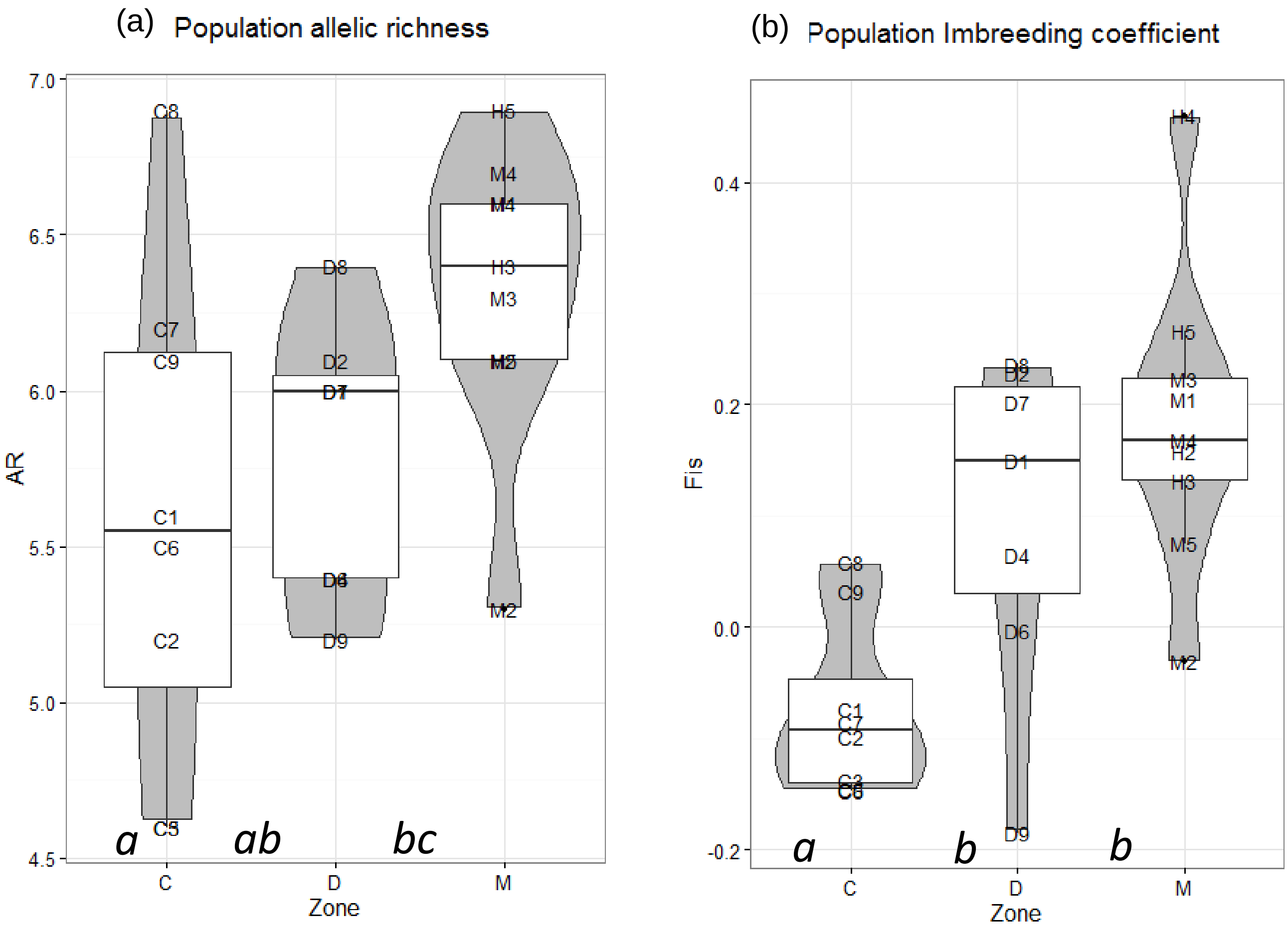
2.11 Appendices

Appendix 2.1 Output of the models of Eq. 2.2 for the correlation with (a) May temperature and (b) June precipitation in the previous year

```
a. Response variable = T May

Call:
lm(formula = mydata[, i] ~ blue + yellow + orange, data = mydata)

Residuals:
      Min        1Q    Median        3Q       Max 
-0.188450 -0.048232 -0.000896  0.067942  0.141996 

Coefficients: (1 not defined because of singularities)
            Estimate Std. Error t value Pr(>|t|)    
(Intercept)  0.32133    0.04299   7.475  2.4e-07 ***
blue        -0.16303    0.06448  -2.528   0.0195 *  
yellow      -0.10660    0.06614  -1.612   0.1219    
orange            NA         NA      NA       NA    
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.08929 on 21 degrees of freedom
Multiple R-squared: 0.2386,	Adjusted R-squared: 0.166 
F-statistic:  3.29 on 2 and 21 DF,  p-value: 0.05717
```

```
b. Response variable = P pJun

Call:
lm(formula = mydata[, i] ~ blue + yellow + orange, data = mydata)

Residuals:
     Min       1Q   Median       3Q      Max 
-0.15482 -0.05540 -0.01077  0.06778  0.15076 

Coefficients: (1 not defined because of singularities)
            Estimate Std. Error t value Pr(>|t|)  
(Intercept)  0.10232    0.04196   2.439   0.0237 *
blue         0.17373    0.06293   2.761   0.0117 *
yellow       0.12596    0.06455   1.951   0.0645 .
orange            NA         NA      NA       NA  
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Residual standard error: 0.08715 on 21 degrees of freedom
Multiple R-squared: 0.2783,	Adjusted R-squared: 0.2096 
F-statistic: 4.049 on 2 and 21 DF,  p-value: 0.03256
```

Appendix 2.2: (a) Mean population allelic richness and (**b**). inbreeding coefficient (Fis) for continuous zone (C), discontinuous zone (D) and marginal zone (M). Different letters indicate a significant difference in the mean value between two groups (*t*-test, $p < 0.05$).



CHAPITRE III

BEYOND THE SOLE CLIMATE EFFECTS ON TREE-RING WIDTH VARIATIONS: THE COMPLEX FUNCTION OF TREE GENETIC, TREE MORPHOLOGY, AND THE ENVIRONMENT

(AU-DELA DU SIMPLE EFFET DU CLIMAT SUR LES VARIATIONS DE CROISSANCE RADIALE : UNE MODULATION COMPLEXE PAR LA GÉNÉTIQUE, LA MORPHOLOGIE DES ARBRES ET LES VARIABLES ENVIRONNEMENTALES)

Johann Housset[1,2,3,4*,] Francine Tremblay[1,2], Renzo Motta[5], Martin P. Girardin[2,6], Yves Bergeron[1,2], Christopher Carcaillet[3,4]

[1]Natural Sciences and Engineering Research Council of Canada Industrial Chair in Sustainable Forest Management, Forest Research Institute, Université du Québec en Abitibi-Témiscamingue, 445 boulevard de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada, [2]Centre d'étude de la forêt, Université du Québec à Montréal, C.P. 8888, Montréal, Québec, H3C 3P8, Canada, [3]Ecole Pratique des Hautes Etudes, F-75014 Paris, France, [4]LEHNA (UMR5023, CNRS), Université Lyon 1, F-69622 Villeurbanne, France, [5]Università degli Studi di Torino – Dip. Agroselviter, Via Leonardo da Vinci 44, I-10095 Grugliasco (TO), Italy, [6]Natural Ressources Canada, Canadian Forest Service, Laurentian Forestry Centre, 1055 du P.E.P.S, PO Box 10380, Stn. Sainte-Foy, Quebec, QC, G1V 4C7, Canada.

*Auteur correspondant: Johann Housset, Centre d'Étude de la Forêt, CP 8888, Montréal, QC, H3C 3P8, Canada. E-mail: housset.johann@courrier.uqam.ca

Manuscrit en préparation au moment de la fin de cette thèse de doctorat..

3.1 Résumé

Dans un contexte de changement climatique, les modifications de croissance et d’abondances des plantes devraient être les plus fortes au niveau des limites d’aires de répartition des espèces. La capacité d’adaptation des populations marginales à leur nouveau climat pourrait être décisive pour les espèces car les prédictions tendent à montrer que la migration sera probablement trop lente pour suivre le déplacement des enveloppes bioclimatiques vers les pôles. Cependant, la diversité génétique intra-populationelle réduite de ces populations pourrait entraver leur capacité d’adaptation. Dans cet article, nous testons l’existence d’une relation entre la structure génétique et la réponse de la croissance radiale annuelle à la variabilité climatique de *Pinus cembra* à sa limite sud-ouest de répartition dans les Alpes. Un total de 444 pins cembro a été échantillonné dans 16 sites forestiers de montagne, à une altitude moyenne de 2018 m. Nous avons testé l’influence de la structure génétique, des conditions climatiques et de variables liées à la morphologie des arbres des populations sur le synchronisme de croissance au niveau du site entre les arbres du même site, et sur la réponse de la croissance radiale annuelle des arbres à la variabilité climatique. Nous avons observé que le synchronisme de croissance des arbres au niveau du site était corrélé à la fois avec la richesse allélique et le régime de précipitation. De plus, nous avons montré que les relations climat-croissance étaient principalement liées au régime climatique régional (notamment les précipitations moyennes annuelles) et à la morphologie des arbres et faiblement liées à la structure génétique. Cependant, la structure génétique présente une relation significative avec la réponse de la croissance radiale annuelle à la température de fin d’automne de l’année précédant la formation du cerne. Contrairement aux études antérieures sur *P. cembra* qui ont seulement pris en compte les paramètres climatiques, nous avons ici démontrent que la croissance radiale des arbres est influencée par des interactions complexes entre la structure génétique et les variables environnementales, y compris le régime climatique régional. Toutefois, l'inclusion de la structure génétique apporte une faible contribution à la modélisation de la croissance radiale à l'échelle régionale.

Mots clés : Adaptation, changements climatiques, dendroclimatologie, structure génétique, populations périphériques, forêt tempérée subalpine, croissance radiale.

3.2 Abstract

Under climatic change, modifications on plants' growth and abundances are expected to be the strongest at species margins. Tree adaptations may thus play a key role as migration is predicted to be too slow to track poleward shifts of bioclimatic envelops. However, reduced intra-population genetic diversity could hinder the adaptation capacity of tree populations to climate change. Here we test for the existence of relationships between the genetic structure and the response of annual tree radial growth to climate variability of *Pinus cembra*, a boreo-mountain pine species, at its southwestern distribution. We tested the influence of genetic structure, climatic conditions and tree morphology variables on the between-trees radial growth synchronicity at site-level, and on the response of annual radial growth of trees to climate variability. We found that the between-trees growth synchronicity was affected by both the allelic richness and the precipitation regime since AD 1900. But, the inter-site growth-climate relationships are mostly linked to environmental and tree-size variables and poorly to genetic structure. However, the genetic structure has significant relationship on the response of annual radial growth to late-fall temperature variability of the year before ring formation. Contrary to former studies on *P. cembra* that only took into account climate parameters, we here demonstrate that tree radial growth at individual-to-stand scale is under complex interactions between genetic and environment including climate. However, the inclusion of the genetic structure remains limited for radial-growth modeling at the regional scale.

Key words: Adaptation, climate change, dendrochronology, genetic structure, peripheral population, temperate subalpine forest, tree growth.

3.3 Introduction

The ongoing warming will cause pole-ward and upward shifts of isotherms and locally-dependent changes in precipitation patterns (Chapin *et al.*, 2011 ; IPCC, 2013). These modifications could change the climatic selection pressures patterns acting on plant distribution, such as temperatures and dryness (Chapin *et al.*, 2011 ; Polechová *et al.*, 2009). Rapid warming raises the question of the ability of tree populations to cope with their new local climatic conditions (Alberto *et al.*, 2013 ; Jump et Peñuelas, 2005). Research investigating the response to selection pressure indicates that population ability to adapt on a given trait involves a genetic control on this trait under selection and the existence of intra-population genetic variability for this trait (Barton, 2001 ; Savolainen *et al.*, 2007). Although many models have implemented the rate of adaptation, the predictive power of these models is limited by insufficient empirical knowledge of the genes involved in the adaptation to local climate and their interactions (Polechová *et al.*, 2009 ; Sexton *et al.*, 2009 ; Shaw et Etterson, 2012). Predictions are also limited by a lack of knowledge on species range-wide genetic variation (Aitken *et al.*, 2008), and by the lack of temporal hindsight on the past evolutionary responses (Polechová *et al.*, 2009). *In situ* studies documenting both genetic structure and plant traits over broad ecological gradients including range limits are needed to calibrate and validate models of adaptation through space and time (Aitken *et al.*, 2008 ; Sexton *et al.*, 2009).

Dendroclimatology focuses on the link between climate and, amongst other things, the annual radial growth of trees, i.e., annual xylem production (E. Cook et Kairiūkštis, 1990 ; Fritts, 1976). The annual radial growth of trees constitutes a valuable source of information to investigate the *in situ* phenotypical response of a tree species to its local climate, via the repeated indirect measurement of the effects of climate on tree physiology. One chief application of dendroclimatology is the investigation of the relations between the annual radial growth of trees and climate variability at sites located near species ecological boundaries (Fritts, 1976). It is often noted that the climatic signal captured in tree-ring time-series is stronger in a stressful or constrained environment (Filion et Payette, 2010 ; Fritts, 1976). Such sites, however, could also be well suited for the study of selection pressure gradients. Indeed, ecological gradients are superimposed with selection force gradients.

We aim to investigate the relationships between genetic structure and the response of annual radial growth of *Pinus cembra* L. subsp. *cembra* (cembra pine also called arolla pine) trees to climate variability over multiple sites at the western edge of the species' distribution. We formulated and tested the following hypotheses:

H3.1: Radial growth synchronicity between trees of a single site is both linked to the intra-population genetic diversity and to similar environmental conditions; by placing a common growth constraint on all trees of a site, a more stressful local climate could lead to a greater synchronicity (King *et al.*, 2013 ; Schweingruber, 1996).

H3.2: Responses of stem radial growth to climate variability is influenced but the genetic structure. The alternative hypothesis is that variability in climate responses among sites is only linked to environmental conditions or tree size (i.e. no effects from genetic structure).

3.4 Material and method

3.4.1 Biological material

Cembra pine is an evergreen long-lived (>500 yrs) and late-succession boreo-mountain tree species (e.g. Genries *et al.*, 2009), with a distribution spanning all the subalpine zone of the Alps, with patchy populations in the Carpathes (Fig. 3.1a). The other subspecies (*P*. c. ssp. *sibirica* and *pumilia*) growth in Asia, from the Ural to the Kamchatka. If moderate disturbances that do not kill trees can affect the radial growth of cembra (e.g., surface fires: Genries *et al.*, 2009), other dominant disturbances in this ecosystem have very low consequences on this productivity trait, chiefly the larch budworm disease (Nola et al. 2006; Battipaglia et al., 2014). Given these characteristics, cembra pine has already proven to be a good species to study the growth-climate relationships (Carrer *et al.*, 2007 ; Leonelli *et al.*, 2009 ; Saulnier *et al.*, 2011 ; Vittoz *et al.*, 2008). However, no attempts were made to explore the contribution of genetic structure on the expression of the relationships between radial growth and climate variability.

3.4.2 Study area

The study area covers the western Alps (latitude 44.1-46.0°N, longitude 5.9-7.5°E). Sampling was focused on the western peripheral populations of cembra pine, including stands from the French and the Italian inner Alps (Fig. 3.1). A total of 16 cembra stands were sampled at a mean (±sd) altitude of 2018 ±129 m, which is representative of the species western distribution in the subalpine and alpine bioclimatic zones. Slopes, aspect and soil depth (up to 60 cm) of each stand were measured in the field, as well as the diameter at breast height (DBH) and height (H) of each tree. Those variables were used as environmental variable in the later analysis. According to the HISTALP database (Auer *et al.*, 2007), the mean (±sd) annual temperature (MAT) of our sample sites averages 2.1 ±0.77 °C over the period 1900-2003, with a mean (±sd) annual precipitation (MAP) averaging 1129 ±289 mm.year^{-1}. The spatial variations in the climatic conditions over our study area are characterized by a decrease in the annual precipitation southward (Table 3.1), resulting in a drought gradient linked to summer Mediterranean influences.

3.4.3 Tree-ring data

During summers 2011 and 2012, up to 30 dominant and co-dominant cembra pines were randomly selected in each stands, for a total of 444 trees. Two cores per tree were collected at 1.3 m above ground. Cores were sanded, with progressively finer sandpaper, up to a grit of 600. Annual rings of each core were visually cross-dated with skeleton-plots and pointer-year identification (E. Cook et Kairiūkštis, 1990). Ring-widths were measured with a Velmex measuring table (Velmex Incorporated, Bloomfield, New York, USA) with 10^{-3} mm precision under 4.5× magnification or on a scanned image of the cores using the software Coo-Recorder (Cybis, Saltsjöbaden, Sweden) with 10^{-2} mm precision. Cross-dating was validated with the software COFECHA (Grissino-Mayer, 2001) for each site. Our study did not include growth data on young (<20 tree-rings) and immature (20 to 70 tree-rings) pines owing to difficulties in recovering long-term growth changes in short time series. The average sample size was 28 trees per site (Table 3.1).

The raw ring-width measurement series were detrended to filter out medium- to low-frequency trends (long-term growth trends) from the ring-width measurements. This procedure aimed at maximizing the high-frequency growth responses associated with year-to-year climatic variability. Therein, each raw ring-width series was detrended using 60-year splines with a 50% frequency response (E. Cook et

Kairiūkštis, 1990) using the R package dplR (Bunn, 2008) to obtain a standardized chronology for each core. An average standard chronology was computed for each tree. Temporal autocorrelation was removed using first-order autoregressive modelling and, a residual chronology was computed for each site using a biweight robust mean (E. Cook et Kairiūkštis, 1990). These site-residual chronologies are hereafter used for evaluating the relationships between radial-growth and inter-annual climatic variability.

3.4.4 Meteorological data

Monthly mean temperatures and total monthly precipitation were obtained for 1900–2003 from the trans-alpine network HISTALP database (www.zamg.ac.at/histalp; Auer *et al.*, 2007). We used homogenized time-series interpolated on a systematic 5×5 arc minutes (~9 km in latitude and 6.5 km in longitude) for monthly mean temperatures (Hiebl *et al.*, 2009) and precipitation (Efthymiadis *et al.*, 2006) over the period 1901-2003. Although the HISTALP database spans older periods, the number of calibration weather stations drops before the 1900s (Auer *et al.*, 2007) and the earlier years were not included in our analysis. For each site, data were averaged from the nine closest grid cells using a $1/d^2$ weight, where d is the distance between the site location and the centre of each cell. Finally, climatic series were normalized and linearly detrended for each site using the period AD 1900-2003 to obtain unbiased data of inter-annual climatic anomalies.

3.4.5 Genetic data

Neutral genetic structure was assessed by the genotyping of 29 (±2) trees in average (±sd) for each sampling site, for seven polymorphic microsatellite loci: pc1b, pc3, pc7, pc18, pc22, pc23, pc25 (Salzer *et al.*, 2009). For each sampled stand, the microsatellites genotyping allowed to calculate various complementary indicators of intra-population genetic diversity (Table 3.1) that will be used in the further analysis: the Allelic Richness (AR), the expected heterozygoty (H_e) and the inbreeding coefficient (F_{is}). AR represents the average number of alleles existing in a population, corrected for population size effect. H_e is another indicator of gene diversity, with values ranging from 0 to 1 for low to high diversities (Eckert *et al.*, 2008). A clustering analysis was performed on all the pooled trees across the study area using the STRUCTURE v. 2.3.2 software (Pritchard *et al.*, 2000). According to a Monte Carlo procedure, the genetic structure was characterized by the presence of four different clusters, hereafter coded by the colours red, green, yellow, and blue (Tremblay et al, unpublished data; Fig. 3.1b). In the further analysis, the genetic structure was identified as the % of each genetic cluster in each sampling site.

3.4.6 Intra-population variability analysis

To assess intra-population phenotypic variability, the growth synchronicity was measured through the calculation of the average correlation between trees within a site ($\bar{r}_{bt}$). The $\bar{r}_{bt}$ statistic was calculated as the average pairwise correlation between single tree detrended chronologies within each site (E. Cook et Kairiūkštis, 1990) using the R package dplR (Bunn, 2008). Growth synchronicity between trees could be influenced by differences in tree size or local edaphic conditions, by a more stressful local climate or, by intra-population genetic variability. Tree size variability was estimated by the standard deviation of tree DBH (sd_{DBH}) and tree height (sd_H) for each sampling site. The soil depth was assessed for each tree and the standard deviations ($sd_{Soil\ Depth}$) was calculated at each site to account for differences in edaphic conditions. The effect of climate on growth synchronicity was assessed through the MAT and the MAP, averaged over the period 1900-2003. Finally, three complementary proxies of intra-population genetic diversity were used: AR, H_e and F_{is}. To determine which variable best explained growing variability in our data, we used model selection based on AICc. In the model selection approach, each hypothesis is associated with a model that can be compared to other model hypotheses through the corrected Akaike Information Criteria (AICc) statistic (Burnham et Anderson, 2010). The model with the lowest AICc corresponds to the model with the highest likelihood and, to the hypothesis with the greatest likelihood to fit the observed data. Models having a difference in AICc greater than two in comparison with the best model can be rejected. The model selection was computed using the R package "AICcmodavg" (Mazerolle, 2015). Each model was a linear regression, having the same number of parameters (K), with $\bar{r}_{bt}$ as response variable and one of the following explanatory variable: sd_{DBH}, sd_H, $sd_{Soil\ Depth}$, MAT, MAP, AR, H_e, and F_{is}.

3.4.7 Genetic and dendroclimatological variability relationships

A mixed effect model was built with the standardized tree-ring index, TRI, as a response variable. The sites and years (1900 to 2003) were incorporated as random effects and the temporal autocorrelation was taken into account through a first order auto regressive modelling term. The fixed effects (explanatory variables) included mean monthly temperature and precipitation, and the interaction between these with the genetic structure (% of each genetic cluster per site), MAT, MAP, relief (aspect, slope %), morphology (mean DBH, mean H) and soil depth. To sum up, the following TRI model was build:

$$TRI \sim \sum clim_i + clim_i * X_{i,j}\ ,\ random = sites/year\ . \qquad \text{(Eq. 3.1)}$$

where $clim_i$ is the i monthly or seasonal climatic variable and $X_{i,j}$ the j explanatory variables.

Our analyzes involve many variables and interactions. It was thus crucial to reduce their number to simplify the mixed effect model. Accordingly, we proceeded in a two-step manner. First, climatic variables were screened for their contribution to explaining variability in annual radial growth and non-relevant ones were eliminated. This was done by examining the relationships between mean monthly temperatures and precipitation, and annual radial growth using correlation and principal component regression analyses (PCR, also known as response function analysis; Biondi & Waikul, 2004) over the period 1900-2003 (Appendix 3.1). PCR is a multiple regression technique that uses the principal components of monthly climatic data to estimate the correlation with the growth time-series. Correlation coefficients on the other hand are computed between a site residual chronology and the matrix of climatic data in order to depict the average relationship for the studied period. Correlation and PCR were tested using the bootstrapping technique: when the confidence interval includes 0, the hypothesis of 'no relationship' cannot be rejected at the 95% level. The months under analysis were from May of the year preceding ring formation (hereafter May[-1]) to October of the year current to ring formation, i.e. two growing seasons and one winter. On the basis of the correlation results, we identified the monthly climatic variables that were significant for more than three sites. Monthly climatic variables were averaged when consecutive months turned out significant and these averages were used in the mixed model. Analyses were conducted using the R package treeclim (Zang et Biondi, 2015).

Second, environmental and genetic variables were screened for their contribution to explaining variability in relationship between annual radial growth and climate variability and non-relevant variables were eliminated. This step was conducted using univariate linear regression models built with the correlation coefficients as a response variable and genetic structure (genetic cluster % per site), annual climatic data (MAT, MAP), relief (aspect, slope %), tree morphology (mean DBH, mean H) and soil depth as explanatory variables. Each site was a replicate. Following this exercise, the explanatory variables having a ΔAICc <2 and whose *p*-value was < 0.1 (see Table 3.2) were kept for the mixed effect model.

3.5 Results

3.5.1 Tree-ring time-series

The chronology lengths ranged between 186 and 697 years (Table 3.1), with a mean (±sd) of 324 ±111 years. The average sample size was 28 trees per site (56 cores), with a minimum tree number of 11 for site MGI (Table 3.1). The Expressed Population Signal (EPS) was high (0.92 ±0.05), confirming that the trees of a same site shared a common signal suitable for dendroclimatic analysis (Table 3.1). The average (±sd) pairwise correlation between trees ($\bar{r}_{bt}$) in a site was 0.26 ±0.07.

3.5.2 Intra-site variability

Model selection revealed that two models were likely to explain the intra-population growth synchronicity ($\bar{r}_{bt}$), having a DeltaAICc lower than 2 (Table 3.3). The best model explaining synchronicity corresponded to the Allelic Richness (AR). The second best models explaining synchronicity included the mean annual precipitation (MAP) as explanatory variable (Delta AICc = 1.83). Subsequently, the model including both AR and MAP was computed to test for those effects. This model explained 38.5% of the variance (adjusted R^2). The $\bar{r}_{bt}$ significantly decreased with AR ($p = 0.018$) and with MAP ($p = 0.042$). Specifically, a higher intra-population genetic-diversity is significantly linked with more differences in the growth time-series of a site. Similarly, sites receiving less precipitation per year appeared to be more synchronous.

3.5.3 Growth-climate relationships

While the correlation analysis was conducted on all the monthly mean temperature and precipitation variables (Appendix 3.1), we only present here the analysis for the main climatic variables of cembra pine radial growth selected following the above mentioned screening method (Fig. 3.2). Hereafter, months followed by "[-1]" show correlations with a monthly climatic variable during the year previous to ring formation. Radial growth was negatively correlated with August to September temperatures of the previous year ($T_{aug\text{-}sep[-1]}$). A negative correlation was also observed across the whole study area with March temperature of the current year (T_{mar}). In contrast, growth was positively correlated with previous November temperature ($T_{nov\text{-}1}$). We also observed a positive correlation with June to July temperatures ($T_{jun\text{-}jul}$) and September (T_{sep}) temperature during the year of ring formation, especially in the northern part of the study area (Fig. 3.2). Radial growth was positively correlated with precipitation of August of the year-1 ($P_{aug[-1]}$) and with previous November to current January precipitation ($P_{nov[-1]}$-P_{jan}). A strong positive correlation was also observed with current July precipitation (P_{jul}).

3.5.4 Genetic structure *vs* inter-site growth-climate variations

The effects of the climatic variables on growth appeared to differ among the sites. The model selection procedure allowed to discriminate which variables best explained this inter-site variability (Table 3.2). The correlation with August and

September temperature of the year-1 was best explained by the mean tree height (H). Sites with taller trees had more negative correlations with $T_{aug\text{-}sep[-1]}$ (p <0.001). The correlation with August[-1] precipitation varied with both mean H and MAP. Sites with taller trees had more positive effects of P_{aug} ($p = 0.003$). However, sites receiving more annual precipitation exhibited a less positive effects of P_{aug} ($p = 0.005$). The best candidate variable to explain the correlation with T_{nov} was the % of genetic cluster: sites with higher proportions of the blue cluster had a less positive correlation with $T_{nov[-1]}$ (p =0.002). Several models had a ΔAICc lower than 2 to describe the variability in the correlation with T_{mar}, corresponding to the following explanatory variables: MAP (ΔAICc = 0), %blue (ΔAICc = 0.77) and %yellow (ΔAICc = 1.75). But, all these models were poorly significant, with p-values of 0.062, 0.092 and 0.157 respectively (Table 3.2). Both $T_{jun\text{-}jul}$ and P_{jul} were best related to MAP. A high MAP was associated with a higher correlation with $T_{jun\text{-}jul}$ ($p < 0.01$) and a lower correlation with P_{jul} ($p < 0.01$). MAP was also the best model to explain the correlation with P_{nov}-$P_{jan[-1]}$, which was lower for sites receiving more precipitation ($p < 0.01$). Finally, the positive effect of September temperature was lower for sites of higher elevation ($p < 0.05$). Correlation with T_{sep} also seemed to be influenced by the % of yellow genetic cluster, although this relation was poor ($0.05 < p < 0.1$).

According to our results, the inter-site variability in the growth-climate correlation is greatly influenced by non-genetic variables (MAP, mean H and MAT) and, in a lesser extent, by the genetic structure (%blue and, weakly, by %yellow). However, the fact that the correlation with a climatic variable is influenced by a modulating factor does not mean that the effect of this interaction significantly influenced the TRI overall. Examining the output of the TRI model (Eq. 3.1) allowed to disentangle the relative effect of each climatic variable and of each modulating factor, and to test their effect on TRI (Fig. 3.3). It reveals that MAP has a significant interaction with $P_{nov[-1]}$-P_{jan} and P_{jul} ($p < 0.001$ in both cases). The interaction between

MAP and $T_{jun\text{-}jul}$ had also a significant modulating effect on TRI ($p < 0.05$ p=0.023). The interaction of mean H and $P_{aug[-1]}$ did not significantly contribute to the prediction of TRI. But mean H interaction with $T_{aug\text{-}sep[-1]\_}$ varied significantly with TRI ($p < 0.01$ p=0.004). Finally, the interaction of the %blue cluster with T_{nov} was also significant ($p < 0.05$ p=0.027) but poor with T_{mar} (p=0.09). The effect of the yellow cluster % on T_{mar} and T_{sep} was finally not significant.

3.6 Discussion

In this research, we tested a novel approach to investigate tree responses to climate change, involving both *in situ* genetic and dendroclimatologic features. Our investigation on the multi-decadal dendroclimatological responses of cembra pine in the western Alps revealed that the genetic structure influenced the correlation with previous year fall temperature at the inter-site scale. However, the climatic regime and tree size accounted for the great majority of the inter-site variability in the effects of temperatures and precipitation on radial-growth. First, we will discuss the links between the genetic diversity, the environmental variables and the intra-population radial-growth synchronicity. Second, the link between the growth-climate relationships of cembra pine across the study area and environmental, size related and genetic modulating factor will be further commented. Finally, the implications for research on eco-evolutionary dynamics and dendroclimatology at biogeographic limits will be briefly exposed.

3.6.1 Intra-site synchronicity of radial growth linked to genetic diversity

At the intra-site scale, we found that the growth synchronicity between trees within a site ($\bar{r}_{bt}$) was negatively correlated to the allelic richness, meaning that more genetically diverse stands have more phenotypical variability for radial growth. Our observation supports the idea that the tree-ring pattern is influenced by its genetic diversity, and not only by annual climate, soil or tree morphology. However, about other boreo-mountain conifers, King et al. (2013) found no link between growth synchronicity and the pairwise genetic relatedness for spruce (*Picea abies* (L.) Karst) and larch (*Larix decidua* Mill.), the pairwise genetic being another proxy of genetic diversity. This difference could be explained by the fact that they investigated growth synchronicity under climatic conditions different from the local climate of the seeds tested: indeed, the genetic provenances under study were planted in a common garden experiment where the dendroclimatology analysis was conducted. In our study, we have an assessment of both *in situ* genetic and dendroclimatology features. According to our results, growth synchronicity measured through dendroclimatology could be an indirect proxy of genetic diversity. But, synchronicity is also greatly influenced by the mean annual sum of precipitation (MAP), as a dryer climate may place a common drought constraint on trees resulting in a higher synchronicity (Schweingruber, 1996). Therefore, genetic diversity cannot unfortunately be directly inferred from synchronicity without taking into account climatic constraints in complex relations.

3.6.2 Modulating factors of between-site variability

As a preliminary result, we identified eight climatic variables influencing growth inter-annual variations in our study area: $T_{aug\text{-}sep[-1]}$, $T_{nov[-1]}$, T_{mar}, $T_{jun\text{-}jul}$, T_{sep}, P_{aug}, $P_{nov[-1]\text{-}jan}$, P_{jul}. This dendroclimatic signature is consistent with other dendroclimatological analyses; in close (Vittoz *et al.*, 2008) or overlapping (Carrer *et* *al.*, 2007) study zones. In addition, we had similar results to Saulnier et al. (2011) study of cembra pine dendroclimatology in the French Alps. Radial growth correlation with previous summer ($T_{aug\text{-}sep[-1]}$) likely reflects an indirect sensibility to the hydric stress. Summer droughts during the year prior to ring formation could lower the accumulation of carbohydrates reserves available for the next growing season (Fritts, 1976). The negative effect of previous summer temperatures could also be linked with a higher loss of carbohydrates due to efforts to maintain respiration (Chapin *et al.*, 2011). The negative correlation with T_{mar} could be related to respiration costs before photosynthesis reactivation (Saulnier *et al.*, 2011). Another possible cause of this negative correlation could be that a warm March could enhance an earlier dormancy termination, indirectly reducing growth through an increased risk of frost injury. A warmer fall decreases the risk of frost injury on bud or cambium (Howe *et al.*, 2003). The negative correlation with previous summer precipitation ($P_{aug[-1]}$) builds on the hypothesis of a previous summer hydric stress. The positive correlation with previous November to current January precipitation ($P_{nov[-1]}$-P_{jan}) may have several biological interpretations. Winter precipitation could decrease the risk of frost injuries thanks to the snow cover insulating properties (Havranek et Tranquillini, 1995). Moreover, winter snow accumulation can reduce the risk of hydric stress during the next growing season with an overwintering effect on soil hydric reserves during the following spring snow melting.

We found that the inter-site variability of the correlation between growth and those climatic factors was primarily influenced by environmental and size-related variables, strengthening the idea that tree-ring width does not have a strong genetic control. This finding is consistent with results from common garden experiments on conifer species phylogenetically different from the cembra pine, in which experiments, different genetic provenances were planted in a common environment, to isolate the genotype effect on growth performances (heritability). Those experiments have shown that trees radial growth is a trait of low heritability

(Beaulieu et Bousquet, 2010 ; Cornelius, 1994). In our data, a variance partitioning on the TRI model (Eq. 3.1) revealed that the climatic variables alone explained 72.5% of the inter-site variance. The interactions with the climatic regime (MAP and MAT) and mean H variables explain 93.3% of the additional 27.5% explained variance, *versus* 6.3% for the interactions with genetic structure variables. Few dendrochronological studies were led on common garden experiment planted trees further reporting a null or very low genetic effects on the growth-climate relationships for several pine species, such as *P. banksiana* (Savva *et al.*, 2008) or *P. sylvestris* (Savva *et al.*, 2002). All those studies point out to a stronger effect of environmental factors on the radial growth inter-site variations.

3.6.3 Precipitation chiefly trigger the radial growth functional response

In our study area, MAP is the most important variable contributing to the variability in cembra pine growth-climate relationships. Sites receiving less precipitation are associated with a higher positive influence of summer precipitation (P_{jul}) and previous winter precipitation ($P_{nov[-1]-jan}$). They also exhibit a lower positive influence of current summer temperature ($T_{jun-jul}$). The positive influence of warm summer is lower for sites receiving less precipitation, which can be explained by a temperature-induced hydric stress under drier precipitation regimes. Ring width formation depends on the number of cell divisions, which could be influenced by the amount of carbohydrates reserves inherited from the previous year (Fritts, 1976). Cell enlargement is another determining factor of ring width variations. It depends largely on water availability for the tree during the year of ring formation, especially during summer where the most important part of the enlargement takes place (Filion et Payette, 2010 ; Gruber *et al.*, 2009). Climatic conditions during the previous summer are, however, less influenced by the precipitation regime. Instead, the differences in tree size (mean H) played a key role in the inter-site variability for the correlation with previous summer temperature ($T_{aug\text{-}sep[-1]}$). Sites with taller trees are more negatively affected by warm summers during the growing period preceding ring formation. This finding supports the hypothesis exposed in the previous paragraph that the negative effect of $T_{aug\text{-}sep[-1]}$ on growth is due to a higher maintenance respiration, which is known to increase proportionally with plant biomass (Lavigne et Ryan, 1997 ; Tang *et al.*, 2014).

3.6.4 Modulating effects of the genetic clusters on the growth-climate relationships

Interestingly, genetic structure was only related to variability in growth-climate relationships for climate variables corresponding to fall temperature ($T_{nov[-1]}$ and T_{sep}) and spring temperature (T_{mar}; Table 3.2). However, the only climatic driver of radial growth being influenced by the genetic structure is the previous November temperatures. This climate-radial growth interaction could be due to the higher genetic control of the frost hardiness (Howe *et al.*, 2003). For instance, not all the genotypes have the same thermal requirements to enter dormancy: researches have shown that the timing of bud set has a higher heritability than radial growth (Howe *et al.*, 2003), reaching 67% for instance in *P. sylvestris* (Savolainen *et al.*, 2004). This trait has an evolutionary implication in tree adaptation to their local climate caused by a trade-off between maximizing the carbohydrate assimilation and minimizing the vulnerability to early fall frosts (Howe *et al.*, 2003). The slight link between genetic structure and the correlation with March temperature could possibly reflect a genetic control of the dormancy termination. The TRI model reproduced quite well the average TRI chronology of our study area, with a spearman correlation of 0.576 between the observed TRI and the predicted TRI time-series. When the genetic structure modulating factors are removed from the equation. 3.1, the spearman correlation only slightly decrease to reach 0.572, meaning that the predictive power of the TRI model is not increased by those factors at the regional scale. Interactions with genetic structure variables accounted for a relatively small proportion of the variance in comparison with the other factors. According to a sensitivity analysis, the genetic structure slightly changed the amplitude of the predicted TRI (Fig. 3.4), mostly through the interaction between the percentage of the blue cluster and $T_{nov[-1]}$. This genetic cluster seems to be more present in western peripheral populations of the study area (Fig. 3.1), thus strengthening the theory of higher rate of genetic differentiation within marginal populations (Eckert *et al.*, 2008). Dendroclimatic studies encompassing marginal populations could therefore increase their predictive power with the inclusion of genetic structure interactions with climate.

3.7 Conclusion

Dendroclimatic signal of *P. cembra* was not strongly correlated with the genetic structure, making it not suitable to use as a proxy for the tree populations response to climate change. Although growth synchronicity was correlated with the intra-population genetic diversity, supporting our hypothesis H3.1, modeling it would require accounting for other environmental variables, such as the precipitation regime. Contrary to our hypothesis H3.2, the between-site variability in the growth-climate relations was mostly influenced by site-specific ecological and tree-size variables. The within site heterogeneity appears linked to genetic diversity. The site-specific ecological variables are the annual precipitation, the mean tree height and the altitude. Nevertheless, the genetic structure was more strongly correlated to the variability of responses to some specific climatic variables, such as the fall temperature in particular. A deeper investigation of this relationship could be complementary to the study of traits related to dormancy phenology, whose genetic control is stronger. Our model of the effects of climate, coupled with interactions with environment and genetic structure variables, allowed to correctly predict the inter-annual radial growth variations. Variations of the genetic structure in our model did not seem to significantly modulate the predictions of TRI time-series and we argue that the inclusion of the genetic structure is not necessary for TRI modeling at the regional scale. It could be useful to take this effect into account in some cases for dendroclimatic studies to slightly increase the predictions of the models, especially for the study of peripheral populations that tend to exhibit higher genetic differentiation.

3.8 Acknowledgements

We are thankful to the institutions that made this study possible through there valuable help : the Mercantour and Vanoise national, the Plan Tuéda national reserve, the Direction Régionale de l'Environnement Rhône-Alpes, and the French forest administration (Office National des Forêts). We warmly thank Jean-Christophe Gattus, Lilian Micas, Daniel Lesieur, Albanie Leduc, Maxime Allard, Maxime Tremblay, Benoit Brossier, Laure Paradis, Mathieu Baconnet, Guillaume, Charles et Francis Tremblay Bergeron, Cécile Leroy, Fabio Meloni, Guido, Paola Nola, Marc Mazerolle. This study was conducted with the financial support of the Natural Sciences and Engineering Research Council of Canada (NSERC) through its CREATE program in Forest Modelling Complexity (PhD grant to JH) and by the ANR/ERA-net BiodivERsA granted to CC. JH obtained a PhD grant from the French programme Paris Nouveau Monde "Humboldt" and, FT a 6-months visiting grant from the French National Centre for Scientific Research (CNRS) and a 2-months from the University of Montpellier 2. This research was also funded by a NSERC strategic grant (STPGP336871) to Francine Tremblay and by the joint French-Canadian laboratory LIA MONTABOR.

3.9 References

Aitken S.N., Yeaman S., Holliday J.A., Wang T., & Curtis McLane S. (2008) Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, **1**, 95–111.

Alberto F.J., Aitken S.N., Alía R., González-Martínez S.C., Hänninen H., Kremer A., Lefèvre F., Lenormand T., Yeaman S., Whetten R., & Savolainen O. (2013) Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, **19**, 1645–1661.

Auer I., Böhm R., Jurkovic A., Lipa W., Orlik A., Potzmann R., Schöner W., Ungersböck M., Matulla C., Briffa K., Jones P., Efthymiadis D., Brunetti M., Nanni T., Maugeri M., Mercalli L., Mestre O., Moisselin J., Begert M., Müller-Westermeier G., Kveton V., Bochnicek O., Stastny P., Lapin M., Szalai S., Szentimrey T., Cegnar T., Dolinar M., Gajic-Capka M., Zaninovic K., Majstorovic Z., & Nieplova E. (2007) HISTALP—historical instrumental climatological surface time series of the Greater Alpine Region. *International Journal of Climatology*, **27**, 17–46.

Barton N.H. (2001) Adaptation at the edge of a species' range. *Special Publication - British Ecological Society*, **14**, 365–392.

Battipaglia G., Büntgen U., McCloskey S.P., Blarquez O., Denis N., Paradis L., Brossier B., Fournier T., & Carcaillet C. (2014) Long-term effects of climate and land-use change on larch budmoth outbreaks in the French Alps. *Clim Res*, **62**, 1–14.

Beaulieu J. & Bousquet J. (2010) Facteurs génétiques affectant la variabilité des cernes annuels chez les espèces arborescentes nordiques. *La dendroécologie: principes, méthodes et applications.* pp. 137–167. Payette, S. and Filion, L., Eds.,

Biondi F. & Waikul K. (2004) DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences*, **30**, 303–311.

Bridle J.R., Polechová J., Kawata M., & Butlin R.K. (2010) Why is adaptation prevented at ecological margins? New insights from individual-based simulations. *Ecology Letters*, **13**, 485–494.

Bunn A.G. (2008) A dendrochronology program library in R (dplR). *Dendrochronologia*, **26**, 115–124.

Burnham K.P. & Anderson D.R. (2010) *Model selection and multi-model inference: A practical information-theoretic approach.* Springer, Carrer M., Nola P., Eduard J.L., Motta R., & Urbinati C. (2007) Regional variability of climate-growth relationships in Pinus cembra high elevation forests in the Alps. *Journal of Ecology*, **95**, 1072–1083.

Chapin F.S.I., Chapin M.C., Matson P.A., & Vitousek P. (2011) *Principles of terrestrial ecosystem ecology.* Springer,

Cook E. & Kairiūkštis L. (1990) *Methods of dendrochronology: applications in the environmental sciences.* Kluwer Academic Publishers, Dordrecht, The Netherlands.

Cornelius J. (1994) Heritabilities and additive genetic coefficients of variation in forest trees. *Canadian Journal of Forest Research*, **24**, 372–379.

Eckert C.G., Samis K.E., & Lougheed S.C. (2008) Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. *Molecular Ecology*, **17**, 1170–1188.

Efthymiadis D., Jones P.D., Briffa K.R., Auer I., Böhm R., Schöner W., Frei C., & Schmidli J. (2006) Construction of a 10-min-gridded precipitation data set for the Greater Alpine Region for 1800–2003. *Journal of Geophysical Research: Atmospheres*, **111**, D01105.

Filion L. & Payette S. (2010) *La Dendroécologie: Principes, Méthodes et Applications.* Les Presses de l'Universite Laval,

Fritts H.C. (1976) *Tree rings and climate.* Academic Press, London, New York, San Francisco.

Genries A., Morin X., Chauchard S., & Carcaillet C. (2009) The function of surface fires in the dynamics and structure of a formerly grazed old subalpine forest. *Journal of Ecology*, **97**, 728–741.

Grissino-Mayer H.D. (2001) Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research*, **57**, 205–221.

Gruber A., Baumgartner D., Zimmermann J., & Oberhuber W. (2009) Temporal dynamic of wood formation in <i>Pinus cembra</i> along the alpine treeline ecotone and the effect of climate variables. *Trees - Structure and Function*, **23**, 623–635.

Hampe A. & Petit R.J. (2005) Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, **8**, 461–467.

Havranek W.M. & Tranquillini W. (1995) Physiological Processes during Winter Dormancy and Their Ecological Significance. *Ecophysiology of coniferous forests*, 95.

Hiebl J., Auer I., Böhm R., Schöner W., Maugeri M., Lentini G., Spinoni J., Brunetti M., Nanni T., Tadić M.P., Bihari Z., Dolinar M., & Müller-Westermeier G. (2009) A high-resolution 1961–1990 monthly temperature climatology for the greater Alpine region. *Meteorologische Zeitschrift*, **18**, 507–530.

Howe G.T., Aitken S.N., Neale D.B., Jermstad K.D., Wheeler N.C., & Chen T.H. (2003) From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany*, **81**, 1247–1266.

IPCC (2013) *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the IPCC.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,.

Jump A.S. & Peñuelas J. (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.

King G.M., Gugerli F., Fonti P., & Frank D.C. (2013) Tree growth response along an elevational gradient: climate or genetics? *Oecologia*, **173**, 1587–1600.

Lavigne M.B. & Ryan M.G. (1997) Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. *Tree Physiology*, **17**, 543–551.

Leonelli G., Pelfini M., Battipaglia G., & Cherubini P. (2009) Site-aspect influence on climate sensitivity over time of a high-altitude Pinus cembra tree-ring network. *Climatic Change*, **96**, 185–201.

Mazerolle M.J. (2015) *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).* R package version 2.0-3, http://CRAN.R-project.org/package=AICcmodavg.

Nola P., Morales M., Motta R., & Villalba R. (2006) The role of larch budmoth (*Zeiraphera diniana* Gn.) on forest succession in a larch (*Larix decidua* Mill.) and Swiss stone pine (*Pinus cembra* L.) stand in the Susa Valley (Piedmont, Italy). *Trees*, **20**, 371–382.

Polechová J., Barton N., & Marion G. (2009) Species' Range: Adaptation in Space and Time. *The American Naturalist*, **174**, E186–E204.

Pritchard J.K., Stephens M., & Donnelly P. (2000) Inference of population structure using multilocus genotype data. *Genetics*, **155**, 945–959.

Saulnier M., Edouard J.-L., Corona C., & Guibal F. (2011) Climate/growth relationships in a Pinus cembra high-elevation network in the Southern French Alps. *Annals of Forest Science*, **68**, 189–200.

Savolainen O., Bokma F., García-Gil R., Komulainen P., & Repo T. (2004) Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of Pinus sylvestris to climatic changes. *Forest Ecology and Management*, **197**, 79–89.

Savolainen O., Pyhäjärvi T., & Knürr T. (2007) Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics*, **38**, 595–619.

Savva Y., Bergeron Y., Denneler B., Koubaa A., & Tremblay F. (2008) Effect of interannual climate variations on radial growth of jack pine provenances in Petawawa, Ontario. *Canadian Journal of Forest Research*, **38**, 619–630.

Savva Y., Schweingruber F.H., Kuzmina N.A., & Vaganov E.A. (2002) Sensitivity of diameter growth to annual weather conditions in Scots pine provenances at a Central Siberian location. *Silvae genetica*, **51**, 49–55.

Schweingruber F.H. (1996) *Tree rings and environment. Dendroecology.* Paul Haupt AG Bern,

Sexton J.P., McIntyre P.J., Angert A.L., & Rice K.J. (2009) Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, **40**, 415–436.

Shaw R.G. & Etterson J.R. (2012) Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *New Phytologist*, **195**, 752–765.

Tang J., Luyssaert S., Richardson A.D., Kutsch W., & Janssens I.A. (2014) Steeper declines in forest photosynthesis than respiration explain age-driven decreases in forest growth. *Proceedings of the National Academy of Sciences*, doi: 10.1073/pnas.1320761111.

Vittoz P., Rulence B., Largey T., & Freléchoux F. (2008) Effects of Climate and Land-Use Change on the Establishment and Growth of Cembran Pine (*Pinus cembra* L.) over the Altitudinal Treeline Ecotone in the Central Swiss Alps. *Arctic, Antarctic, and Alpine Research*, **40**, 225–232.

Zang C. & Biondi F. (2015) treeclim: an R package for the numerical calibration of proxy-climate relationships. Ecography.

3.10 Tables

Table 3.1 Main geographic, climatic, and dendrochronological features of the *Pinus cembra* sampling sites.

Sites are ordered by decreasing latitude. Annual climatic data were averaged over the period 1900-2003. The first letter of the site codes represents the marginal (M) or central (C) distribution zones. MAT: Mean Annual Temperature; MAP: Mean Annual Precipitation; $\bar{r}_{bt}$: mean pairwise correlation between trees; EPS: Expressed Population Signal (a statistic representing the strength of the common signal in all the trees of a sampling site).

Site	Location	Latitude (dd)	Longitude (dd)	Altitude (m)	MAT (°C)	MAP (mm)	N trees	1^{st} year measured	$\bar{r}_{bt}$	EPS
MFL	Flaine	46.001	6.71	1946	1.7	1528	30	1734	0.27	0.94
CBL	Chamonix	45.917	6.897	1976	2.2	1666	29	1731	0.27	0.94
MAR	Aravis	45.897	6.471	1900	2.4	1639	22	1699	0.18	0.86
MGI	Gilly s. Isere	45.597	6.383	1971	1.4	1391	11	1826	0.20	0.76
CTU	Méribel	45.364	6.587	1735	4.2	1031	30	1735	0.28	0.95
CLV	Lanslevillard	45.287	6.949	2150	1.6	1071	27	1613	0.19	0.9
CAU	Aussois	45.255	6.719	2119	1.9	897	28	1704	0.22	0.92
COR	Orelle	45.193	6.535	1932	3.0	960	30	1698	0.17	0.9
MCH	Chamrousse	45.112	5.891	1923	2.8	1317	28	1661	0.24	0.93
CSC	Serre Chevallier	44.923	6.545	2092	1.8	904	30	1704	0.26	0.94
CLP	Lago Perso	44.906	6.795	2016	2.5	799	30	1713	0.40	0.97
CAY	Bois des Ayes	44.821	6.655	1988	2.7	850	30	1716	0.37	0.96
CMI	Lac Miroir	44.631	6.794	2256	1.0	871	30	1650	0.26	0.94
CAL	Bosco di Aleve	44.611	7.08	2012	2.3	945	30	1781	0.36	0.96
CBR	Vallon Braisse	44.286	6.807	2213	1.4	1125	29	1315	0.23	0.93
MMO	Moulière	44.189	6.565	2069	2.0	1073	30	1736	0.31	0.95

Table 3.2 Results of the model selection explaining the among site variability in the growth-climate correlation coefficients r_i for each of the main climatic variables (columns).

Values represent differences in the corrected Akaike Information Criteria (ΔAICc) between a given model and the best model, the weight of each model, the associated β coefficient and p values. Capital letters represent climate conditions prevailing during the current year of ring formation ; small letters represent climate conditions prevailing during the year preceding ring formation. For each climatic variable, the best model (ΔAICc = 0) is highlighted by dark gray shading. Other models having a ΔAICc < 2 are highlighted by paler gray shading.

r_i	T aug-sep [-1]				T nov [-1]				T MAR				T JUN-JUL			
Model	ΔAICc	Weigth	*β*	*p*	ΔAICc	Weigth	*β*	*p*	ΔAICc	Weigth	*β*	*p*	ΔAICc	Weigth	*β*	*p*
r_i ~ %blue	11.93	0			0	0.92	-0.21	0.002 **	0.77	0.19	-0.11	0.092 .	7.22	0.02		
r_i ~ %yellow	13.29	0			9.97	0.01			1.75	0.12	0.10	0.157	8.49	0.01		
r_i ~ %green	12.01	0			6.9	0.03			4.02	0.04			5.68	0.03		
r_i ~ annual P	7.04	0.03			10.67	0			0	0.28	-0.08	0.062 .	0	0.59	0.24	0.006 **
r_i ~ MAT	7.83	0.02			9.14	0.01			2.25	0.09			4.61	0.06		
r_i ~ mean DBH	13.29	0			9.72	0.01			3.83	0.04			7.77	0.01		
r_i ~ mean H	0	0.94	-0.03	<0.001 ***	9.69	0.01			2.11	0.1			1.72	0.25	-0.03	0.013 *
r_i ~ Slope	12.93	0			10.95	0			3.47	0.05			8.84	0.01		
r_i ~ Aspect	11.45	0			9.35	0.01			3.87	0.04			8.81	0.01		
r_i ~ Soil Depth	12.1	0			10.64	0			3.71	0.04			8.04	0.01		

r_i / Model	T SEP				P aug [-1]				P nov-dec [-1]-JAN				P JUL			
	ΔAICc	Weigth	*β*	*p*	ΔAICc	Weigth	*β*	*p*	ΔAICc	Weigth	*β*	*p*	ΔAICc	Weigth	*β*	*p*
r_i ~ %blue	1.41	0.12	-0.17	0.204	8	0.01			10.3	0.01			10.64	0		
r_i ~ %yellow	0.1	0.22	0.227	0.099 .	10.37	0			8.73	0.01			7.3	0.02		
r_i ~ %green	3.22	0.05			5.43	0.04			11.22	0			4.94	0.06		
r_i ~ annual P	3.18	0.05			1.19	0.32	-0.22	0.005 **	0	0.9	-0.38	0.002 **	0	0.68	-0.39	0.003 **
r_i ~ MAT	0	0.24	0.056	0.094 .	9.65	0			11.6	0			9.4	0.01		
r_i ~ mean DBH	2.29	0.08			10.21	0			8.23	0.01			9.11	0.01		
r_i ~ mean H	1.52	0.11	0.013	0.216	0	0.59	0.025	0.003 **	8.75	0.01			3.41	0.12		
r_i ~ Slope	3.12	0.05			9.92	0			8.02	0.02			5.36	0.05		
r_i ~ Aspect	3.32	0.04			9.83	0			10.68	0			9.45	0.01		
r_i ~ Soil Depth	3.26	0.05			6.62	0.02			6.73	0.03			5.43	0.05		

Table 3.3 Results of the model selection explaining the radial growth synchronicity between trees of a site ($\bar{r}_{bt}$).

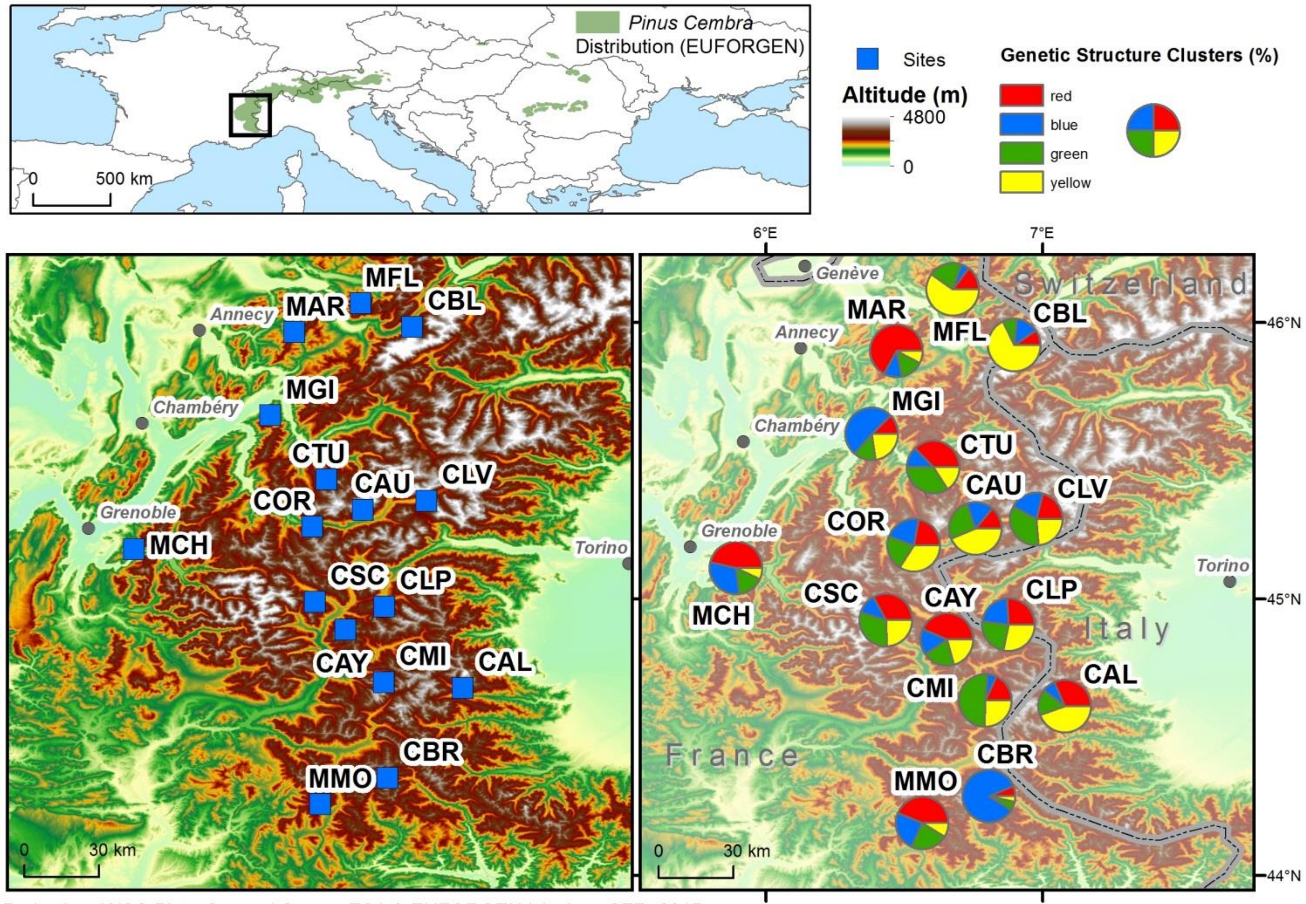
Each model had one of the following explanatory variables: standard deviation of the trees diameters at breast height and total height (sd_{DBH} and sd_H), standard deviation of the soil depth around sampled trees ($sd_{Soil\ Depth}$), allelic richness (AR), expected heterozygoty (H_e), inbreeding coefficient (F_{is}), mean annual temperature (MAT) and mean annual precipitation MAP). Models are sorted by increasing AICc, the best model being at the top. The best model (ΔAICc = 0) is highlighted by dark gray shading. Models having a ΔAICc < 2 are highlighted by paler gray shading.

Model	K	AICc	ΔAICc	Weight	LL
$\bar{r}_{bt}$ ~ AR	3	-38.11	0	0.44	23.06
$\bar{r}_{bt}$ ~ MAP	3	-36.28	1.83	0.18	22.14
$\bar{r}_{bt}$ ~ He	3	-34.16	3.95	0.06	21.08
$\bar{r}_{bt}$ ~ sd_{DBH}	3	-34.02	4.09	0.06	21.01
$\bar{r}_{bt}$ ~ Aspect	3	-33.97	4.14	0.06	20.99
$\bar{r}_{bt}$ ~ sd_H	3	-33.7	4.41	0.05	20.85
$\bar{r}_{bt}$ ~ $sd_{Soil\ Depth}$	3	-33.4	4.71	0.04	20.7
$\bar{r}_{bt}$ ~ F_{is}	3	-33.39	4.72	0.04	20.69
$\bar{r}_{bt}$ ~ Altitude	3	-33.37	4.74	0.04	20.68
$\bar{r}_{bt}$ ~ MAT	3	-33.35	4.76	0.04	20.68

3.11 Figures

Figure 3.1 *Pinus cembra* distribution area, sampling sites and genetic structure.

(**a**) Study area at the western margin of *Pinus cembra* distribution area (source EUFORGEN). (**b**) Location of the sampling sites (blue squares) across the western Alps. (**c**) Spatial repartition of the genetic clusters (each coded by a single color) determined by the STRUCTURE v. 2.3.2 software (Pritchard *et al.*, 2000).



Projection: WGS Plate Carree | Souce: ESA & EUFORGEN | Author: CFR, 2015

Figure 3.2 Bootstrapped correlation coefficients computed between the main climatic variables of *Pinus cembra* growth and residual chronologies of each site, over the period 1900-2003.

Months in capital letters represent the current year, small letters code for climate variables during the year preceding ring formation. Significant correlations are represented by dots for the bootstrapped response function method and by circles for the bootstrapped correlation function. Sites are sorted by decreasing latitude. T: mean temperature, P: precipitation.

Figure 3.3 Effects of climatic, environmental, morphologic and genetic variables on *Pinus cembra* tree ring index.

Black points represent the β coefficients of the scaled explanatory variables of the TRI model (Eq. 3.1), showing the effect of climate variables and their interactions with environmental, morphologic and genetic variables to predict the tree ring index (TRI). Thick bars represent sampling error (1×SE). Thin bars represent 2×SE. Variables for which 2×SE exclude zero are significant.

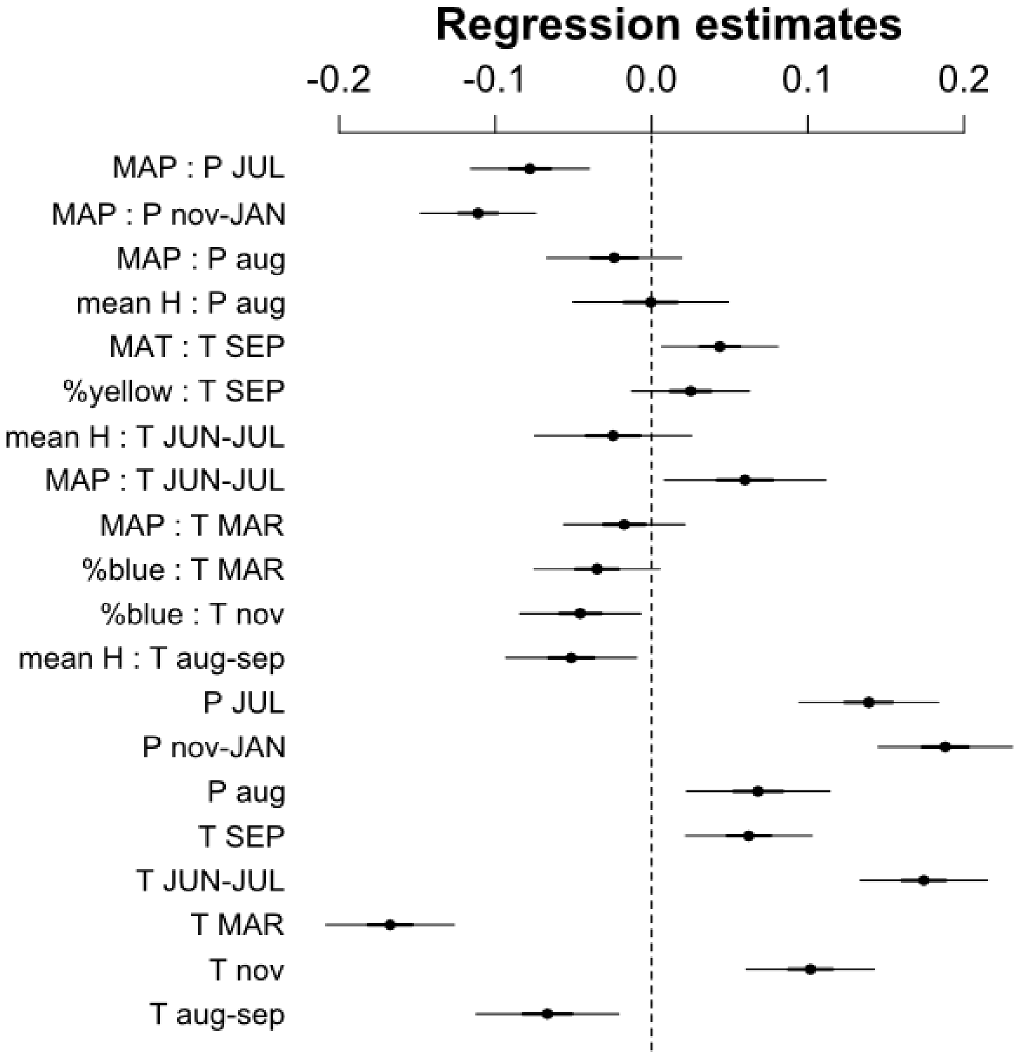
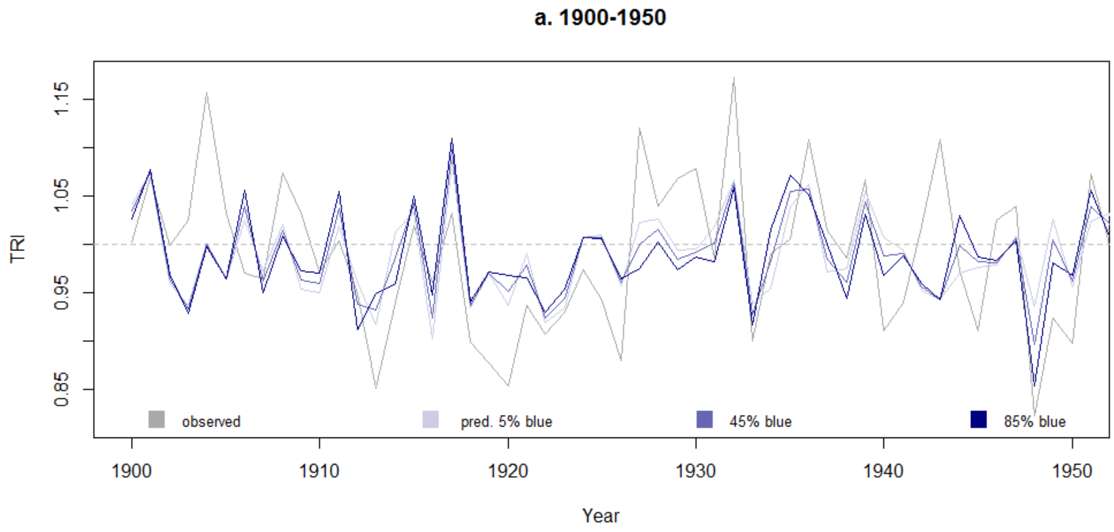
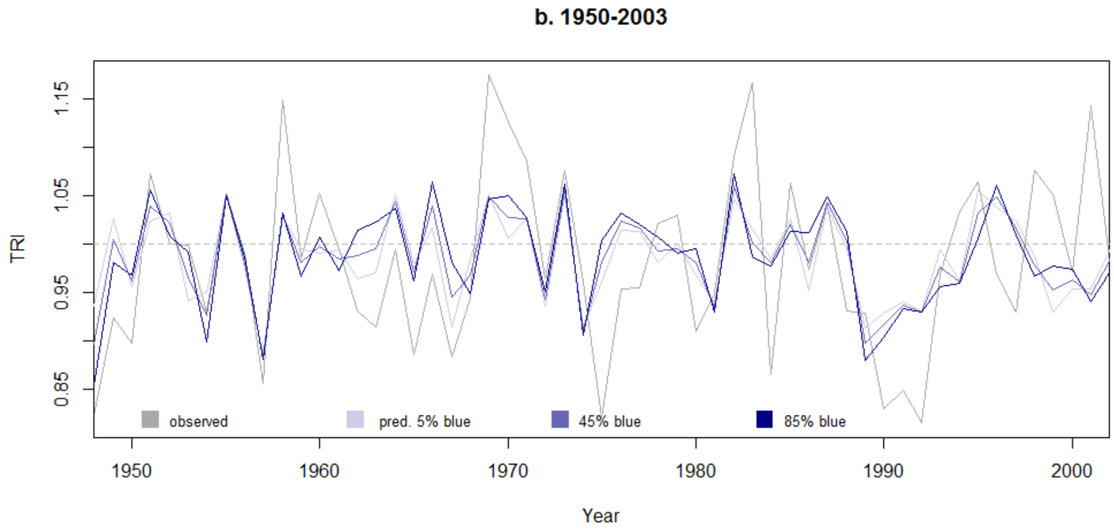


Figure 3.4 Sensitivity analysis of the effect of the genetic structure on the TRI model

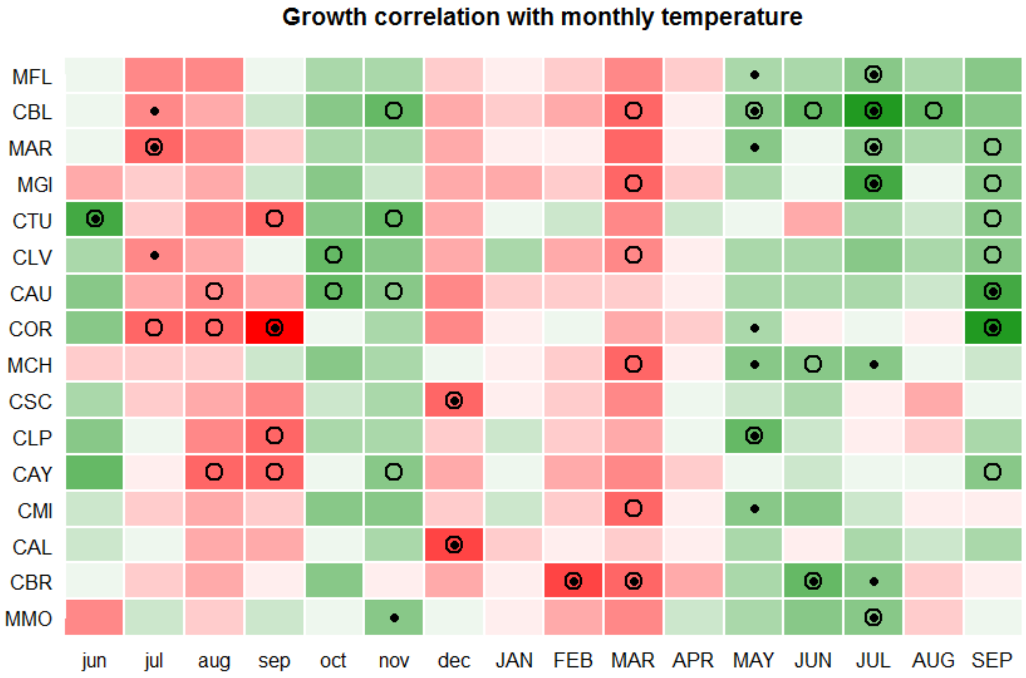
Observed Tree Ring Index (TRI) chronology averaged over the whole study area *versus* predictions from the TRI model (Eq. 3.1) for a varying range of blue genetic cluster, over (**a**) the 1900-1950 period and (**b**) the 1950-2003 period.

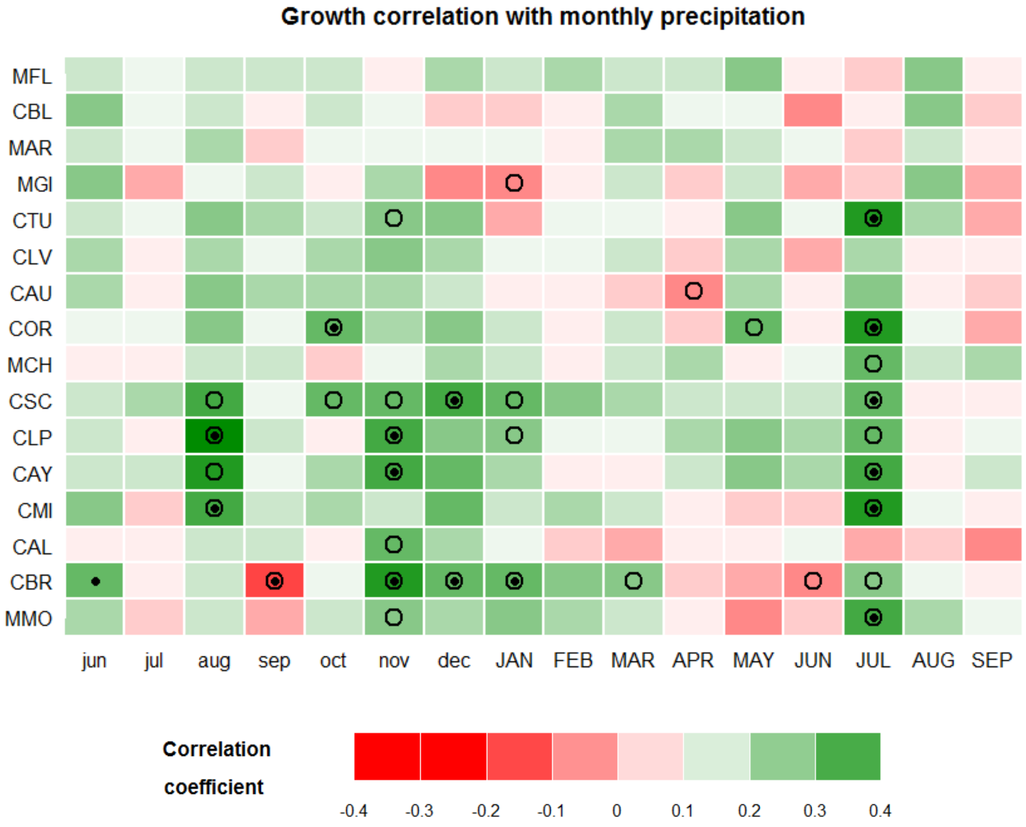




3.12 Supplementary material

Appendix 3.1 Bootstrapped correlation coefficients computed between *Pinus cembra* residual chronology and the normalized detrended monthly mean temperature (**a**) and monthly total precipitation (**b**) during the period 1900-2003. Months in capital letters represent the current year, small letters code for climate variables during the year preceding ring formation. Significant correlations are represented by dots for the bootstrapped response function method and by circles for the bootstrapped correlation function. Sites are sorted by decreasing latitude.


Growth correlation with monthly temperature
MFL
CBL
MAR
MGI
CTU
CLV
CAU
COR
MCH
CSC
CLP
CAY
CMI
CAL
CBR
MMO
jun jul aug sep oct nov dec JAN FEB MAR APR MAY JUN JUL AUG SEP


Growth correlation with monthly precipitation
MFL
CBL
MAR
MGI
CTU
CLV
CAU
COR
MCH
CSC
CLP
CAY
CMI
CAL
CBR
MMO
jun jul aug sep oct nov dec JAN FEB MAR APR MAY JUN JUL AUG SEP
Correlation coefficient
-0.4 -0.3 -0.2 -0.1 0 0.1 0.2 0.3 0.4

CONCLUSION GÉNÉRALE

Dans un premier temps de cette discussion, je rappellerai les principales conclusions de chaque chapitre. Puis, je m’efforcerai de faire une synthèse plus transversale de ces conclusions pour répondre plus généralement à la question de recherche de départ, qui visait à faire émerger, ou non, des mécanismes communs en étudiant le comportement de populations marginales de deux espèces d’arbres au regard des changements climatiques en cours. Les limites de l’approche que j’ai adoptée et les pistes de recherches futures pour continuer de répondre à cette question seront notamment abordées avant de discuter des implications de mes résultats pour la mise en place de mesures d’aménagement forestiers durables des populations marginales.

Diminution de croissance radiale des populations marginales de thuya induite par le réchauffement (chapitre 1)

Le premier article de cette thèse était consacré aux effets du réchauffement climatique encouru au cours de la période 1953-2010 sur la croissance radiale des populations marginales nordiques du thuya. Contrairement à l’hypothèse H1.1[1], ce réchauffement n'a entrainé aucune accélération de la croissance. Bien au contraire, une diminution de la croissance a été observée pour les populations marginales, indiquant que les températures auraient dépassé le seuil optimal pour ces populations

---

[1] La croissance de thuya est significativement et positivement corrélée avec les variations de température. La croissance augmente au cours du XXème siècle en fonction du réchauffement climatique, et cette augmentation est la plus forte dans la zone marginale nordique

nordiques. Les données indiquent que ce seuil aurait été atteint vers les années 1980. Cela suggère que le froid n'est plus le principal facteur limitant de la croissance à la marge septentrionale de l'aire de distribution de l'espèce *Thuja occidentalis*. Nos résultats suggèrent qu'il s'est produit une substitution de facteurs limitants causée par une augmentation du stress hydrique induite par l’augmentation des températures. Ce résultat est surprenant compte tenu de la supposition largement acceptée, et somme toute très intuitive, que les limites froides des espèces incluant les zones alticoles en montagne connaitraient un gain de productivité lié au réchauffement climatique (e.g. Kramer *et al.*, 2000). Nos résultats confortent d’autres études qui indiquent une tendance à la diminution de croissance dans certains contextes écologiques en forêt boréale (D’Arrigo *et al.*, 2004 ; Girardin *et al.*, 2014 ; Wilmking *et al.*, 2004). D’après les données satellitaires, il existe de fortes variations spatiales dans les tendances de productivité de la végétation dans la zone boréale autour du globe (Hicke *et al.*, 2002 ; Myneni *et al.*, 2001). S’il existe des zones où celle-ci augmente, les données satellitaires confirment l’existence d’une baisse de croissance au niveau de notre zone d’étude. L'étude de la réponse dendroclimatique du thuya sur un vaste gradient de latitude, allant des populations marginales nordiques (~50°N lat.) jusqu'à sa zone de distribution continue plus au sud au cœur de la forêt boréale mixte (47-48°N lat.), indique que les relations climat-croissance sont grandement influencées par les facteurs environnementaux des peuplements forestiers tels que les conditions de sols, le régime des précipitations ou la taille moyenne des arbres (ce qui est conforme à notre hypothèse H2.2[1]). Ainsi, les secteurs ayant un volume de précipitation plus important pendant la période de croissance semblent moins souffrir du stress hydrique. En revanche, les sites ayant des arbres de plus grand diamètre en

---

[1] La réponse de la croissance du thuya aux variations climatiques dépend localement du régime régional de précipitations, de la qualité du site et des conditions associées d'humidité de sol.

moyenne semblent être plus affectés, ce qui pourrait être causé par une demande accrue en eau et une plus grande perte de production primaire de carbohydrates due à la respiration pour la maintenance des tissus. La situation édaphique particulière des populations marginales de thuya (hydrique à mésique) entraîne une grande influence de la saisonnalité des précipitations. Nous avons observé un effet négatif des précipitations sur la productivité au début de la saison de croissance (mai), principalement dans les sites les plus froids et dont les sols sont le plus longtemps saturés en eau. Une augmentation des précipitations de printemps, synchrones avec la fonte des neiges, pourrait provoquer une élévation de la nappe de l'eau dans les zones tourbeuses ou un épisode d'inondation aux abords des lacs et rivières, entraînant l'asphyxie des racines et un retard de croissance. Les arbres développent des racines superficielles dans les sites hydriques, ce qui augmente la vulnérabilité aux sécheresses en été lorsque le niveau de la nappe d'eau redescend. Les modèles de niche[1] projettent une montée vers le nord de l'aire de répartition future du thuya causée par le réchauffement des températures (McKenney *et al.*, 2007). Notre étude *in situ* apporte des conclusions contradictoires avec ces modèles statistiques et montre la nécessité de prendre en compte la saisonnalité du climat et les conditions édaphiques, qui influeront sur la réponse de la marge nordique de l'aire du thuya. Par ailleurs, nos résultats suggèrent que les populations marginales nordiques du thuya feront face à une pression de sélection liée à un stress hydrique. La contribution des populations marginales à la migration du thuya vers le nord et leur capacité de persistance *in situ*, sera dépendante des capacités d'adaptation face à cette pression évolutive.

---

[1] Modèles de projection statistique basés uniquement sur l'enveloppe bioclimatique réalisée des espèces

Capacités d’adaptation des populations marginales de thuya en réponse au réchauffement pour les traits de la croissance radiale (chapitre 2)

Le deuxième chapitre constitue une première tentative pour évaluer les capacités d'adaptation des populations marginales de thuya en réponse à la pression de sélection mise en évidence dans le premier chapitre. Nous proposons ici une approche innovante en testant le lien entre la structure génétique et la réponse dendroclimatique du thuya. Il ressort de nos analyses que les variables environnementales (régime climatique, variables édaphiques ou diamètre des arbres) sont prépondérantes pour expliquer les variations inter-sites de relations climat-croissance, ce qui est cohérent avec les conclusions des autres travaux de recherches dans ce domaine. Néanmoins, nos analyses ont montré que la structure génétique module la sensibilité de la croissance vis-à-vis de la température de printemps (mai) et au stress hydrique en juin de l'année précédant la formation du cerne de croissance. Notre hypothèse H2.1[1] est donc partiellement vérifiée pour ces deux cas particuliers. Ce constat pourrait s'expliquer par un contrôle génétique des traits liés à la résistance à la sécheresse et à la phénologie de la dormance. L'adaptation génétique évolutive nécessite à la fois l'existence pour un trait donné (i) d'un contrôle génétique, (ii) d'une pression de sélection et (iii) d'une variabilité intra-populationnelle (Polechová *et al.*, 2009 ; Savolainen *et al.*, 2007). Dans le contexte du changement climatique, la sélection naturelle pourrait donc agir sur les populations marginales de thuya pour sélectionner les individus les mieux adaptés aux nouvelles conditions climatiques. En

---

[1] La réponse de la croissance radiale à la variabilité du climat est influencée par la structure génétique des populations de thuya.

effet, contrairement aux suppositions du modèle central-marginal (H2.2[1]), les populations marginales nordiques de thuya ne présentent pas de diminution de leur diversité génétique intra-population, malgré un taux plus élevé de reproduction entre individus apparentés, dit communément taux de « consanguinité ». De plus, la variabilité phénotypique de croissance, mesurée dans cette étude par le synchronisme de croissance moyenne entre les arbres d'un site ($\bar{r}_{bt}$), n'est pas non plus réduite dans les populations marginales. En réponse à l'hypothèse H2.3[2], il semble que le synchronisme de croissance soit affecté à la fois par le climat et par la diversité génétique intra-population. Le synchronisme de croissance était plus faible pour les populations ayant une plus grande diversité génétique. Autrement dit, les sites avec des arbres plus variables d'un point de vue génétique présentent des comportements de croissances également plus variables. Cependant, c'est le niveau moyen du volume de précipitation qui contrôle le plus le synchronisme d'après nos analyses. Les sites recevant le moins de précipitations ont des croissances plus synchrones, car tous les arbres subissent alors une même contrainte liée au manque d'eau. Dans une perspective à plus long terme, l'adaptation dépendra de l'acquisition de nouvelles combinaisons génétiques par la reproduction sexuée, la migration des gènes provenant d'autres populations ou mutation. Il serait également nécessaire d'étudier la régénération sexuée du thuya dans les populations marginales, car c'est l'un des principaux moyens d'apparition de nouvelles combinaisons génétiques dans une population. Paul et al. (2014) ont montré que la production de semences et les taux de

---

[1] La variabilité phénotypique intra-population pour les caractères liés à la croissance radiale et la diversité génétique intra-population est plus faible pour les populations marginales, selon l'hypothèse du modèle central-marginal.

[2] Le synchronisme de croissance radiale entre les arbres d'un même site diminue avec la diversité génétique intra-population. Une autre hypothèse est que le synchronisme de croissance est plus lié aux conditions climatiques.

germination ne diminuent pas vers la marge nord de thuya du Québec. Toutefois, le recrutement et le taux de survie des semis y sont diminués. Comprendre les facteurs écologiques associés à ce blocage permettrait de mieux anticiper la réponse évolutive possible de ces populations marginales.

Structure génétique et croissance radiale des populations marginales de pin cembro dans les Alpes (chapitre 3)

Dans le troisième chapitre nous avons transposé la question de recherche sur une autre espèce boréo-montagnarde poussant dans un autre biome, celui des montagnes tempérées dans l'étage forestier d'altitude dit subalpin. Nous avons testé ici l'existence d'une influence de la structure génétique sur la croissance radiale du pin cembro à sa limite occidentale et méridionale d'aire de répartition dans les Alpes. La question de la vitesse d'adaptation des populations marginales a fait l'objet de nombreux efforts de modélisation (Bridle *et al.*, 2010 ; Kirkpatrick et Barton, 1997 ; Polechová *et al.*, 2009). Toutefois, l'applicabilité de ces modèles reste très faible car il existe très peu de données sur les variations passées de la structure génétique, ce qui rend difficile la calibration de ces modèles et empêche leur application au-delà du cadre théorique. Dans le cas d'une forte corrélation entre la structure génétique et la réponse dendroclimatique, il a été envisagé ici d'utiliser la réponse au climat en termes de croissance radiale comme proxy de leur réponse évolutive aux variations du climat pour contribuer à l'effort de calibration des modèles d'adaptation. D'après nos analyses, le synchronisme de croissance des arbres diminue significativement pour les sites ayant la plus grande diversité génétique (richesse allélique, AR) ce qui conforte l'hypothèse H3.1[1]. Toutefois, le synchronisme de croissance est également fortement influencé par le régime de précipitations. En effet, nous avons observé que les sites les moins arrosés connaissaient un synchronisme accru probablement dû à un stress hydrique affectant communément les arbres du site. Ce constat confirme que l'étude de la croissance radiale des arbres est un défi en raison des processus complexes dont elle résulte. Pareillement, nos résultats tendent à indiquer que nous ne

---

[1] Le synchronisme de croissance radiale entre les arbres d'un même site est lié à la diversité génétique intra-population.

pouvons pas vérifier de façon certaine l'hypothèse H3.2[1]. Si les relations climat-croissance apparaissent majoritairement influencées par les variables environnementales (régime climatique ou taille des arbres), comme nous l'avions observé pour le thuya, il reste que, chez le pin cembro, la structure génétique influence plus spécifiquement les corrélations avec certains facteurs climatiques. En l'occurrence, sur notre zone d'étude, la sensibilité aux températures de l'automne de l'année précédant la formation du cerne est altérée par la structure génétique.

Plusieurs études génétiques ont montré que les traits liés à la résistance au froid avaient une plus grande héritabilité (part du phénotype observé contrôlé par la génétique). Il y a notamment une sélection des arbres sur la date de la mise en place des bourgeons avant l'entrée en dormance, qui présenterait un plus fort contrôle génétique que la croissance radiale elle-même (Alberto *et al.*, 2013 ; Howe *et al.*, 2003). La structure génétique aurait également une légère influence sur la sensibilité aux températures de printemps, traduisant sûrement le contrôle génétique plus faible sur la sortie de dormance. Compte-tenu de ces résultats, il ne semble pas possible d'utiliser la réponse dendroclimatique comme seul proxy pour étudier l'adaptation génétique. En incorporant les interactions entre le climat et les variables environnementales et génétiques, nous avons construit un modèle empirique de prédictions des variations interannuelles de croissance (Tree Ring Index, TRI). D'un point de vue dendroclimatologique, il est intéressant de vérifier qu'il ne soit pas crucial d'incorporer la structure génétique dans l'étude des relations climat-croissance. Le dogme dans la discipline est de négliger, voire d'ignorer, la contribution du génome considérant l'espèce comme une entité sans variabilité inter-

---

[1] Les relations climat-croissance sont modulées par la structure génétique du pin cembro.

individuelle[1], alors même que les recherches théoriques très récentes soulignent l'importance de la variabilité de traits en réponse à l'environnement (Violle *et al.*, 2012). Néanmoins, il semble que cela pourrait permettre d'accroître, dans certains contextes, le pouvoir prédictif dans la modélisation du TRI. Bien comprendre le rôle régulateur de la structure génétique nécessiterait cependant des recherches plus approfondies, notamment sur la structure génétique adaptative du pin cembro en particulier, et des espèces en général.

Synthèses des travaux et enseignement transversal sur la croissance des arbres

Il est intéressant de vérifier qu'il existe des convergences dans nos résultats pour les deux espèces étudiées, dans deux écosystèmes pourtant assez distincts bien que soumis à des contraintes proches ou analogues.

Devenir des populations marginales dans le contexte du réchauffement

Les analyses dendroclimatiques ont permis de mieux comprendre les facteurs limitants de la croissance radiale des populations marginales du thuya et du pin cembro. Nos résultats suggèrent que les populations marginales du thuya au Québec boréal (limite nordique) et du pin cembro dans les Alpes occidentales subiront une pression de sélection liée au stress hydrique. Ce constat dénote avec une idée couramment répandue voulant que ces espèces se trouvant dans des écosystèmes froids seront favorisées par le réchauffement climatique (Kramer *et al.*, 2000). Bien que cela se vérifie pour les boisements se situant vers la limite des arbres en forêt

---

[1] quelques rares travaux récent portent néanmoins sur la variabilité individuelle (e.g. Carrer, 2011) ou interpopulationnelle de la croissance radiale (e.g. Lévesque *et al.*, 2014)

boréale (Lloyd *et al.*, 2011 ; Rehfeldt *et al.*, 2002), des diminutions de croissances ont été rapportées dans des écosystèmes froids situés en deçà de cette écotone (Girardin *et al.*, 2014 ; Lloyd *et al.*, 2011). Il existe une forte hétérogénéité spatiale dans les effets du réchauffement sur la croissance des arbres en raison notamment des variations spatiales des conditions édaphiques et des régimes de précipitations (R. de Jong *et al.*, 2012 ; Lévesque *et al.*, 2014 ; Lloyd *et al.*, 2011). Cela va dans le sens des résultats de cette thèse qui montre que les relations climat-croissance sont fortement influencées par le régime régional de précipitations pour les deux espèces étudiées, et aussi par les conditions édaphiques dans le cas du thuya. Ainsi les populations marginales nordiques de thuya et les populations marginales occidentales de pin cembro devraient subir une pression de sélection exercée par le stress hydrique. Dans le cas du pin cembro, la contrainte liée au stress hydrique sera plus prononcée dans les secteurs les moins arrosés en moyenne.

Le devenir des populations marginales dépendra donc de leurs capacités d'adaptation à la pression de sélection. Bien que de nombreux modèles théoriques portent sur les dynamiques évolutives aux marges de distribution (Bridle *et al.*, 2010 ; Kirkpatrick et Barton, 1997 ; Sexton *et al.*, 2009), le manque de données de calibration ne permet pas de leur conférer une valeur prédictive (Polechová *et al.*, 2009). Une des contributions de cette thèse consistait à collecter des données empiriques pour renseigner sur la réponse au climat de populations périphériques par des mesures répétées dans le temps. D'après les recherches de modélisation, la variabilité génétique est un des principaux facteurs permettant l'adaptation d'une population à une pression de sélection (Polechová *et al.*, 2009 ; Savolainen *et al.*, 2007). Nos données suggèrent que les populations marginales de thuya et de pin cembro ne présentent pas de forte diminution de leur diversité vers les marges de distribution. Les caractéristiques génétiques et phénotypiques observées pour le thuya, suggèrent qu'il existe une capacité d'adaptation génétique des populations étudiées face à cette pression de sélection. L'existence d'une adaptation génétique au climat local a par ailleurs été démontrée pour le pin cembro (Mosca *et al.,* 2012). Toutefois, notre étude exploratoire du lien entre le signal dendroclimatique et la structure génétique ne permet pas de déterminer quelle sera la vitesse d'adaptation face aux changements climatiques rapides attendus d'ici la fin du XXI$^{\text{ième}}$ siècle et d'autres recherches seraient nécessaires pour pouvoir anticiper correctement le devenir des populations marginales.

Lien génétique-dendrochronologie

Une des contributions scientifiques de cette thèse est d'explorer le lien entre la dendroclimatologie et la structure génétique des populations forestières, domaine qui est encore peu étudié. Je me suis concentré sur des traits phénotypiques liés à la croissance radiale des arbres, à savoir le synchronisme de croissance et la variabilité intersites dans les relations climat-croissance radiale. Ces réponses de variables ont été comparées à la structure génétique neutre de ces mêmes sites. Cette approche se distingue de celles des précédentes études des relations entre la génétique et la dendroclimatologie, qui étudiait des provenances plantées dans des sites expérimentaux de tests de provenances (King *et al.*, 2013 ; Savva *et al.*, 2002, 2008).

Pour les deux espèces, les relations climat-croissance étaient principalement modulées par des variables liées aux conditions environnementales du site ainsi qu'à la taille des arbres (diamètre ou hauteur moyens) - 55% de la variance expliquée pour le thuya, 94% pour le pin cembro - avec une contribution beaucoup plus faible de la structure génétique seule - 9% et 7%, respectivement. Nos résultats sont comparables à ceux d'autres études testant l'influence de la génétique sur la réponse dendroclimatique et qui concluaient sur une incidence nulle pour *Pinus banksiana* en forêt boréale canadienne (Savva *et al.*, 2008) ou faible pour *Pinus sylvestris* en forêt boréale russe (Savva *et al.*, 2002). D'après les tests de provenances réalisés dans des *common garden*, la croissance des arbres est d'ailleurs un trait qui est connu pour avoir un faible contrôle génétique, avec une forte influence des variables environnementales (Alberto *et al.*, 2013 ; Yang *et al.*, 2015). Nous avons néanmoins observé un effet de la structure génétique sur la réponse dendroclimatique sur quelques variables climatiques bien précises, qui ne sont pas les mêmes pour les deux espèces. Pour le thuya, la corrélation avec les températures du printemps était influencée par la structure génétique, ce qui pourrait traduire un effet de la génétique sur la sensibilité thermique du débourrement au printemps. Dans le cas du pin cembro il s'agissait des températures de l'automne de l'année précédant la formation du cerne. Cette observation pourrait s'expliquer par un contrôle génétique de la résistance au gel, traduisant un compromis évolutif entre une maximisation de la période de croissance et une diminution du risque de blessure par gel (Howe *et al.*, 2003 ; Savolainen *et al.*, 2004). Les traits liés à la phénologie de dormance ont généralement un plus fort contrôle génétique que la croissance elle-même (Alberto *et al.*, 2013).

Par ailleurs, pour les deux espèces, le synchronisme de la croissance était influencé à la fois par le régime de précipitations et par la diversité génétique intra-population. Pour les deux espèces, une plus grande richesse allélique (AR) était positivement associée à une plus grande variabilité phénotypique de croissance ($\bar{r}_{bt}$). Ce résultat diffère de ceux de l'étude menée par King et al. (2013), qui ne met pas en évidence de lien entre le synchronisme de croissance et la diversité génétique des populations de *Larix decidua* et de *Picea abies* le long d'un gradient d'altitude. Cette différence pourrait être due au fait que les populations intégrées dans ce dispositif couvrent une étendue géographique plus faible que celui présenté ici, et qu'elle n’intègre pas de populations marginales qui sont *a priori* plus différentiées (Aitken *et al.*, 2008 ; Alberto *et al.*, 2013 ; Lesica et Allendorf, 1995).

Nos recherches ont également permis de tester le modèle théorique central-marginal au travers de deux exemples différents de marges de distribution. Pour les populations marginales boréales nordiques (« leading edge » dans la figure 0.1) du thuya nous n’avons pas observé de diminution de diversité génétique vers les marges à l’échelle de la population étudiée, bien qu’il y ait une perte de diversité au niveau de l’arbre se traduisant par une plus grande homozygotie (Xu *et al.*, 2012). Pour le pin cembro, l’histoire des migrations postglaciaires est plus complexe en raison des reliefs prononcés et la complexité des voies de migration possible. Les populations marginales occidentales pourrait correspondre à la conjonction de gènes issus de refuges glaciaires des Carpates et d’autres situés au nord-est de l’Italie (Mosca *et al.*, 2012). Il semble qu’il y ait une légère diminution de la diversité génétique vers la marge sud-ouest de l’espèce (Dzialuk *et al.*, 2014 ; Höhn *et al.*, 2009) avec les populations les plus occidentales se différentiant significativement de celle de l’est et du centre de l’Europe (Mosca *et al.*, 2012) ce que nos données conforteraient. Ainsi, nos résultats rejoignent les conclusions de synthèses sur le modèle central-marginal qui indiquent que les diminution de diversité génétique ne sont pas systématiquement observées pour les populations marginales, et qu’elles sont relativement faibles lorsqu’elles sont observées (Eckert *et al.*, 2008 ; Gaston, 2009). Nos résultats indiquent que cette perte de diversité génétique n’est pas accompagnée d’une diminution significative dans la variabilité phénotypique de croissance. En effet, aucune diminution dans le synchronisme de croissance entre les arbres d’un site ($\bar{r}_{bt}$) n’a été observée vers les marges de distribution.

Pistes de recherches futures

Nos analyses ont permis une première exploration du lien entre la dendroclimatologie et la structure génétique neutre du thuya et du pin cembro. Il serait également nécessaire de tester le lien entre la génétique adaptative et les relations climat-croissance. La structure génétique neutre est en effet *a priori* moins corrélée à l'environnement et au climat local. Elle renseigne plus sur les ressemblances génétiques entre les populations testées, dont l'interprétation se rapproche plus de celle des lignées génétiques. Les études génétiques récentes portant sur l'adaptation au climat local mettent en évidence des relations significatives entre certains gènes et le climat dans lequel poussent ces arbres (Aitken *et al.*, 2008 ; Savolainen, 2011), notamment pour le pin cembro (Mosca *et al.*, 2012). En testant le lien entre la génétique adaptative et la dendrochronologie, on pourrait s'attendre à des corrélations plus élevées relativement à celle des variables non-génétiques. Toutefois, il apparaît ici une limite en raison du manque de connaissances de l'architecture génétique[1] de ces deux espèces qui sont de faibles enjeux commerciaux, et dont la génétique quantitative est encore peu étudiée. Il pourrait être également pertinent de tester le lien entre la génétique et la dendrochronologie au niveau de l'arbre, pour augmenter le pouvoir statistique des analyses dans la discrimination des effets de la génétique d'une part, et de l'environnement et de la taille des arbres d'autre part. En effet, les espèces forestières se caractérisent par une diversité génétique intra-populationnelle plus grande que la diversité inter-populationnelle (Alden et Loopstra, 1987 ; Beaulieu et Bousquet, 2010 ; Savva *et al.*, 2002) et il est possible qu'une grande partie des informations soient perdues en faisant une moyenne au niveau du site. Par exemple, Cole et ses collaborateurs (2010) ont trouvé un effet positif significatif de l'hétérozygotie sur la croissance radiale de *Populus tremuloides* au

---

[1] Cartographie des gènes et de leurs interactions entre eux et avec l'environnment lors de leur expression.

niveau de l'arbre. Enfin, dans le prolongement de nos travaux, il sera possible d'utiliser le modèle de prédiction de la croissance radiale (TRI) développé dans le chapitre 3 pour le pin cembro pour générer des prédictions de croissance future plus précises pour notre zone d'étude en tenant compte des facteurs d'interactions environnementaux et génétiques. Il serait également envisageable de faire des reconstitutions de variables climatiques dans le passé pour des périodes antérieures aux séries météorologiques compte tenu des longueurs des chronologies dont on dispose.

Nos travaux apportent une réponse partielle à la question du devenir des populations marginales en réponse aux changements climatiques. Pour y répondre pleinement il serait nécessaire d'adopter une approche transdisciplinaire pour considérer l'ensemble des processus biologiques altérés, tels que les dynamiques de régénération des boisements, mais aussi les conséquences sur les variations des régimes de perturbations (feux, avalanches, attaques d'insectes, pathogènes). D'autres travaux réalisés dans le cadre du projet de recherche BOREALP, dans lequel s'inscrit nos recherches, ont apporté de premiers éléments de réponse. Il semble que les populations marginales de thuya au Québec présentent une faible expansion via l'apparition de semis à la marge des forêts matures (Visnadi, 2014). Par ailleurs, on observe un déficit de survie des semis issus de régénérations naturelles au sein des populations marginales de thuya (Paul *et al.*, 2014), et la multiplication végétative reste le mode garantissant actuellement le maintien des populations de thuya (Paul *et al.*, 2014 ; Visnadi, 2014). Étant donné que la reproduction sexuée est le principal vecteur d'apparition de nouvelles combinaisons génétiques (Savolainen, 2011), l'adaptation génétique des populations marginales pourrait être limitée par ce déficit de recrutement de semis.

Enfin, les recherches sur la réponse des arbres aux changements climatiques doivent faire appel aux méthodes d'études des systèmes complexes. De trop nombreux mécanismes de réponses adaptatives impliquent des interactions entre les gènes et l'environnement et des équilibres dynamiques entre les populations et le climat. Des effets de seuil ont également été observés dans nos données, avec par exemple le basculement d'un facteur limitant thermique de la croissance vers un facteur limitant lié au stress hydrique autour des années 1980 pour les populations marginales de thuya (chapitre I). L'utilisation des techniques des systèmes complexes permettrait de mieux caractériser la réponse de la croissance aux changements climatiques.

Implications potentielles pour la gestion forestière durable

La rapidité sans précédent des changements climatiques (IPCC, 2013) et les multiples pressions de sélection que subiront les arbres laissent penser que l'adaptation des arbres devra jouer un rôle prépondérant dans cette réponse si les espèces ne peuvent pas migrer assez rapidement pour suivre le déplacement de leur enveloppe bioclimatique (Alberto *et al.*, 2013 ; Thompson *et al.*, 2009). Dès lors le principe de précaution voudrait que le gestionnaire sylvicole essaye de favoriser les capacités d'adaptation génétique des arbres dans la gestion des ressources ligneuses forestières.

Favoriser la variabilité génétique

Ce facteur est primordial pour l'adaptation rapide des populations en permettant une réponse immédiate au changement climatique par la sélection parmi les variations déjà existante (Kelly *et al.*, 2003 ; Antoine Kremer *et al.*, 2012 ; Savolainen, 2011).

Cela permettra d’augmenter l’adaptabilité des espèces à un panel plus large de scénarios futurs en termes de climat ou en termes de perturbations. Les principaux moyens pour y parvenir sont d’éviter la simplification génétique par des plantations de provenances homogènes ou de clones, de favoriser le brassage génétique par reproduction sexuée entre un grand nombre de populations (Thompson *et al.*, 2009).

Faciliter le flux de gènes à travers toute l’aire de distribution

L’adaptation d’une espèce aux changements climatiques nécessite un flux de gènes sur toute son aire de répartition (Davis *et al.*, 2005 ; Savolainen *et al.*, 2007). Il est donc primordial de limiter la fragmentation anthropique et de maintenir une continuité écologique reliant les extrêmes écologiques et géographiques de l’aire de répartition des espèces (Alberto *et al.*, 2013 ; Hampe et Petit, 2005 ; Lesica et Allendorf, 1995). Les réseaux internationaux d’aires protégées et le maintien d’îlots de forêts matures au sein des zones exploitées pourraient contribuer à la conservation des ressources génétiques propices à l’adaptation (Kohler *et al.*, 2009 ; Koskela *et al.*, 2007). À titre d’exemple, la conservation *in situ* de peuplements autochtones vastes, abondants et inter-fertiles est recommandées pour la conservation et l’adaptabilité du pin cembro en Europe (Ulber *et al.*, 2003).

Conserver les populations marginales

D’après nos travaux, certaines populations marginales ont des structures génétiques et des réponses dendroclimatiques qui leurs sont propres. La conservation des populations marginales fortement différenciées génétiquement permet de faciliter l’adaptabilité des espèces (Lesica et Allendorf, 1995). Leur conservation *in situ* donnera donc plus de chances à l'espèce de présenter des phénotypes adaptés à la pression de sélection induite par les changements climatiques. En particulier, le flux de gènes des marges chaudes vers les marges froides permettent de faciliter l’adaptation aux changements climatiques (Davis et Shaw, 2001 ; Savolainen *et al.*, 2007). Selon la théorie du « *shifting-balance* » de Wright (1988), plus une population isolée connaît des conditions éloignées de son optimum de *fitness*, plus sa vitesse d’adaptation augmente. Ainsi ces populations pourraient servir de laboratoires naturels d’expérimentations pour l’apparition rapide de nouvelles combinaisons génétiques. Les populations disjointes pourraient même être le lieu de phénomènes de spéciation dans le futur (Lesica et Allendorf, 1995). Il apparaît donc souhaitable de les conserver, pour permettre le déroulement naturel des processus évolutifs et favoriser la résilience des espèces par plasticité génétique.

RÉFÉRENCES GÉNÉRALES

Aitken, S. N., Yeaman, S., Holliday, J. A., Wang, T. et Curtis McLane, S. (2008). Adaptation, migration or extirpation: climate change outcomes for tree populations. *Evolutionary Applications*, *1*(1), 95‑111. http://dx.doi.org/10.1111/j.1752-4571.2007.00013.x

Alberto, F. J., Aitken, S. N., Alía, R., González-Martínez, S. C., Hänninen, H., Kremer, A., Lefèvre, F., Lenormand, T., Yeaman, S., Whetten, R. et Savolainen, O. (2013). Potential for evolutionary responses to climate change – evidence from tree populations. *Global Change Biology*, *19*(6), 1645–1661. http://dx.doi.org/10.1111/gcb.12181

Alden, J. et Loopstra, C. (1987). Genetic diversity and population structure of Picea glauca on an altitudinal gradient in interior Alaska. *Canadian journal of forest research*, *17*(12), 1519–1526.

Ali, A. A., Carcaillet, C., Talon, B., Roiron, P. et Terral, J. (2005). Pinus cembra L. (arolla pine), a common tree in the inner French Alps since the early Holocene and above the present tree line: a synthesis based on charcoal data from soils and travertines. *Journal of Biogeography*, *32*(9), 1659‑1669. http://dx.doi.org/10.1111/j.1365-2699.2005.01308.x

Archambault, S. et Bergeron, Y. (1992a). An 802-year tree-ring chronology from the Québec boreal forest. *Canadian Journal of Forest Research*, *22*, 674–682. http://dx.doi.org/111

Archambault, S. et Bergeron, Y. (1992b). Discovery of a Living 900 Year-old Northem White Cedar, Thuja occidentalis, in Northwestem Québec, (972), 192–195. http://dx.doi.org/1112

Auer, I., Böhm, R., Jurkovic, A., Lipa, W., Orlik, A., Potzmann, R., Schöner, W., Ungersböck, M., Matulla, C., Briffa, K., Jones, P., Efthymiadis, D., Brunetti, M., Nanni, T., Maugeri, M., Mercalli, L., Mestre, O., Moisselin, J., Begert, M., Müller-Westermeier, G., Kveton, V., Bochnicek, O., Stastny, P., Lapin, M., Szalai, S., Szentimrey, T., Cegnar, T., Dolinar, M., Gajic-Capka, M., Zaninovic, K., Majstorovic, Z. et Nieplova, E. (2007). HISTALP—historical instrumental climatological surface time series of the Greater Alpine Region. *International Journal of Climatology*, *27*(1), 17‑46. http://dx.doi.org/10.1002/joc.1377

Barton, N. H. (2001). Adaptation at the edge of a species' range. *Special Publication - British Ecological Society*, *14*, 365–392.

Battipaglia, G., Büntgen, U., McCloskey, S. P., Blarquez, O., Denis, N., Paradis, L., Brossier, B., Fournier, T. et Carcaillet, C. (2014). Long-term effects of climate and land-use change on larch budmoth outbreaks in the French Alps. *Clim Res*, *62*, 1–14.

Beaudoin, A., Bernier, P. Y., Guindon, L., Villemaire, P., Guo, X. J., Stinson, G., Bergeron, T., Magnussen, S. et Hall, R. J. (2014). Mapping attributes of Canada's forests at moderate resolution through *k*NN and MODIS imagery. *Canadian Journal of Forest Research*, *44*(5), 521‑532. http://dx.doi.org/10.1139/cjfr-2013-0401

Beaulieu, J. et Bousquet, J. (2010). Facteurs génétiques affectant la variabilité des cernes annuels chez les espèces arborescentes nordiques. Dans *La dendroécologie: principes, méthodes et applications.* (Presses de l'Université Laval, p. 137‑167). [s.l.] : Payette, S. and Filion, L., Eds.

Bebi, P., Kulakowski, D. et Rixen, C. (2009). Snow avalanche disturbances in forest ecosystems—State of research and implications for management. *Forest Ecology and Management*, *257*(9), 1883‑1892. http://dx.doi.org/10.1016/j.foreco.2009.01.050

Beck, P. S. A., Juday, G. P., Alix, C., Barber, V. A., Winslow, S. E., Sousa, E. E., Heiser, P., Herriges, J. D. et Goetz, S. J. (2011). Changes in forest productivity across Alaska consistent with biome shift. *Ecology Letters*, *14*(4), 373–379. http://dx.doi.org/10.1111/j.1461-0248.2011.01598.x

Belyea, R. M., Fraser, D. A. et Rose, A. H. (1951). Seasonal growth of some trees in Ontario. *The Forestry Chronicle*, *27*(4), 300‑305. http://dx.doi.org/10.5558/tfc27300-4

Benito Garzón, M., Alía, R., Robson, T. M. et Zavala, M. A. (2011). Intra-specific variability and plasticity influence potential tree species distributions under climate change. *Global Ecology and Biogeography*, *20*(5), 766–778. http://dx.doi.org/10.1111/j.1466-8238.2010.00646.x

Berner, L. T., Beck, P. S. A., Bunn, A. G., Lloyd, A. H. et Goetz, S. J. (2011). High-latitude tree growth and satellite vegetation indices: Correlations and trends in Russia and Canada (1982–2008). *Journal of Geophysical Research: Biogeosciences*, *116*(G1), G01015. http://dx.doi.org/10.1029/2010JG001475

Biondi, F. et Waikul, K. (2004). DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Computers & Geosciences*, *30*(3), 303-311. http://dx.doi.org/10.1016/j.cageo.2003.11.004

Blarquez, O., Carcaillet, C., Elzein, T. M. et Roiron, P. (2012). Needle accumulation rate model-based reconstruction of palaeo-tree biomass in the western subalpine Alps. *The Holocene*, *22*(5), 579-587. http://dx.doi.org/10.1177/0959683611427333

Boisvenue, C. et Running, S. W. (2006). Impacts of climate change on natural forest productivity – evidence since the middle of the 20th century. *Global Change Biology*, *12*(5), 862–882. http://dx.doi.org/10.1111/j.1365-2486.2006.01134.x

Bradshaw, A. D. (1991). The Croonian Lecture, 1991: Genostasis and the Limits to Evolution. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences*, *333*(1267), 289-305. http://dx.doi.org/10.1098/rstb.1991.0079

Breshears, D. D., Myers, O. B., Meyer, C. W., Barnes, F. J., Zou, C. B., Allen, C. D., McDowell, N. G. et Pockman, W. T. (2008). Tree die-off in response to global change-type drought: mortality insights from a decade of plant water potential measurements. *Frontiers in Ecology and the Environment*, *7*(4), 185-189. http://dx.doi.org/10.1890/080016

Bridle, J. R., Polechová, J., Kawata, M. et Butlin, R. K. (2010). Why is adaptation prevented at ecological margins? New insights from individual-based simulations. *Ecology Letters*, *13*(4), 485–494. http://dx.doi.org/10.1111/j.1461-0248.2010.01442.x

Bridle, J. R., Polechová, J. et Vines, T. H. (2009). Patterns of biodiversity and limits to adaptation in time and space. *Speciation and patterns of biodiversity Butlin RK, Bridle JR, Schluter D*, 77–101.

Buckley, B. M., Wilson, R. J. S., Kelly, P. E., Larson, D. W. et Cook, E. R. (2004). Inferred summer precipitation for southern Ontario back to AD 610, as reconstructed from ring widths of Thuja occidentalis. *Canadian Journal of Forest Research*, *34*(12), 2541–2553.

Bunn, A. G. (2008). A dendrochronology program library in R (dplR). *Dendrochronologia*, *26*(2), 115‑124. http://dx.doi.org/10.1016/j.dendro.2008.01.002

Büntgen, U., Esper, J., Frank, D. C., Nicolussi, K. et Schmidhalter, M. (2005). A 1052-year tree-ring proxy for Alpine summer temperatures. *Climate Dynamics*, *25*(2-3), 141‑153. http://dx.doi.org/10.1007/s00382-005-0028-1

Burnham, K. P. et Anderson, D. R. (2010). *Model selection and multi-model inference: A practical information-theoretic approach*. [s.l.] : Springer. (Cited by 19932).

Burns, R. M. et Honkala, B. H. (1990). *Silvics of North America.* (Agriculture Handbook). Washington : USDA Forest Service. (Cited by 1523). Récupéré de http://www.cabdirect.org/abstracts/19910653295.html

Carcaillet, C., Bergeron, Y., Richard, P. J. H., Fréchette, B., Gauthier, S. et Prairie, Y. T. (2001). Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? *Journal of Ecology*, *89*(6), 930‑946. http://dx.doi.org/10.1111/j.1365-2745.2001.00614.x

Carcaillet, C. et Richard, P. J. H. (2000). Holocene changes in seasonal precipitation highlighted by fire incidence in eastern Canada. *Climate Dynamics*, *16*(7), 549‑559. http://dx.doi.org/10.1007/s003820000062

Carcaillet, C., Richard, P. J. H., Bergeron, Y., Fréchette, B. et Ali, A. A. (2010). Resilience of the boreal forest in response to Holocene fire-frequency changes assessed by pollen diversity and population dynamics. *Int. J. Wildland Fire*, *19*(8), 1026‑1039.

Carrer, M. (2011). Individualistic and Time-Varying Tree-Ring Growth to Climate Sensitivity. *PLoS ONE*, *6*(7), e22813. http://dx.doi.org/10.1371/journal.pone.0022813

Carrer, M., Nola, P., Eduard, J. L., Motta, R. et Urbinati, C. (2007). Regional variability of climate-growth relationships in Pinus cembra high elevation forests in the Alps. *Journal of Ecology*, *95*(5), 1072‑1083.

Carrer, M. et Urbinati, C. (2004). Age-dependent tree-ring growth responses to climate in Larix decidua and Pinus cembra. *Ecology*, *85*(3), 730–740.

Chapin, F. S. I., Chapin, M. C., Matson, P. A. et Vitousek, P. (2011). *Principles of terrestrial ecosystem ecology*. [s.l.] : Springer.

Chapin, F. S. I., Jefferies, R. L., Reynolds, J. F., Shaver, G. R. et Svoboda, J. (1992). *Arctic ecosystems in a changing climate: An ecophysiological perspective* (Academic Press Inc.). San Diego, CA, USA : [s.n.].

Chauchard, S., Beilhe, F., Denis, N. et Carcaillet, C. (2010). An increase in the upper tree-limit of silver fir (Abies alba Mill.) in the Alps since the mid-20th century: A land-use change phenomenon. *Forest Ecology and Management*, *259*(8), 1406‑1415. http://dx.doi.org/10.1016/j.foreco.2010.01.009

Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences*, *365*(1555), 3149‑3160. http://dx.doi.org/10.1098/rstb.2010.0142

Cole, C. T., Anderson, J. E., Lindroth, R. L. et Waller, D. M. (2010). Rising concentrations of atmospheric CO2 have increased growth in natural stands of quaking aspen (Populus tremuloides). *Global Change Biology*, *16*(8), 2186–2197. http://dx.doi.org/10.1111/j.1365-2486.2009.02103.x

Cook, E. et Kairiūkštis, L. (1990). *Methods of dendrochronology: applications in the environmental sciences*. Dordrecht, The Netherlands : Kluwer Academic Publishers.

Cook, E. R. et Peters, K. (1981). The smoothing spline: a new approach to standardizing forest interior tree-ring width series for dendroclimatic studies. *Tree-Ring Bulletin*, *41*, 45‑53.

Cornelius, J. (1994). Heritabilities and additive genetic coefficients of variation in forest trees. *Canadian Journal of Forest Research*, *24*(2), 372‑379. http://dx.doi.org/10.1139/x94-050

D’Arrigo, R. D., Kaufmann, R. K., Davi, N., Jacoby, G. C., Laskowski, C., Myneni, R. B. et Cherubini, P. (2004). Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. *Global Biogeochemical Cycles*, *18*(3), GB3021. http://dx.doi.org/10.1029/2004GB002249

Darrigo, R., Wilson, R., Liepert, B. et Cherubini, P. (2008). On the ‘Divergence Problem’ in Northern Forests: A review of the tree-ring evidence and possible causes. *Global and Planetary Change*, *60*(3-4), 289–305. http://dx.doi.org/10.1016/j.gloplacha.2007.03.004

Davis, M. B. et Shaw, R. G. (2001). Range shifts and adaptive responses to quaternary climate change. *Science*, *292*(5517), 673-679. http://dx.doi.org/10.1126/science.292.5517.673

Davis, M. B., Shaw, R. G. et Etterson, J. R. (2005). Evolutionary responses to changing climate. *Ecology*, *86*(7), 1704-1714. http://dx.doi.org/10.1890/03-0788

De Jong, G. (2005). Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. *New Phytologist*, *166*(1), 101–118. http://dx.doi.org/10.1111/j.1469-8137.2005.01322.x

de Jong, R., Verbesselt, J., Schaepman, M. E. et de Bruin, S. (2012). Trend changes in global greening and browning: contribution of short-term trends to longer-term change. *Global Change Biology*, *18*(2), 642-655. http://dx.doi.org/10.1111/j.1365-2486.2011.02578.x

Denneler, B., Bergeron, Y. et Bégin, Y. (2010). Flooding effects on tree-ring formation of riparian eastern white-cedar (*Thuja occidentalis* L.), northwestern Quebec, Canada. *Tree-Ring Research*, *66*(1), 3–17. http://dx.doi.org/10.3959/2008-11.1

Denneler, B., Bergeron, Y., Bégin, Y. et Asselin, H. (2008). Growth responses of riparian *Thuja occidentalis* to the damming of a large boreal lake. *Botany*, *86*(1), 53–62. http://dx.doi.org/10.1139/B07-116

Deslauriers, A., Morin, H., Urbinati, C. et Carrer, M. (2003). Daily weather response of balsam fir (*Abies balsamea* (L.) Mill.) stem radius increment from dendrometer analysis in the boreal forests of Québec (Canada). *Trees*, *17*(6), 477-484. http://dx.doi.org/10.1007/s00468-003-0260-4

Duchesne, L., Houle, D. et D’Orangeville, L. (2012). Influence of climate on seasonal patterns of stem increment of balsam fir in a boreal forest of Québec, Canada. *Agricultural and Forest Meteorology*, *162–163*, 108-114. http://dx.doi.org/10.1016/j.agrformet.2012.04.016

Dzialuk, A., Chybicki, I., Gout, R., Mączka, T., Fleischer, P., Konrad, H., Curtu, A. L., Sofletea, N. et Valadon, A. (2014). No reduction in genetic diversity of Swiss stone pine (Pinus cembra L.) in Tatra Mountains despite high fragmentation and small population size. *Conservation Genetics*, *15*(6), 1433‑1445. http://dx.doi.org/10.1007/s10592-014-0628-6

Eckert, C. G., Samis, K. E. et Lougheed, S. C. (2008). Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. *Molecular Ecology*, *17*(5), 1170–1188. http://dx.doi.org/10.1111/j.1365-294X.2007.03659.x

Efthymiadis, D., Jones, P. D., Briffa, K. R., Auer, I., Böhm, R., Schöner, W., Frei, C. et Schmidli, J. (2006). Construction of a 10-min-gridded precipitation data set for the Greater Alpine Region for 1800–2003. *Journal of Geophysical Research: Atmospheres*, *111*(D1), D01105. http://dx.doi.org/10.1029/2005JD006120

Ettinger, A. K., Ford, K. R. et HilleRisLambers, J. (2011). Climate determines upper, but not lower, altitudinal range limits of Pacific Northwest conifers. *Ecology*, *92*(6), 1323‑1331. http://dx.doi.org/10.1890/10-1639.1

EUFORGEN. (2015). *European Forest Genetics Resources Programme*. http://www.euforgen.org/distribution-maps/ : *Pinus cembra* distribution map. (00000).

Fan, S., Grossnickle, S. C. et Russell, J. H. (2008). Morphological and physiological variation in western redcedar (*Thuja plicata*) populations under contrasting soil water conditions. *Trees*, *22*(5), 671‑683. http://dx.doi.org/10.1007/s00468-008-0225-8

Filion, L. et Payette, S. (2010). *La Dendroécologie: Principes, Méthodes et Applications*. [s.l.] : Les Presses de l'Universite Laval.

Franklin, J. F., Shugart, H. H. et Harmon, M. E. (1987). Tree Death as an Ecological Process. *BioScience*, *37*(8), 550‑556. http://dx.doi.org/10.2307/1310665

Fraser, D. A. (1952). Initiation of cambial activity in some forest trees in Ontario. *Ecology*, *33*(2), 259‑273. http://dx.doi.org/10.2307/1930644

Fritts, H. C. (1976). *Tree rings and climate*. London, New York, San Francisco. : Academic Press.

Gaston, K. J. (2009). Geographic range limits: achieving synthesis. *Proceedings of the Royal Society B: Biological Sciences*, *276*(1661), 1395–1406.

Genries, A., Morin, X., Chauchard, S. et Carcaillet, C. (2009). The function of surface fires in the dynamics and structure of a formerly grazed old subalpine forest. *Journal of Ecology*, *97*(4), 728‑741. http://dx.doi.org/10.1111/j.1365-2745.2009.01518.x

Girardin, M. P., Ali, A. A. et Hély, C. (2010). Wildfires in boreal ecosystems: past, present and some emerging trends. *Int. J. Wildland Fire*, *19*(8), 991‑995.

Girardin, M. P., Guo, X. J., De Jong, R., Kinnard, C., Bernier, P. et Raulier, F. (2014). Unusual forest growth decline in boreal North America covaries with the retreat of Arctic sea ice. *Global Change Biology*, *20*(3), 851–866. http://dx.doi.org/10.1111/gcb.12400

Greene, D., Zasada, J. C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I. et Simard, M. J. (1999). A review of the regeneration dynamics of North American boreal forest tree species. *Canadian Journal of Forest Research*, *29*(6), 824–839.

Gričar, J., Zupančič, M., Čufar, K., Koch, G., Schmitt, U. W. E. et Oven, P. (2006). Effect of local heating and cooling on cambial activity and cell differentiation in the stem of Norway spruce (*Picea abies*). *Annals of Botany*, *97*(6), 943–951.

Grissino-Mayer, H. D. (2001). Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Research*, *57*(2), 205–221.

Gruber, A., Baumgartner, D., Zimmermann, J. et Oberhuber, W. (2009). Temporal dynamic of wood formation in <i>Pinus cembra</i> along the alpine treeline ecotone and the effect of climate variables. *Trees - Structure and Function*, *23*(3), 623‑635. http://dx.doi.org/10.1007/s00468-008-0307-7

Guo, Q., Taper, M., Schoenberger, M. et Brandle, J. (2005). Spatial-temporal population dynamics across species range: from centre to margin. *Oikos*, *108*(1), 47‑57. http://dx.doi.org/10.1111/j.0030-1299.2005.13149.x

Hampe, A. et Petit, R. J. (2005). Conserving biodiversity under climate change: the rear edge matters. *Ecology Letters*, *8*(5), 461–467. http://dx.doi.org/10.1111/j.1461-0248.2005.00739.x

Hättenschwiler, S. et Körner, C. (1995). Responses to recent climatewarming of Pinus sylvestris and Pinus cembra within their montane transition zone in the Swiss Alps. *Journal of Vegetation Science*, *6*(3), 357‑368. http://dx.doi.org/10.2307/3236235

Havranek, W. M. et Tranquillini, W. (1995). Physiological Processes during Winter Dormancy and Their Ecological Significance. *Ecophysiology of coniferous forests*, 95.

Hicke, J. A., Asner, G. P., Randerson, J. T., Tucker, C., Los, S., Birdsey, R., Jenkins, J. C. et Field, C. (2002). Trends in North American net primary productivity derived from satellite observations, 1982–1998. *Global Biogeochemical Cycles*, *16*(2), 2‑1. http://dx.doi.org/10.1029/2001GB001550

Hiebl, J., Auer, I., Böhm, R., Schöner, W., Maugeri, M., Lentini, G., Spinoni, J., Brunetti, M., Nanni, T., Tadić, M. P., Bihari, Z., Dolinar, M. et Müller-Westermeier, G. (2009). A high-resolution 1961–1990 monthly temperature climatology for the greater Alpine region. *Meteorologische Zeitschrift*, *18*(5), 507‑530. http://dx.doi.org/10.1127/0941-2948/2009/0403

Higuera, P. E., Brubaker, L. B., Anderson, P. M., Hu, F. S. et Brown, T. A. (2009). Vegetation mediated the impacts of postglacial climate change on fire regimes in the south-central Brooks Range, Alaska. *Ecological Monographs*, *79*(2), 201‑219. http://dx.doi.org/10.1890/07-2019.1

Hofmeyer, P. V., Kenefic, L. S. et Seymour, R. S. (2009). Northern white-cedar ecology and silviculture in the northeastern United States and southeastern Canada: a synthesis of knowledge. *Northern Journal of Applied Forestry*, *26*(1), 21–27.

Höhn, M., Gugerli, F., Abran, P., Bisztray, G., Buonamici, A., Cseke, K., Hufnagel, L., Quintela-Sabarís, C., Sebastiani, F. et Vendramin, G. G. (2009). Variation in the chloroplast DNA of Swiss stone pine (Pinus cembra L.) reflects contrasting post-glacial history of populations from the Carpathians and the Alps. *Journal of Biogeography*, *36*(9), 1798‑1806. http://dx.doi.org/10.1111/j.1365-2699.2009.02122.x

Housset, J. M., Girardin, M. P., Baconnet, M., Carcaillet, C. et Bergeron, Y. (2015). Unexpected warming-induced growth decline in *Thuja occidentalis* at its northern limits in North America. *Journal of Biogeography*, *42*, 1233–1245. http://dx.doi.org/10.1111/jbi.12508

Howe, G. T., Aitken, S. N., Neale, D. B., Jermstad, K. D., Wheeler, N. C. et Chen, T. H. (2003). From genotype to phenotype: unraveling the complexities of cold adaptation in forest trees. *Canadian Journal of Botany*, *81*(12), 1247‑1266. http://dx.doi.org/10.1139/b03-141

IPCC. (2013). *Climate change 2013: the physical science basis. Contribution of Working Group I to the Fifth Assessment Report of the IPCC.* Cambridge, United Kingdom and New York, NY, USA, : Cambridge University Press. (00000).

Jokela, J. J., Cyr, C. L. et others. (1977). Performance of northern white-cedar in central Illinois. Dans *Proceedings of the Thirteenth Lake States Forest Tree Improvement Conference* (p. pp. 100–106). USDA For. Serv. Récupéré de http://www.nrs.fs.fed.us/pubs/gtr/gtr_nc050/gtr_nc050_100.pdf

Jump, A. S., Mátyás, C. et Peñuelas, J. (2009). The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology & Evolution*, *24*(12), 694‑701. http://dx.doi.org/10.1016/j.tree.2009.06.007

Jump, A. S. et Peñuelas, J. (2005). Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, *8*(9), 1010–1020. http://dx.doi.org/10.1111/j.1461-0248.2005.00796.x

Kelly, C. K., Chase, M. W., De Bruijn, A., Fay, M. F. et Woodward, F. I. (2003). Temperature-based population segregation in birch. *Ecology Letters*, *6*(2), 87–89. http://dx.doi.org/10.1046/j.1461-0248.2003.00402.x

King, G. M., Gugerli, F., Fonti, P. et Frank, D. C. (2013). Tree growth response along an elevational gradient: climate or genetics? *Oecologia*, *173*, 1587–1600. http://dx.doi.org/10.1007/s00442-013-2696-6

Kirkpatrick, M. et Barton, N. H. (1997). Evolution of a Species' Range. *The American Naturalist*, *150*(1), 1‑23. http://dx.doi.org/10.1086/286054

Kohler, Y., Scheurer, T. et Ullrich, A. (2009). Réseaux écologiques dans l'Arc alpin. *Journal of Alpine Research | Revue de géographie alpine*, (97-1). http://dx.doi.org/10.4000/rga.798

Koskela, J., Buck, A. et Teissier du Cros, E. (2007). *Climate change and forest genetic diversity. Implications for sustainable forest management in Europe* (p. 111). Rome, Italy : European Forest Genetic Resources Programme (EUFORGEN).

Kramer, K., Leinonen, I. et Loustau, D. (2000). The importance of phenology for the evaluation of impact of climate change on growth of boreal, temperate and Mediterranean forests ecosystems: an overview. *International Journal of Biometeorology, 44*(2), 67‑75. http://dx.doi.org/10.1007/s004840000066

Kremer, A. et Le Corre, V. (2012). Decoupling of differentiation between traits and their underlying genes in response to divergent selection. *Heredity, 108*(4), 375‑385. http://dx.doi.org/10.1038/hdy.2011.81

Kremer, A., Ronce, O., Robledo-Arnuncio, J. J., Guillaume, F., Bohrer, G., Nathan, R., Bridle, J. R., Gomulkiewicz, R., Klein, E. K., Ritland, K., Kuparinen, A., Gerber, S. et Schueler, S. (2012). Long-distance gene flow and adaptation of forest trees to rapid climate change. *Ecology Letters*, *15*(4), 378–392. http://dx.doi.org/10.1111/j.1461-0248.2012.01746.x

Lafontaine, G. et Payette, S. (2010). The origin and dynamics of subalpine white spruce and balsam fir stands in boreal Eastern North America. *Ecosystems*, *13*(6), 932‑947. http://dx.doi.org/10.1007/s10021-010-9366-x

Lavigne, M. B. et Ryan, M. G. (1997). Growth and maintenance respiration rates of aspen, black spruce and jack pine stems at northern and southern BOREAS sites. *Tree Physiology*, *17*(8-9), 543‑551. http://dx.doi.org/10.1093/treephys/17.8-9.543

Legendre, P. et Legendre, L. (2012). *Numerical Ecology*. Kidlington, Oxford, UK : Elsevier. (08775).

Lenoir, J., Gégout, J. C., Marquet, P. A., de Ruffray, P. et Brisse, H. (2008). A significant upward shift in plant species optimum elevation during the 20th century. *Science*, *320*(5884), 1768 ‑1771. http://dx.doi.org/10.1126/science.1156831

Leonelli, G., Pelfini, M., Battipaglia, G. et Cherubini, P. (2009). Site-aspect influence on climate sensitivity over time of a high-altitude Pinus cembra tree-ring network. *Climatic Change*, *96*(1-2), 185‑201. http://dx.doi.org/10.1007/s10584-009-9574-6

Lesica, P. et Allendorf, F. W. (1995). When are peripheral populations valuable for conservation? *Conservation Biology*, *9*(4), 753‑760. http://dx.doi.org/10.1046/j.1523-1739.1995.09040753.x

Lévesque, M., Rigling, A., Bugmann, H., Weber, P. et Brang, P. (2014). Growth response of five co-occurring conifers to drought across a wide climatic gradient in Central Europe. *Agricultural and Forest Meteorology*, *197*, 1‑12. http://dx.doi.org/10.1016/j.agrformet.2014.06.001

Lingua, E., Cherubini, P., Motta, R. et Nola, P. (2008). Spatial structure along an altitudinal gradient in the Italian central Alps suggests competition and facilitation among coniferous species. *Journal of Vegetation Science*, *19*(3), 425‑436. http://dx.doi.org/10.3170/2008-8-18391

Li, P. et Adams, W. T. (1994). Genetic variation in cambial phenology of coastal Douglas-fir. *Canadian Journal of Forest Research*, *24*(9), 1864‑1870. http://dx.doi.org/10.1139/x94-240

Little, E. L. J. (1971). *Atlas of United States trees, volume 1. Conifers and important hardwoods.* (Miscellaneous publication 1146). Washington : USDA Forest Service. (00108).

Lloyd, A. H., Bunn, A. G. et Berner, L. (2011). A latitudinal gradient in tree growth response to climate warming in the Siberian taiga. *Global Change Biology*, *17*(5), 1935–1945. http://dx.doi.org/10.1111/j.1365-2486.2010.02360.x

Logan, J. A., Régnière, J. et Powell, J. A. (2003). Assessing the impacts of global warming on forest pest dynamics. *Frontiers in Ecology and the Environment*, *1*(3), 130‑137. http://dx.doi.org/10.1890/1540-9295(2003)001[0130:ATIOGW]2.0.CO;2

Mazerolle, M. J. (2015). *AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c).* http://CRAN.R-project.org/package=AICcmodavg : R package version 2.0-3. Récupéré de http://CRAN.R-project.org/package=AICcmodavg

McKenney, D. W., Pedlar, J. H., Lawrence, K., Campbell, K. et Hutchinson, M. F. (2007). Beyond Traditional Hardiness Zones: Using Climate Envelopes to Map Plant Range Limits. *BioScience*, *57*(11), 929‑937. http://dx.doi.org/10.1641/B571105

McLachlan, J. S., Clark, J. S. et Manos, P. S. (2005). MOLECULAR INDICATORS OF TREE MIGRATION CAPACITY UNDER RAPID CLIMATE CHANGE. *Ecology*, *86*(8), 2088‑2098. http://dx.doi.org/10.1890/04-1036

Moreira, B., Castellanos, M. C. et Pausas, J. G. (2014). Genetic component of flammability variation in a Mediterranean shrub. *Molecular Ecology*, *23*(5), 1213‑1223. http://dx.doi.org/10.1111/mec.12665

Mosca, E., Eckert, A. J., Di Pierro, E. A., Rocchini, D., La Porta, N., Belletti, P. et Neale, D. B. (2012). The geographical and environmental determinants of genetic diversity for four alpine conifers of the European Alps. *Molecular Ecology, 21*(22), 5530‑5545. http://dx.doi.org/10.1111/mec.12043

Motta, R. et Edouard, J. L. (2005). Stand structure and dynamics in a mixed and multilayered forest in the Upper Susa Valley, Piedmont, Italy. *Canadian Journal of Forest Research*, *35*(1), 21‑36. http://dx.doi.org/10.1139/x04-153

Mudelsee, M. (2003). Estimating Pearson's Correlation Coefficient with Bootstrap Confidence Interval from Serially Dependent Time Series. *Mathematical Geology*, *35*(6), 651‑665. http://dx.doi.org/10.1023/B:MATG.0000002982.52104.02

Myneni, R. B., Dong, J., Tucker, C. J., Kaufmann, R. K., Kauppi, P. E., Liski, J., Zhou, L., Alexeyev, V. et Hughes, M. K. (2001). A large carbon sink in the woody biomass of Northern forests. *Proceedings of the National Academy of Sciences*, *98*(26), 14784‑14789. http://dx.doi.org/10.1073/pnas.261555198

Nienstaedt, H. (1974). Genetic variation in some phenological characteristics of forest trees. Dans H. Lieth (dir.), *Phenology and seasonality modeling* (p. 389‑400). Berlin Heidelberg : Springer. (00038). Récupéré de http://link.springer.com/chapter/10.1007/978-3-642-51863-8_33

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, B., Simpson, G. L., Solymos, P., Stevens, M. H. H. et Wagner, H. (2013). *vegan: Community Ecology Package.* http://CRAN.R-project.org/package=vegan : R package v. 2.0-10. (03661).

Oribe, Y., Funada, R., Shibagaki, M. et Kubo, T. (2001). Cambial reactivation in locally heated stems of the evergreen conifer *Abies sachalinensis* (Schmidt) Masters. *Planta*, *212*(5-6), 684‑691. http://dx.doi.org/10.1007/s004250000430

Oribe, Y. et Kubo, T. (1997). Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. *Tree Physiology*, *17*(2), 81–87.

Paul, V., Bergeron, Y. et Tremblay, F. (2014). Does climate control the northern range limit of eastern white cedar (*Thuja occidentalis* L.)? *Plant Ecology*, *215*(2), 181‑194. http://dx.doi.org/10.1007/s11258-013-0288-5

Payette, S. (2007). Contrasted dynamics of northern Labrador tree lines caused by climate change and migrational lag. *Ecology*, *88*(3), 770‑780. http://dx.doi.org/10.1890/06-0265

Peakall, R. et Smouse, P. E. (2012). GenAlEx 6.5: genetic analysis in Excel. Population genetic software for teaching and research—an update. *Bioinformatics*, *28*(19), 2537‑2539. http://dx.doi.org/10.1093/bioinformatics/bts460

Pigliucci, M. (2005). Evolution of phenotypic plasticity: where are we going now? *Trends in Ecology & Evolution*, *20*(9), 481‑486. http://dx.doi.org/10.1016/j.tree.2005.06.001

Polechová, J., Barton, N. et Marion, G. (2009). Species' Range: Adaptation in Space and Time. *The American Naturalist*, *174*(5), E186‑E204.

Porter, T. J. et Pisaric, M. F. J. (2011). Temperature-growth divergence in white spruce forests of Old Crow Flats, Yukon Territory, and adjacent regions of northwestern North America. *Global Change Biology*, *17*(11), 3418–3430. http://dx.doi.org/10.1111/j.1365-2486.2011.02507.x

Pritchard, J. K., Stephens, M. et Donnelly, P. (2000). Inference of population structure using multilocus genotype data. *Genetics*, *155*(2), 945‑959.

Raj, S., Bräutigam, K., Hamanishi, E. T., Wilkins, O., Thomas, B. R., Schroeder, W., Mansfield, S. D., Plant, A. L. et Campbell, M. M. (2011). Clone history shapes *Populus* drought responses. *Proceedings of the National Academy of Sciences*, *108*(30), 12521‑12526. http://dx.doi.org/10.1073/pnas.1103341108

Régnière, J. et Bolstad, P. (1994). Statistical simulation of daily air temperature patterns in Eastern North America to forecast seasonal events in insect pest management. *Environmental Entomology*, *23*(6), 1368‑1380.

Rehfeldt, G. E., Tchebakova, N. M., Parfenova, Y. I., Wykoff, W. R., Kuzmina, N. A. et Milyutin, L. I. (2002). Intraspecific responses to climate in Pinus sylvestris. *Global Change Biology*, *8*(9), 912–929.

Richter, S., Kipfer, T., Wohlgemuth, T., Calderón Guerrero, C., Ghazoul, J. et Moser, B. (2012). Phenotypic plasticity facilitates resistance to climate change in a highly variable environment. *Oecologia, 169*(1), 269‑279. http://dx.doi.org/10.1007/s00442-011-2191-x

Risch, A. C., Jurgensen, M. F., Page-Dumroese, D. S., Wildi, O. et Schütz, M. (2008). Long-term development of above- and below-ground carbon stocks following land-use change in subalpine ecosystems of the Swiss National Park. *Canadian Journal of Forest Research*, *38*(6), 1590‑1602. http://dx.doi.org/10.1139/X08-014

Russell, J. H., Burdon, R. D. et Yanchuk, A. D. (2003). Inbreeding depression and variance structures for height and adaptation in self-and outcross *Thuja plicata* families in varying environments. *Forest Genetics*, *10*(3), 171–184.

Salzer, K., Sebastiani, F., Gugerli, F., Buonamici, A. et Vendramin, G. G. (2009). Isolation and characterization of polymorphic nuclear microsatellite loci in Pinus cembra L. *Molecular Ecology Resources, 9*(3), 858‑861. http://dx.doi.org/10.1111/j.1755-0998.2008.02396.x

Saulnier, M., Edouard, J.-L., Corona, C. et Guibal, F. (2011). Climate/growth relationships in a Pinus cembra high-elevation network in the Southern French Alps. *Annals of Forest Science, 68*, 189‑200. http://dx.doi.org/10.1007/s13595-011-0020-3

Savolainen, O. (2011). The Genomic Basis of Local Climatic Adaptation. *Science*, *334*(6052), 49‑50. http://dx.doi.org/10.1126/science.1213788

Savolainen, O., Bokma, F., García-Gil, R., Komulainen, P. et Repo, T. (2004). Genetic variation in cessation of growth and frost hardiness and consequences for adaptation of Pinus sylvestris to climatic changes. *Forest Ecology and Management*, *197*(1–3), 79‑89. http://dx.doi.org/10.1016/j.foreco.2004.05.006

Savolainen, O., Pyhäjärvi, T. et Knürr, T. (2007). Gene flow and local adaptation in trees. *Annual Review of Ecology, Evolution, and Systematics*, *38*(1), 595‑619. http://dx.doi.org/10.1146/annurev.ecolsys.38.091206.095646

Savva, Y., Bergeron, Y., Denneler, B., Koubaa, A. et Tremblay, F. (2008). Effect of interannual climate variations on radial growth of jack pine provenances in

Petawawa, Ontario. *Canadian Journal of Forest Research, 38*(3), 619‑630. http://dx.doi.org/10.1139/X07-178

Savva, Y., Schweingruber, F. H., Kuzmina, N. A. et Vaganov, E. A. (2002). Sensitivity of diameter growth to annual weather conditions in Scots pine provenances at a Central Siberian location. *Silvae genetica*, *51*(2-3), 49‑55.

Schweingruber, F. H. (1996). *Tree rings and environment. Dendroecology.* (Birmensdorf, Swiss Federal Institute for Forest, Snow and Landscape Research). [s.l.] : Paul Haupt AG Bern. (00910). Récupéré de http://www.cabdirect.org/abstracts/19980602476.html

Sexton, J. P., McIntyre, P. J., Angert, A. L. et Rice, K. J. (2009). Evolution and Ecology of Species Range Limits. *Annual Review of Ecology, Evolution, and Systematics*, *40*(1), 415‑436. http://dx.doi.org/10.1146/annurev.ecolsys.110308.120317

Shaw, R. G. et Etterson, J. R. (2012). Rapid climate change and the rate of adaptation: insight from experimental quantitative genetics. *New Phytologist*, *195*(4), 752–765. http://dx.doi.org/10.1111/j.1469-8137.2012.04230.x

Sirois, L. (1997). Distribution and dynamics of balsam fir (*Abies balsamea* L. Mill.) at its northern limit in the James Bay area. *Ecoscience*, *4*(3), 340–352.

Soja, A. J., Tchebakova, N. M., French, N. H. F., Flannigan, M. D., Shugart, H. H., Stocks, B. J., Sukhinin, A. I., Parfenova, E. I., Chapin, F. S. et Stackhouse, P. W. (2007). Climate-induced boreal forest change: Predictions versus current observations. *Global and Planetary Change*, *56*(3-4), 274‑296. http://dx.doi.org/10.1016/j.gloplacha.2006.07.028

Tang, J., Luyssaert, S., Richardson, A. D., Kutsch, W. et Janssens, I. A. (2014). Steeper declines in forest photosynthesis than respiration explain age-driven decreases in forest growth. *Proceedings of the National Academy of Sciences*, doi: 10.1073/pnas.1320761111. http://dx.doi.org/10.1073/pnas.1320761111

Tardif, J. et Bergeron, Y. (1997). Comparative dendroclimatological analysis of two black ash and two white cedar populations from contrasting sites in the Lake Duparquet region, northwestern Quebec. *Canadian Journal of Forest Research, 27*(1), 108‑116. http://dx.doi.org/10.1139/x96-150

Tardif, J., Flannigan, M. et Bergeron, Y. (2001). An Analysis of the Daily Radial Activity of 7 Boreal Tree Species, Northwestern Quebec. *Environmental*

Monitoring and Assessment, *67*(1-2), 141‑160. http://dx.doi.org/10.1023/A:1006430422061

Tardif, J. et Stevenson, D. (2001). Radial growth-climate association of *Thuja occidentalis* L. at the northwestern limit of its distribution, Manitoba, Canada. *Dendrochronologia*, *19*(2), 179–187.

Thompson, I., Mackey, B., McNulty, S. et Mosseler, A. (2009). Forest resilience, biodiversity, and climate change. Dans *A synthesis of the biodiversity/resilience/stability relationship in forest ecosystems. Secretariat of the Convention on Biological Diversity, Montreal. Technical Series* (Vol. 43).

Tremblay, M. F., Bergeron, Y., Lalonde, D. et Mauffette, Y. (2002). The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (Acer rubrum L.) populations at the northern limit of the species range. *Journal of Biogeography*, *29*(3), 365‑373. http://dx.doi.org/10.1046/j.1365-2699.2002.00665.x

Ulber, M., Gugerli, F. et Bozic, G. (2003). *Technical Guidelines for genetic conservation and use for Swiss stone pine (*Pinus cembra*).* Rome, Italy : EUFORGEN, Inter- national Plant Genetic Resources Institute.

Van Mantgem, P. J. et Stephenson, N. L. (2007). Apparent climatically induced increase of tree mortality rates in a temperate forest. *Ecology Letters*, *10*(10), 909‑916. http://dx.doi.org/10.1111/j.1461-0248.2007.01080.x

Violle, C., Enquist, B. J., McGill, B. J., Jiang, L., Albert, C. H., Hulshof, C., Jung, V. et Messier, J. (2012). The return of the variance: intraspecific variability in community ecology. *Trends in Ecology & Evolution*, *27*(4), 244‑252. http://dx.doi.org/10.1016/j.tree.2011.11.014

Visnadi, I. (2014). *Régénération et dynamique des populations marginales de* Thuja occidentalis *L. en forêt boréale* (Mémoire de maîtrise en biologie). Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, Québec. Récupéré de http://www.archipel.uqam.ca/6539/

Vittoz, P., Rulence, B., Largey, T. et Freléchoux, F. (2008). Effects of Climate and Land-Use Change on the Establishment and Growth of Cembran Pine (*Pinus cembra* L.) over the Altitudinal Treeline Ecotone in the Central Swiss Alps.

Arctic, Antarctic, and Alpine Research, *40*(1), 225-232. http://dx.doi.org/10.1657/1523-0430(06-010)[VITTOZ]2.0.CO;2

Wang, Z., Yang, B., Qin, C. et Shi, F. (2012). Research progress in monitoring and simulating stem radius growth: an overview. *Sciences in Cold and Arid Regions*, *4*(2), 0175–0183.

Williams, J. W., Shuman, B. N., Thompson Webb III, Bartlein, P. J. et Leduc, P. L. (2004). Late-Quaternary Vegetation Dynamics in North America: Scaling from Taxa to Biomes. *Ecological Monographs*, *74*(2), 309-334.

Wilmking, M., Juday, G. P., Barber, V. A. et Zald, H. S. J. (2004). Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Global Change Biology*, *10*(10), 1724-1736. http://dx.doi.org/10.1111/j.1365-2486.2004.00826.x

Wright, S. (1988). Surfaces of selective value revisited. *The American Naturalist, 131*(1), 115-123.

Xu, H., Tremblay, F., Bergeron, Y., Paul, V. et Chen, C. (2012). Genetic consequences of fragmentation in « arbor vitae, » eastern white cedar (*Thuja occidentalis* L.), toward the northern limit of its distribution range. *Ecology and Evolution*, *2*(10), 2506–2520. http://dx.doi.org/10.1002/ece3.371

Yakovlev, I. A., Asante, D. K. A., Fossdal, C. G., Junttila, O. et Johnsen, Ø. (2011). Differential gene expression related to an epigenetic memory affecting climatic adaptation in Norway spruce. *Plant Science*, *180*(1), 132-139. http://dx.doi.org/10.1016/j.plantsci.2010.07.004

Yamaguchi-Shinozaki, K. et Shinozaki, K. (2006). Transcriptional regulatory networks in cellular responses and tolerance to dehydration and cold stresses. *Annual Review of Plant Biology*, *57*(1), 781-803. http://dx.doi.org/10.1146/annurev.arplant.57.032905.105444

Yang, J., Pedlar, J. H., McKenney, D. W. et Weersink, A. (2015). The development of universal response functions to facilitate climate-smart regeneration of black spruce and white pine in Ontario, Canada. *Forest Ecology and Management*, *339*, 34-43. http://dx.doi.org/10.1016/j.foreco.2014.12.001

Zang, C. et Biondi, F. (2015). treeclim: an R package for the numerical calibration of proxy-climate relationships. *Ecography*, n/a‑n/a. http://dx.doi.org/10.1111/ecog.01335