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NORTHEASTERN CHINA AND EASTERN CANADA

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PREFACE

The present thesis is comprised of five parts, including the General Introduction, the Chapter I, Chapter II, Chapter III, and the General Conclusion presenting a publication associated with my Ph.D. study. All the papers and contexts involved in the thesis together are the original contributions to my Ph.D. in the program of Doctorat en sciences de l'environnement that I pursued and accomplished at Université du Québec en Abitibi-Témiscamingue, Canada. The Chapters I-III are correspondingly based on the following three publications:

1. Zhang, Y., Drobyshev, I., Gao, L.S., Zhao, X.H., Bergeron, Y. 2013. Disturbance and regeneration dynamics of a mixed Korean pine dominated forest on Changbai Mountain, North-Eastern China. *Dendrochronologia*, 31: 21-31 (IF 2012: 1.480)
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To meet the requirements of the jury of this thesis, let me clarify the role of each author in these publications. The leading author developed all the experimental designs with Dr. Yves Bergeron, Dr. Xiuhai Zhao, and Dr. Igor Drobyshev, and conducted all the fieldwork with Dr. Drobyshev. The leading author conducted all the laboratory work in all three studies. The leading author conducted all data analyses as well as wrote the three manuscripts and the thesis. Dr. Bergeron constantly financed, supervised, and discussed all Ph.D. project, and commented on early versions of the manuscripts. Dr. Zhao constantly financed, supervised, and discussed the Chapter I and II. Dr. Drobyshev guided data analyses of the three chapters, discussed and commented the early versions of manuscripts of the three chapters. Dr. Gao discussed and commented the early versions of manuscripts of Chapter I and II. Dr. Wang contributed to the field and laboratory work of Chapter II and commented the early version of manuscript of Chapter II. The comments and suggestions from all the co-authors greatly improved the quality of the papers, and I greatly appreciated their contributions.

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RÉSUMÉ

Afin d'évaluer la réponse de la croissance des arbres au changement climatique à leur limite de répartition et d'identifier les changements potentiels de leur aire de répartition, nous avons utilisé des méthodes dendrochronologiques en laboratoire et sur le terrain. Les zones d'étude se situaient dans des zones de transition forestière dans le nord de la Chine et dans l'ouest du Québec. Toutes deux présentaient une structure forestière similaire (forêt mixte) avec de nombreuses espèces situées à leur limite de répartition. De part et d'autre de celle-ci, les forêts étaient influencées par le climat et les perturbations, nous permettant ainsi de détecter les facteurs contrôlant les écotones forestiers. Dans le nord de la Chine, nous nous sommes concentrés sur trois conifères dominants le long d'un gradient altitudinal (750-1800 m) dans le Massif Changbai. Les forêts étudiées étaient composées du pin de Corée (*Pinus koraiensis* Siebold et Zuccarini), de l'épinette Jezo (*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu) et du sapin de Mandchourie (*Abies nephrolepis* (Trautv.) Maxim.). Nous avons également discuté d'un éventuel changement de la position altitudinale des écotones dans le contexte de réchauffement climatique. Dans l'ouest du Québec, nous avons analysé les modèles de croissance et de sensibilité de la croissance au climat de l'érable rouge (*Acer rubrum* L.) le long du gradient latitudinal (47-49° N). A la limite nordique de l'aire de répartition, nous avons examiné les effets directs et indirects des changements climatiques futurs sur la croissance et la position de la limite nordique.

Comme les chablis sont les principales perturbations affectant la croissance des espèces et la dynamique forestière dans le Massif Changbai, nous avons d'abord (chapitre I) reconstitué l'historique des perturbations dans la zone d'étude au cours de la période 1770-2000, sur la base de l'analyse des reprises de croissance et du patron de recrutement. Les pourcentages de reprises de croissance dans la canopée étaient inférieurs à 6 % dans la plupart des décennies, suggérant que les perturbations initiant ces reprises étaient de faible intensité. Les vents forts étaient la cause la plus probable de ces perturbations modérées. Deux épisodes avec des taux élevés de perturbations (19% et 13%) correspondaient aux décennies 1920 et 1980. Le recrutement du mélèze de la Baie d'Olga (*Larix olgensis* Henry), espèce intolérante à l'ombre, a eu lieu principalement avant les années 1860. Le recrutement du pin de Corée, espèce mi-tolérante à l'ombre, s'est produit via plusieurs vagues de régénération d'intensité modérée (décennies 1820, 1850, 1870, 1880, 1930 et 1990 et 2000). La régénération de l'épinette Jezo et du sapin de Mandchourie, espèces tolérantes à l'ombre, était continue au cours des dernières 220 et 130 années respectivement. Un meilleur recrutement du pin de Corée, de l'épinette Jezo et du sapin de Mandchourie a été observé au cours des décennies 1930 et 1990, coïncidant avec une augmentation de la fréquence des reprises de croissance lors des décennies 1920 et 1980. Cela suggère des perturbations d'intensité modérée.

Nous avons étudié la densité de régénération, l'accumulation de la biomasse et la sensibilité de la croissance au climat du pin de Corée, de l'épinette Jezo et du sapin de Mandchourie à leurs limites respectives de répartition altitudinale dans le Massif Changbai (Chapitre II). Les densités de la régénération ne différaient pas significativement entre les élévations, sauf pour l'épinette de Jezo qui a montré une densité de régénération nettement plus faible à sa limite inférieure par rapport à sa limite supérieure. Les trois espèces avaient une surface terrière significativement plus élevée au milieu du gradient altitudinal de répartition par rapport aux limites inférieure et supérieure du gradient. Elles ont également montré une plus grande sensibilité aux températures qu'aux précipitations à leurs limites supérieures de répartition et la tendance inverse a été observée à leurs limites inférieures. Aux limites supérieures respectives, les températures estivales (pour le pin de Corée et l'épinette de Jezo) et printanières (pour le sapin de Mandchourie) de l'année en cours affectaient positivement la croissance des arbres. Aux limites inférieures respectives, les précipitations automnales de l'année précédente avaient un effet positif sur la croissance. Notre étude suggère que les limites altitudinales de la végétation forestière ont été entravées par des facteurs climatiques affectant la croissance des espèces dominantes plutôt que par des facteurs contrôlant la densité de la régénération. Les changements climatiques auraient probablement modifié les limites altitudinales de l'optimum climatique pour la croissance des espèces dominantes se traduisant par des changements dans les compositions spécifiques et la localisation des écotones.

Dans le chapitre III, nous avons examiné les taux de croissance et la sensibilité de la croissance de l'érable rouge face aux conditions climatiques, en analysant les données dendrochronologiques de neuf sites situés le long d'un transect latitudinal de 300 km (47-49 °N) couvrant trois domaines bioclimatiques dans l'ouest du Québec. Les trois variables de croissance étudiées étaient les taux de croissance au cours des 30 premières années de la vie de l'érable, la croissance cumulative de la surface terrière au cours de la dernière décennie (2000-2009) et le taux de croissance annuelle pendant toute la durée de vie de l'érable. Toutes trois étaient positivement corrélées à la latitude. Sur l'ensemble du transect, la variation annuelle de la croissance de l'érable était positivement affectée par les températures de septembre de l'année précédente. Les températures de juillet de l'année en cours et les précipitations de décembre de l'année précédente ont eu un effet positif sur la croissance dans la partie nord du transect (48-49 °N). La croissance était limitée au milieu de l'été (juillet) par la sécheresse à l'extrémité sud du transect (47-48 °N). La contradiction apparente entre les résultats de la croissance absolue et ceux de la fonction de réponse a été interprétée par l'effet de l'histoire du peuplement sur le modèle de croissance de l'érable rouge. Plus précisément, les érables recrutés après de fortes perturbations, comme à la suite d'un feu, dans le nord, pourraient profiter des niveaux de luminosité plus élevés, nécessaires à la croissance, par rapport au peuplement plus au sud qui se sont probablement développés dans des trouées. Les changements climatiques prévus pourraient favoriser la croissance de l'érable rouge dans la sapinière à bouleau à papier, résultant en une migration de l'érable dans la forêt boréale mixte. Cependant, les régimes de perturbations naturelles et anthropiques

qui affectent les conditions de croissance à l'échelle du site semblent contrôlés la productivité de la biomasse de l'éérable rouge au sein de son aire de répartition actuel.

Notre étude suggère que les limites de répartition des espèces étudiées étaient contrôlées par les effets directs du climat et des perturbations sur leur recrutement et leur croissance. Les effets directs des changements climatiques futurs pourraient influencer positivement la croissance des arbres et le recrutement aux limites altitudinales (Massif Changbai) et latitudinales (ouest du Québec). Alors que les effets des changements des régimes de perturbations sur le maintien des espèces forestières étaient différents entre les deux zones d'étude, les réponses à ces changements dépendent principalement de la stratégie de vie et des caractéristiques écologiques des espèces. Dans le Massif Changbai, l'augmentation des températures et des tempêtes pourraient faciliter la migration des arbres vers de plus hautes altitudes, conduisant à un déplacement de la position actuelle de l'écotone feuillus-pin coréen / épinette-sapin. Dans l'ouest du Québec, un effet cumulée d'un climat plus chaud et d'une activité des feux pourrait favoriser une meilleure croissance de l'éérable. De meilleures projections de la dynamique des précipitations, qui contrôlent directement les niveaux d'activité des feux dans le contexte du réchauffement climatique, pourraient améliorer notre capacité à prévoir les changements futurs à la limite de distribution septentrionale de l'éérable rouge.

ABSTRACT

To understand how tree growth responds to climate change at tree distribution limits and what are the potential changes in tree distribution ranges under the future climate, we used dendrochronological and field survey methods to investigate tree responses to climate variability at the transitional zones in northeastern China and western Quebec. The selected study areas are dominated by mixed forests with many tree species growing at their distribution limits. In northeastern China, we focused on three dominant conifers of an elevational gradient (750-1800 m) in Changbai Mountain. The trees studied included Korean pine (*Pinus koraiensis* Siebold et Zuccarini), Jezo spruce (*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu), and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim.). We observed climatic controls of growth of the dominant species and potential shifts in altitudinal position of vegetational ecotones as a result of climate change. In eastern Canada, we analyzed climate-growth relationships of red maple (*Acer rubrum* L.) along a latitudinal gradient (47-49° N) at its northern distribution limit, and discussed direct and indirect climatic effects on its future distribution.

Since windthrows are main disturbances affecting tree growth and forest dynamics in Changbai Mountain, we first reconstructed disturbance history in the study area over the period 1770-2000 (Chapter I), based on the analyses of growth release and recruitment patterns. Percentages of growth releases in subcanopy trees were below 6% in most decades, suggesting that disturbances initiating these releases were of low severity. Strong winds possible cause of moderate disturbance events. Two episodes with increased disturbance rates (19% and 13%) were dated to the 1920s and 1980s. Shade-intolerant Olga bay larch (*Larix olgensis* Henry) recruited mainly before the 1860s. Recruitment of mid-tolerant Korean pine occurred as several regeneration waves (1820s, 1850s, 1870-1880s, 1930s, and 1990-2000s) of moderate intensity. Shade-tolerant Jezo spruce and Manchurian fir regenerated continuously over the last 220 and 130 years, respectively. An enhanced recruitment of Korean pine, Jezo spruce, and Manchurian fir was observed during the 1930s and 1990s, which were coincided with an increased growth release frequency in the 1920s and 1980s, suggesting disturbance events of moderate intensity.

We studied regeneration density, biomass accumulation, and growth sensitivity of Korean pine, Jezo spruce, and Manchurian fir at their respective distribution limits in Changbai Mountain (Chapter II). Regeneration densities did not differ significantly among the elevations except for the Jezo spruce, which showed a significantly lower regeneration at its lower limit than at upper limit. All three species showed a significantly higher basal area increment (BAI) at the middle part of their distribution ranges than at their limits. They also showed higher growth sensitivity to temperature than to precipitation at their upper limits and the inverse pattern was observed at their lower limits. At respective upper limits, summer temperatures of the current year (for Korean pine and Jezo spruce)

and spring temperature of the current year (for Manchurian fir) positively affected tree growth. At respective lower limits, precipitation in autumn of the previous year had a positive effect on growth. The study suggested that elevational limits of forest vegetation were constrained by climate factors affecting growth of dominant species rather than those controlling regeneration density. We concluded that climate change would likely shift the elevational positions of the climate optima for the growth of canopy dominants, leading to changes in the species and ecotone ranges.

In Chapter III, we examined growth rate and growth sensitivity to climate of red maple by analyzing dendrochronological data from nine sites located along a 300 km transect (47-49 °N) covering three bioclimatic domains in western Quebec. All three growth variables, i.e., growth rates during the first 30 years of maple lifespan, cumulative basal area increment over the most recent decade (2000-2009), and annual growth rate over the whole tree lifespan, were positively related to latitude. Annual variability of maple growth was positively affected by the previous year September temperature across the whole transect. July temperature of the current year and December precipitation of the previous year had a positive influence on the growth in the northern part of transect (48-49 °N). Mid-summer (July) drought limited the growth in the southern part of transect (47-48 °N). We interpreted an apparent discrepancy between the results of absolute growth analyses and response function analyses by the overriding effect of stand history on the growth pattern of red maple. Specifically, maples recruited after large disturbance events such as stand replacing fire in the north could take advantages of primarily higher light levels for the growth, compared to those in the south which likely occurred in canopy gaps. Expected climate change would likely favor red maple growth in the northern balsam fir - paper birch domain, resulting in an extension of maple distribution to the northern boreal mixedwoods. However, the natural and human disturbance regimes affecting the growth conditions at the site level appear to be dominant controls of the actual biomass productivity of red maple at its present distribution range.

Our study suggested that distribution limits of studied species were controlled through a combination of direct climatic and disturbance-mediated effects on their recruitment and growth. The direct effects of future climate change may positively affect tree growth and recruitment at higher elevational (Changbai Mountain) or latitudinal limits (western Quebec). While the effects of changes in disturbance regimes on trees maintenance in the forest were differed in two study area, responses to these changes were mainly dependent on species life strategy and ecological traits. In Changbai Mountain, increases in temperatures and wind disturbances may facilitate trees migration towards higher elevation, leading to an upward shift of altitudinal position of broadleaf-Korean pine/spruce-fir ecotone. While in western Quebec, negative influences of increases in fire activity and severity may override positive effects of direct climate on maple growth. We believe that better projections in precipitation dynamics, which will directly control levels of fire activity in the context of climate warming, may enhance our ability to project future changes in northern distribution limit of red maple.

GENERAL INTRODUCTION

0.1 CONTEXT

Global climate change have had profound effects on tree growth and forest structure (Hansen *et al.*, 2001; Walther, 2003), by affecting tree physiology and growth rates (Prentice *et al.*, 1992; Reinhardt *et al.*, 2011) and also modifying site conditions (Drobyshev *et al.*, 2010), and regional disturbance regimes (Bergeron *et al.*, 2010), as well as biotic interactions (Gavin and Hu 2006). Temperature, precipitation, solar radiation, and wind have been often considered as the main climatic factors which affect tree growth and vegetation dynamics (Huntley and Webb, 1989; Hofgaard *et al.*, 1991; Liu, 1997; Frank and Esper, 2005; Gworek *et al.*, 2007). However, recent studies have demonstrated that disturbance events play an important role in affecting species possibilities for recruitment and migration (see review in Dale *et al.*, 2001).

The influences of climate change on forest may be more apparent at the transitional zones (Allen and Breshears, 1998; Peñuelas and Boada, 2003), since the geographical distribution of vegetation zones has long been thought to be mainly limited by climate and only moderately modified by natural disturbances like forest fires (Walter, 1973; Stephenson, 1990; Woodward *et al.*, 1994; Tardif *et al.*, 2006; Messaoud *et al.*, 2007; Landhäusser *et al.*, 2010).

Recruitment and tree growth at transitional zones (termed ecotones, Odum 1983), encompassing species distribution limits, are particularly sensitive to environmental changes (Ries *et al.*, 2004), due to an increased frequency of sub-optimal environmental conditions causing seedling mortality and growth declines (Brubaker, 1986; Lescop-Sinclair and Payette, 1995; Wang *et al.*, 2006). Climate warming since 1950s has induced northward and elevationally upward shifts of tree species at the distribution limits (Kullman, 1993; Suarez *et al.*, 1999; Wilmking *et al.*, 2004; Griesbauer and Green, 2010) and these extensions have been expected to be further if warming continues (McKenney *et al.*,

2007; Berteaux *et al.*, 2010). Indeed, the evolution and migration of species to higher latitudes and altitudes occurred during the warming period of the Holocene (Delcourt and Delcourt, 1987; Richard, 1993).

Ecological niches defined as a species can maintain its populations without immigration under a set of conditions (Grinnell, 1917). Typically, structure and pattern in species assemblages originate from niche differentiation as the way species partition the resources and respond to microclimate. When a species' niche changes, it means that position possible move within a multivariate environmental niche space (Petitpierre *et al.*, 2012). The process of position change of a species is characterized by three distinct stages: introduction, naturalization and spread (Richardson *et al.* 2000). Invasive species often experience substantial shifts in climatic conditions during introduction from their native to non-native ranges (Kolbe *et al.*, 2012). Naturalization is defined as the ability to self-sustain populations following introduction into a new climatic conditions, whereas invasion is only achieved by a subset of naturalized species that spread away from founding populations to become widespread and abundant (Pyšek *et al.* 2008).

0.1.1 Climate change

Climate change at global scale

The air temperature, CO₂ concentration, precipitation, and radiation have exhibited significant changes during the recent 100 years. Global mean surface temperature has increased 0.74 °C from 1906 to 2005, (IPCC, 2007). This recent warming is mostly attributed to the effects of greenhouse gas (GHG) emissions (Meehl *et al.*, 2004). The mean global atmospheric CO₂ concentration has increased 30% since preindustrial times at a progressively faster rate each decade, 70% of the increase occurred between 1970 and 2005 (IPCC, 2007). Globally, precipitation over land shows a small upward trend

of approximately 1.1 mm per decade since 1901, with trends varying over time and space (IPCC, 2007). Precipitation has increased significantly in eastern parts of North America and northern Asia, while precipitation has declined in the Mediterranean and parts of southern Asia (IPCC, 2007). Dimming was widely reported between 1950s and the late 1980s (Abakumova *et al.*, 1996; Stanhill and Cohen, 2001), while a pronounced increasing trend in radiation has been observed since the late 1980s (Wild, 2009). As well, some extreme weather events have changed in frequency and/or intensity over the last 50 years (IPCC, 2007). It is very likely that cold days, cold nights, and frosts have become less frequent over most land areas, while hot days and hot nights have become more frequent. It is also likely that the frequency of heavy precipitation events has increased over most areas.

Temperature, precipitation, and phenology in northeastern China

The climate of northeastern China has become warmer and drier over the last century (Zhai *et al.*, 1999; Qian and Zhu, 2001; Qian and Qin, 2006). Climate records have shown an increase in annual mean temperature by 2 °C between the 1900s and 1990s (Qian and Zhu, 2001) and a decrease in summer precipitation by -0.81 mm yr⁻¹ between the 1960s and 2000s (Liang *et al.* 2011). Climate models predict a further increase in temperature by 4.6 °C towards the end of the 21st century (He *et al.* 2005). Regional climate model PRECIS has predicted increases in temperatures of spring (3.1°C), summer (4.7°C), and autumn (3.6°C), and a minor increases in precipitation during these seasons (2, 1, and 0%, respectively, Xu *et al.*, 2006). These changes in climate appeared to lengthen the growing season in northeastern China. The growing season has been extended by 1.4 days per year across temperate northeastern China between 1982 and 1993 (Chen *et al.*, 2005). The growing season of both boreal and broadleaf forests has been prolonged during 1982-2003, with obvious advance of the beginning dates of growth (Guo *et al.*, 2010).

Temperature, precipitation, and phenology in eastern Canada

In Canada, annual mean temperature and annual total precipitation over the 20th century have increased by 0.5 - 1.5 °C and 5 - 35%, respectively (Zhang *et al.*, 2000). It may further increase by an additional 1.5 - 4.5 °C by 2050, accompanied by 10 to 25% higher amount of precipitation (Boer *et al.*, 2000; Plummer *et al.*, 2006). In eastern Canada, climate models predict that temperatures will rise by an additional 2.2-3.5 °C by 2050 with more increases in winter (3.0-4.4 °C) than in other seasons. Studies project little change in summer precipitation and a decrease in snow accumulation during winter (Ouranos, 2010).

The increases in temperatures may translate into a longer growing season. The earlier spring warming has induced an increase in the length of the growing season (2 days/decade) since 1950 in Canada and the contiguous USA (Bonsal *et al.*, 2001; Easterling, 2002; Bonsal and Prowse, 2003; Feng and Hu, 2004). Longer growing season was also found in Quebec by an observation in earlier flowering of coltsfoot (*Tussilago farfara* L.) (Lavoie and Lachance, 2006). An average 5 to 6 day advance in spring phenology of lilacs has been reported in North America between 1959 and 1993 (Schwartz and Reiter, 2000). A simulation study by climate models has indicated that sugar maple (*Acer saccharum* Marsh.) buds could begin to open earlier by 1.5 days in Quebec over recent 100 years (Raulier and Bernier, 2000). In the 21st century, leaves of many tree species in Quebec could emerge earlier by 9.2 days due to climate warming (Morin *et al.*, 2009).

0.1.2 Impact of climate change on tree growth and forest at high latitudes of the Northern Hemisphere

Effects of climate change on tree growth and impacts of natural disturbances on forest structure in Changbai Mountain, northeastern China

Climatic factors are important in affecting tree growth in Changbai Mountain of northeastern China, and recent warming has increased tree and forest growth. Changbai Mountain hosts the major forest types of northeastern China with many tree species exhibiting their elevational distribution limits. Temperature, precipitation, and drought were found to be the main factors controlling tree growth in this area (Yu *et al.*, 2011). In general, tree growth was more limited by precipitation at the low elevation and by temperature at the high elevation (Yu *et al.*, 2013; Wang *et al.*, 2013). Growth of Erman's birch (*Betula ermanii* Cham.) at tree line has shown to positively correlate to temperature of the growing season (Wang *et al.*, 2013), and recent climate warming has induced an extension of this tree line (Zhang *et al.*, 2001). A tree-ring research has indicated that warming would increase the radial growth of tree species in Changbai Mountain (Wang *et al.*, 1995) and there was increased carbon sequestration in mixed forests during the 1981-2010 period in the area (Dai *et al.*, 2012). Plant growth in northeastern China has shown an enhancement in recent 30 years, resulting in a significant increase not only in greenness but also in forest carbon stocks (Piao *et al.*, 2003, 2005).

Volcanism and wind are two main natural disturbance factors affecting forest dynamics in Changbai Mountain (Manchida *et al.*, 1987; Liu, 1997; Dai *et al.*, 2011). Volcanism results in large-scale (over 100 km²) and stand-replacing disturbances in the area (Liu, 1997), while wind causes a wide range of disturbance events ranging from large blowdowns to single and multiple tree falls (Dai *et al.*, 2011). Wind disturbances are important for the maintenance of the mixed forest in this mountain area, since large scale wind disturbances (> 1000 m²) and wind-induced small canopy gaps are important for persistence of shade intolerant species such as Olga bay larch (*Larix olgensis* Henry) and mid-tolerant species such as Korean pine (*Pinus koraiensis* Siebold et Zuccarini), respectively (Yang *et al.*, 1994; Okitsu *et al.*, 1995; Liu, 1997; Dai *et al.*, 2011).

Effects of climate change on tree growth and impacts of natural disturbances on forest structure in eastern Canada

Tree growth in northern boreal forest of eastern Canada is enhancing, as a response to recent warming associated with the increase in the length of the growing season (Payette and Delwaide, 1994). For example, black spruce is a major species in its boreal forests and its growth has been positively related to warmer and conditions (Lavoie and Payette, 1992). In boreal zone of Quebec, radial growth rate of black spruce has been increasing since the 1930s, a trend which is likely associated with recent warming (Payette and Delwaide, 1994). Recent increases in height growth of black spruce and a positive trend in leader shoot elongation were also reported in the northern forest-tundra sites of Quebec (Gamache and Payette, 2004). The acceleration of height growth in spruce has been suggested to promote the change from krummholz to arborescent trees and reforestation of tundra uplands and the northward expansion of the boreal forest (Lescop-Sinclair and Payette, 1995). Annual GPP and NEP increases in Canadian black spruce (*Picea mariana* Mill.) forests were positively related to increases in net CO₂ uptake with climate warming (Grant *et al.*, 2009). Increases of NPP have been observed in eastern Canada between 1982 and 1998 (Hicke *et al.*, 2002).

In southern boreal and mixed-boreal transitional zones of Canada, moisture conditions appeared to be more important than temperature for tree growth, since major environment controls upon growth may change due to changes in the composition of canopy trees. The effects of drought stress on xylem structure of red maple (*Acer rubrum* L) have been observed in Central Ontario (De Silva *et al.*, 2012), they found that summer drought negatively affected red maple growth. Negative influences of summer water deficits on tree growth in the southern boreal forest of Quebec have been observed in sugar maple (Tardif *et al.*, 2001), white oak (*Quercus alba* L.) (Tardif *et al.*, 2006), trembling aspen (*Populus tremuloides* Michx.), and paper birch (*Betula papyrifera* Mash.) (Huang *et al.*, 2010). Similar drought stress limiting tree growth has also been reported in Boreal Plains of Manitoba (Girardin and Tardif, 2005).

Changes in disturbance regimes (forest fire and insect outbreaks) would be another critical factor influencing tree growth and forest structure in the boreal forest (Bergeron *et al.*, 1985; Gillett *et al.*, 2004; Duchesne and Prévost, 2013). Changes in fire frequency and severity are deemed to be of particular importance since these factors often control species distribution in boreal and temperate landscapes (Bergeron and Gagnon, 1987; Asselin *et al.*, 2003; Tardif *et al.*, 2006). For instance, high fire severity has been shown to be the main factor controlling the northern distribution limit of red pine (*Pinus resinosa* Ait.) (Bergeron and Brisson, 1994). Low fire frequency and small fire area were the most important factors determining the northern distribution limit of Jack pine (Asselin *et al.*, 2003), whereas Jack pine and black spruce were more suitable for short fire cycles than balsam fir (*Abies balsamea* (L.) Mill., Greene and Johnson, 2000). Insect outbreaks often induce huge damage of mature and overmature conifers and thus cause changes in forest structure (Messaoud, 2007). It may cause change in forest composition after insect outbreaks, if regeneration of affected species is insufficient (Bergeron *et al.*, 1995).

0.2 RATIONALE FOR CARRYING OUT THE STUDY IN TWO AREAS

We focus on Changbai Mountains (northeastern China) and the mixed-boreal zones of Abitibi-Témiscamingue (eastern Canada). Two features of these areas are vital in the context of our project: (1) strong dependence of local economies on forest resources, and (2) geographical location at the transition between boreal and temperate biomes (ecotone), where one could expect the most pronounced changes in vegetation cover as a result of future climatic changes. All these give us a background to better understand development of forest in both areas and vegetation response to climate change.

Forest resources play an important role in economies of both Changbai Mountain and Quebec. Forests in northeastern China have been being very important timber source since 1950s (Zhao *et al.*, 1998).

Changbai Mountain is one of the largest biosphere Reserve in the area and still keep large amount of natural forests due to its remote location and relatively high elevation. In Quebec, forests account for a large area and play a major economic, social, and environmental role. Québec's forests account for 20% of the total Canadian forest and 2% of the world's forests. In Québec, dense forests cover an area of 761,100 km², 55% of the total area is productive forest (source: <http://www.mrnfp.gouv.qc.ca/english/international/forests.jsp>).

Climate change may affect tree growth and forest dynamics by changing soil temperature, mineral nutrients, and water efficiency, extending growing season, rising CO₂ to enhance plant photosynthesis, and affecting disturbance regimes (Bergeron, 1991; Bazzaz, 1996; Menzel and Fabian, 1999; Volney and Fleming, 2001; Luo *et al.*, 2004; Körner, 2006). These effects can cause changes in species composition and community structure, finally leading to the variation of vegetation type.

Forest dynamics in northeastern China (Changbai Mountain) and eastern Canada are both driven by natural processes, and climate and natural disturbances are both important in modulating vegetation dynamics in two sides (Liu *et al.*, 1997; Bergeron *et al.*, 2004; Yu *et al.*, 2011). The similarity of forest type, climate, and soil in both sides has been recognized (Burger and Zhao, 1988; Barnes *et al.*, 1991). Forest composition is similar and have many tree species in the same genus, such as *Pinus*, *Abies*, *Picea*, *Acer*, *Quercus*, *Fraxinus*, *Betula*, *Populus* etc. In addition, two study area have transitional zones where forest structure, climate (cold in winter and warm and moist in summer), and soil condition (mainly sandy) is similar. A study covering such similar areas may therefore help assess generality in the patterns of climate impact on dynamics of vegetation cover.

Furthermore, two areas have a environment gradient which can help understand effects of climate variation on tree growth and forest dynamics. In Changbai mountain, it is an altitudinal gradient where temperatures decrease and precipitation increase as elevation increase, whereas there is a

latitudinal gradient in western Quebec (Abitibi-Témiscamingue region) where temperatures decrease as latitude increase. Although one is an altitudinal gradient and the other one is a latitudinal gradient, both gradients provide good sites to investigate impacts of climate variation on tree growth and forest composition.

0.3 GENERAL OBJECTIVES AND HYPOTHESES

The main aims of the study were (1) to evaluate the role of disturbances in the growth dynamics of selected species at their distribution limits, (2) to investigate climate effects on tree growth and forest dynamics by using recruitment and annual growth data, (3) to discuss effects of future climate on tree growth and forest dynamics in ecotones, i.e. transitional zones between different vegetation types.

I hypothesized that (1) effects of climate and disturbance regime both regulate tree growth and forest structure at the two ecotone areas, (2) temperature is main factor affecting tree growth at higher elevations or higher latitudes while precipitation regulates tree growth at lower elevations or lower latitudes.

0.4 STUDY AREA

0.4.1 Changbai Mountain in northeastern China

Our study was carried out on the northern slope of Changbai Mountain (41°31'-42°28'N, 127°9'-128°55'E) along an altitudinal gradient from 750 to 1800 m. The area has a temperate, continental climate, with long, cold winters and warm summers. Annual mean temperatures vary from 7.3 °C in the lowest reaches of the reserve to 2.8 °C near Heaven Lake on the top of mountain, and annual mean precipitation varies from 750 to 1340 mm (Zhao, 1981; He *et al.*, 2005). Even before the reserve was established in the 1950s, forest harvesting and other human disturbances inside the

reserve had been minor compared to those at areas of lower elevation (Shao *et al.*, 1994; Zhao *et al.*, 1998).

Changbai Mountain is one of the most important biosphere Reserve in northeastern China, due to its rich and well protected forest resource, Temperate Broadleaf and Mixed Forest, which is the most typical forest type in the region. The World Conservation Monitoring Centre of the United Nations Environment Programme (UNEP-WCMC) has published a forest classification system which divides the world's forests into 26 major types, reflecting climatic zones as well as the principal types of trees (http://www.unep-wcmc.org/forest/fp_background.htm). These 26 major types have been grouped into 6 broader categories. One of these is the Temperate Broadleaf and Mixed Forest (TBMF) which occurs in three major regions in the northern hemisphere: in eastern North America, in central and eastern Europe, and in north-east Asia (northeastern China, northern Korea, the Far East of Russia, and northern Japan; Fig. 0.1).

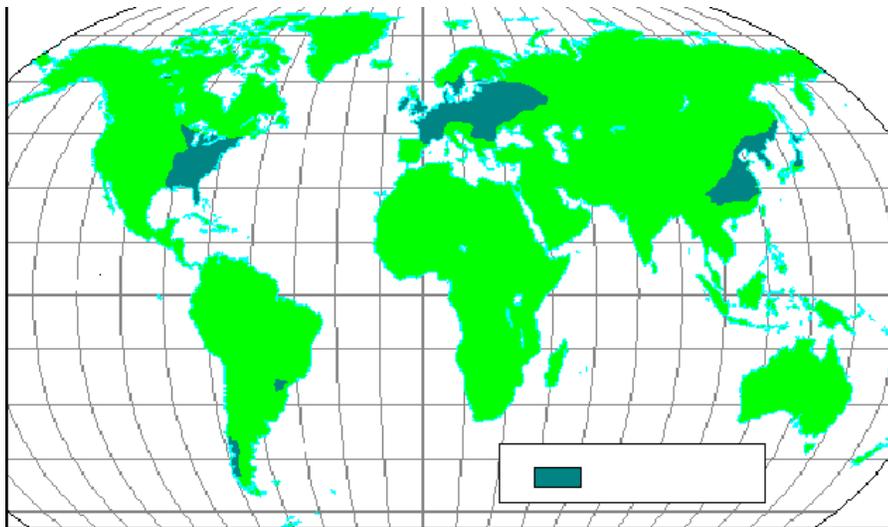


Figure 0.1. Geographical distribution of the temperate broadleaf and mixed forests (see dark green and also <http://www.runet.edu/~swoodwar/CLASSES/GEOG235/biomes/tbdf/tbdf.html>).

Topographic and geological features along with climate variations result in a vertical distribution of major forest ecosystems especially distinct along the northern slope (Wang *et al.*, 1980; Barnes *et al.*, 1992; Zhao *et al.*, 2004). From 1100 m and below, is a broadleaf-Korean pine forests dominated by Korean pine, basswood (*Tilia amurensis* Rupr.), Korean aspen (*Populus davidiana* Dode), Asian white birch (*Betula platyphylla* Suk.), Manchurian ash (*Fraxinus mandshurica* Rupr.), and Usugumo maple (*Acer mono* Maxim.). Transitional forests of Broadleaf-Korean pine forests and spruce-fir forests occur between 1000 to 1300 m. From 1300 to 1700 m, is spruce-fir forest (also known as dark conifer forest) including Jezo spruce (*Picea jezoensis* Carr. var. *komarovii* (V. Vassil.) Cheng et L.K.Fu), Olga bay larch, and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim.), with typical characteristics of boreal forest in North America. Alpine birch forest is from 1700-2000 m dominated by dwarf birch (*B. ermanii*). Above 2000 m, there are tundra, bare rock, and a volcanic crater lake. Such a vertical structure provides a condense picture of vastly distributed temperate and boreal forests found across northeastern China.

0.4.2 Western Quebec of eastern Canada

The distribution of vegetation in Quebec is determined mainly by climatic factors. There are three main vegetation zones (Fig. 0.2), namely northern temperate zone, dominated by hardwood and mixed stands; the boreal zone, characterized by softwood stands; and the Arctic zone, where the vegetation is mostly made of shrubs and herbaceous plants (Ministère des Ressources Naturelles du Québec, 2000).

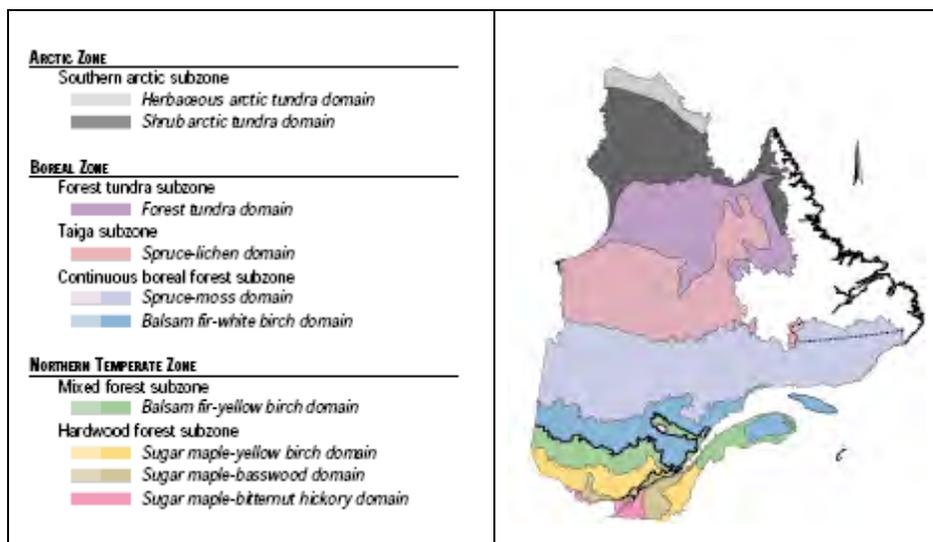


Figure 0.2. Vegetation zones and bioclimatic domains in Québec (Ministere des Ressources Naturelles du Québec, 2000).

Our study sites were located in the mixed forest zone between boreal and deciduous forests, which go across the balsam fir-white birch, balsam fir-yellow birch (*Betula alleghaniensis* Britt.), and sugar maple-yellow birch climatic domains. As the name implies, this vegetation zone is a transitional one, whose ecology is shaped largely by both fire and insect disturbance regimes (Bergeron and Dubuc, 1989; Bergeron, 2000). The average annual temperature is 0.8 °C, daily mean temperature is -17.9 °C for January and 16.8°C for July, and the average annual precipitation totals 856.8 mm (Environment Canada, 1993). The frost free period lasts 64 days, but occasional frost episodes may occur anytime during the growing season. The composition of the vegetation in the study area varies along a successional gradient, topography, disturbance like fire, insect epidemics, and logging would affect vegetation distribution. This mixed forest region is dominated by balsam fir, paper birch, white cedar (*Thuja occidentalis* L.), black spruce, white spruce (*Picea glauca* (Moench) Voss), red maple, trembling aspen, and Jack pine.

0.5 SPECIFIC OBJECTIVES AND RELATIONS BETWEEN CHAPTERS

In this study, we used dendrochronological techniques on Korean pine, Manchurian fir, Jezo spruce in Changbai Mountains (northeastern China) along an elevational gradient, and red maple at northern distribution limit in western Quebec along a latitudinal gradient. We also used detailed vegetation inventories in Changbai Mountain to investigate size structure, tree density, and recruit pattern of main tree species at broadleaf-Korean pine/spruce-fir ecotone.

The reason we chose conifers in Changbai mountain but broadleaf species in western Quebec is due to tree species distributions at respective areas. The three conifers were the only tree species cover three transitional zones along the whole altitudinal gradient in Changbai mountain, and study on their growth dynamics can reveal potential impacts of climate and disturbance on forest composition in the transitional zones. Similarly, red maple is the only tree species presented along the whole latitudinal gradient in the transitional zones (mixed-boreal forest) in Abitibi-Témiscamingue region. In addition, we also have many *Acer* species in Changbai mountain, among them one species *Acer mono* play a similar role in the forest as red maple in western Quebec, i.e. understory trees in the forest and reaching its upper limits (similar to northern limit as limited by low temperature) at transitional zones between broadleaf and boreal forest, therefore understanding factors affecting red maple growth and its northern distributional limit may help understand growth dynamics of *Acer* species in Changbai mountain.

The chapter I focused on forest dynamics in the broadleaved-Korean pine/spruce-fir ecotone based on analyses of size structure, age structure of regeneration and adult trees, and disturbance frequency and severity. It aimed at investigating recruitment pattern, to reconstruct local disturbance history, and to understand the relationship between disturbance history, species coexistence, and forest composition.

After the first goal detecting disturbance effects on forest composition, we are interested in how climate affects tree growth and forest dynamics. Therefore, the chapter II aimed to detect climate-growth associations of three dominant species (Korean pine, Jezo spruce, and Manchuria fir) along the altitudinal gradient (750-1800 m, covering these species upper and lower distribution limits) in Changbai Mountain, and to further understand the factors controlling the forest structure of broadleaved-Korean pine/spruce-fir forest ecotone and its dynamics under the future climate. The combined results of chapter I and chapter II can reveal which is main factor (disturbances or climates) or both mediated tree growth and forest dynamics in Changbai mountain.

The results of Chapter I and II indicates how disturbances and climate would affect tree growth and forest dynamics at the transitional zones in Changbai mountain. Is the regime affecting tree growth dynamics similar at the transitional zone in western Quebec? The chapter III mainly aimed to evaluate the effects of climate on the growth of red maple, examining biomass accumulation rates, growth sensitivity to annual weather, and competition interactions along a 300 km latitudinal gradient (47-49 °N) stretching from the southern mixed forest to the frontier maple populations in western Quebec.

The relations between chapters are: the first two chapters may help us to understand the role of indirect and direct effects of climate change on forest, through evaluating role of historical disturbances on species dynamics (chapter I) and analysis of direct effects of climate on regeneration and growth (chapter II). We believe that changes in disturbance regimes (chapter I) may be affected by climate change, therefore we may understand the order of importance of both effects (indirect and direct) affecting forest and mechanisms controlling dynamics of ecotone. The chapter III showed the importance of direct effects of climate on red maple growth and its variation in forest composition at ecotone in Canada, we also discussed the importance of disturbances on forest structure in the area according to other findings. The study in both area indicated that forest structure at ecotone were in unequilibrium status, both climate factors and disturbances were important in regulating forest

structure. Broadleaved species may expand into higher altitude or latitude. This could help us better understand the response of vegetation cover to future climate change.

Note: This thesis is written in the form of a collection of articles published or submitted to scientific journals. Thus there are a few repetitions in the texts between the General Introduction, the Chapter papers, and General Conclusion.

CHAPTER I

DISTURBANCE AND REGENERATION DYNAMICS OF A MIXED KOREAN PINE DOMINATED FOREST ON CHANGBAI MOUNTAIN, NORTH-EASTERN CHINA

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1.1 RÉSUMÉ

Nous avons utilisé des méthodes dendrochronologiques pour étudier l'histoire des perturbations de la forêt mixte dominée par le pin de Corée (*Pinus koraiensis* Siebold et Zuccarini) sur le versant nord de la montagne Changbai, au Nord-Est de la Chine, sur la période 1770 - 2000. La forêt étudiée, qui n'a connu aucun processus de succession au cours de la période d'intérêt, est dominée par un régime de perturbations naturelles caractérisé par des trouées de petite taille fréquentes et des trouées de taille moyenne peu fréquentes. Les pourcentages des rejets de croissance dans la canopée étaient inférieurs à 6 % dans la plupart des décennies, suggérant que les perturbations initiant ces rejets étaient de faible intensité. Les vents forts étaient la cause probable de ces perturbations modérées. Deux épisodes avec des taux élevés de perturbations (19% et 13%) correspondaient aux décennies 1920 et 1980. L'événement de 1980 était concordant avec un ouragan survenu en 1986 sur le versant ouest du Massif Changbai. Les analyses de la structure d'âge et des rejets de croissance ont révélé des stratégies de régénération spécifiques aux espèces de la canopée. Le recrutement du mélèze de la Baie d'Olga (*Larix olgensis* Henry), espèce intolérante à l'ombre, a eu lieu principalement avant les années 1860. Le recrutement de *P. koraiensis*, espèce mi-tolérante à l'ombre, s'est produit via plusieurs vagues de régénération d'intensité modérée (décennies 1820, 1850, 1870, 1880, 1930 et 1990 et 2000). La régénération de l'épinette Jezo (*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et LKFu) et du sapin de Mandchourie (*Abies nephrolepis* (Trautv.) Maxim.), espèces tolérantes à l'ombre, était continue au cours dernières 220 et 130 années respectivement. Un meilleur recrutement du pin de Corée, de l'épinette Jezo et du sapin de Mandchourie a été observé au cours des décennies 1930 et 1990, coïncidant à une augmentation de la fréquence des rejets de croissance lors des décennies 1920 et 1980. Cela suggère des perturbations d'intensité modérée. Nos résultats indiquent que le régime de perturbations actuel de la forêt mixte dominée par le pin de Corée maintient la coexistence d'espèces héliophiles et tolérantes à l'ombre et qu'un changement de l'activité des vents peut être particulièrement important pour la composition forestière future.

1.2 ABSTRACT

We used dendrochronological methods to study disturbance history of a mixed Korean pine (*Pinus koraiensis* Siebold et Zuccarini) dominated forest on the northern slope of Changbai Mountain, North Eastern China, over 1770-2000. Frequent small-scale canopy gaps and infrequent medium-scale canopy disturbances dominated natural disturbance regime in the forest, which didn't experience stand-replacing disturbances over the studied period. Percentages of growth releases in subcanopy trees were below 6% in most decades, suggesting that disturbances initiating these releases were of low intensity. Strong winds were likely cause of moderate disturbance events. Two episodes with increased disturbance rates (19% and 13%) were dated to the 1920s and 1980s, timing of the 1980s event was consistent with a hurricane occurred in 1986 on the western slope of the Changbai Mountain. Age structure and growth release analyses revealed species-specific regeneration strategies of canopy dominants. Shade-intolerant Olga bay larch (*Larix olgensis* Henry) recruited mainly before the 1860s. Recruitment of moderately shade-tolerant *P. koraiensis* occurred as several regeneration waves (1820s, 1850s, 1870-1880s, 1930s, and 1990-2000s) of moderate intensity. Shade-tolerant Jezo spruce (*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu) and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim.) regenerated continuously over the last 220 and 130 years, respectively. Enhanced recruitment of *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis* was observed during the 1930s and 1990s, coinciding with increased growth release frequency in the 1920s and 1980s, and suggesting disturbance events of moderate intensity. Our results indicate that the current disturbance regime of the mixed Korean pine dominated forest maintains coexistence of light-demanding and shade-tolerant species and that change in wind climate may be particularly important for future forest composition.

Keywords: Canopy gaps Dendroecology Disturbance regime Growth release Old-growth forest

1.3 INTRODUCTION

Natural disturbances have profound effects on forest dynamics, influencing growth, regeneration, diversity, and coexistence of tree species (Frelich and Lorimer, 1991; Abrams *et al.*, 1999; Kubota, 2000; Bergeron *et al.*, 2004). Studies in forest disturbance history are critical for understanding the present forest composition and predicting the future forest structure under different climate and management scenarios (Girardin *et al.*, 2001; Kuuluvainen, 2002; Dang *et al.*, 2009). Dendroecological techniques are widely applied to reconstruct forest history, disturbance regimes, and past forest dynamics (Brisson *et al.*, 1992; Tardif *et al.*, 2001; Fraver and White, 2005). Tree ring analyses allow reconstruction of forest disturbance history through dating of growth release and analyzing the establishing dates in sampled individuals (Lorimer and Frelich, 1989; Frelich and Lorimer, 1991; Black and Abrams, 2003).

Disturbance regimes in the mixed forest are important in promoting coexistence of tree species (Runkle, 1985; Liu, 1997; Bergeron, 2000). In closed-canopy temperate forests, the gradient in forest disturbance severity ranges from small canopy gaps created by single or multiple treefalls to large-scale stand-replacing events (Runkle, 1985; Runkle and Yetter, 1987; Foster *et al.*, 1998; Romme *et al.*, 1998; Turner *et al.*, 1998; Ilisson *et al.*, 2005; Margolis *et al.*, 2007). Variation in the size and frequency of disturbances causes spatial and temporal heterogeneity in environment affecting establishment, growth, and survival of trees (Liu, 1997; Mori and Takeda, 2004). Species may respond differently to the range of disturbance sizes and severities, depending on their own ecological characteristics such as shade tolerance and regeneration requirements (Runkle and Yetter, 1987; Bergeron *et al.*, 1998; Drobyshev, 1999). Typically, shade-tolerant trees benefit from advanced regeneration and often colonize small canopy gaps, whereas shade-intolerant trees reveal faster growth rates but require large disturbance patches for establishment (Runkle and Yetter, 1987; Kobe *et al.*, 1995; Liu, 1997).

Diversity in disturbance events may therefore allow coexistence of both groups of trees within a community.

Mixed Korean pine (*Pinus koraiensis* Siebold et Zuccarini) dominated forest is a major forest type in the Northeastern China with Changbai Mountain as its core distribution area. Volcanism and wind are two main natural disturbance factors affecting forest dynamics in Changbai Mountain (Manchida *et al.*, 1987; Liu, 1997; Dai *et al.*, 2011). Volcanism results in large-scale and stand-replacing disturbances in the area. The most severe volcanic eruption in the Changbai Mountain occurred around 1100 AD and destroyed vegetation over the area of 100 km², the current vegetation cover originating largely after that event (Zhao, 1981). The most recent eruptions occurred in 1597, 1668, and 1702 and had spatially limited effects on local forests (Zhao, 1981; Manchida *et al.*, 1987). Instead, wind mainly causes a wide range of disturbance events ranging from large blowdowns to single and multiple tree falls (Dai *et al.*, 2011), all of which are considered important for forest dynamics in the Changbai Mountain. Large scale wind disturbances (> 1000 m²) are important for persistence of shade intolerant species in the forest canopy, such as Olga bay larch (*Larix olgensis* Henry) (Yang *et al.*, 1994; Okitsu *et al.*, 1995; Liu, 1997). Wind-induced small canopy gaps maintain mid-tolerant *P. koraiensis* in broadleaf-Korean pine forest (Dai *et al.*, 2011). Jezo spruce (*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu) and Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim.) appear to be less dependent on canopy disturbances due to their shade tolerance (Yang *et al.*, 1994; Okitsu *et al.*, 1995; Liu, 1997). Historical records on the frequency and intensity of disturbance events themselves are largely missing, which precludes a deeper understanding of community dynamics in this part of the Eastern Asian temperate zone.

In an attempt to quantify the multi-century pattern of natural disturbances in Asian mixed temperate forests, we studied forest disturbance history and regeneration dynamics in a primary mixed Korean pine forest, the most typical forest type in the Changbai Mountain. Our specific objectives were (1) to

investigate temporal patterns of tree species regeneration, (2) to reconstruct local disturbance history of this mixed forest, and (3) to understand the relationship between disturbance history and species coexistence. Based on our field observations and published studies (Yang *et al.*, 1994; Okitsu *et al.*, 1995; Liu, 1997; Dai *et al.*, 2011), we hypothesized that (1) the forest disturbance regime is dominated by frequent small-scale disturbances, whereas medium or large-scale disturbances (> 1 ha) are infrequent, and (2) both regeneration and growth patterns of three dominant species (*P. koraiensis*, *P. jezoensis*, and *A. nephrolepis*) are synchronized by the canopy disturbances. Understanding the level of control exercised by the disturbance regime upon trees' regeneration is crucial for modeling future species population dynamics. We therefore discuss our results in the context of potential effects of climatic variability on natural disturbance regime and dynamics of the mixed Korean pine forests.

1.4 MATERIALS AND METHODS

1.4.1 Study area and climate

The study was conducted on the northern slope of Changbai Mountain in North Eastern China (1900 km², 41°31' - 42°28' N, 127°9' - 128°55' E, Fig. 1.1), within the territory of Changbaishan Natural Reserve. The area has a temperate continental climate, with long, cold, and windy winters and short, warm, and rainy summers. Annual mean temperatures vary from 7.3 °C at the low elevations (700 m a.s.l.) to 2.8 °C at the top of the mountain (2691 m a.s.l.). The mean annual precipitation along this gradient varies from 750 to 1340 mm (Zhao, 1981). The frequency of storms (episodes with wind speeds above 17 m s⁻¹) varies from 30 days yr⁻¹ at 770 m a.s.l. to 267 days yr⁻¹ at 2600 m a.s.l. (Liu, 1997). The topography of the area below 1700 m is gentle with slope inclinations being below five degrees. Above 1700 m, the slope is relatively steep with an average angle above 20 degrees. Volcanic soils overlaying a deep layer of volcanic ash are common across the study area (Shao, 1996).

Distinctive vegetation zones are present along the elevation gradient on the northern slope of Changbai Mountain (Wang *et al.*, 1980). From 750 to 1100 m, broadleaf-Korean pine forest is dominated by *P. koraiensis*, Amur linden (*Tilia amurensis* Rupr.), Korean aspen (*Populus davidiana* Dode), Asian white birch (*Betula platyphylla* Suk.), Manchurian ash (*Fraxinus mandschurica* Rupr.), and Usugumo maple (*Acer mono* Maxim.). Between 1000 and 1300 m, there is a transitional zone represented by mixed Korean pine dominated forest. In this zone, shade-intolerant *L. olgensis*, mid-tolerant *P. koraiensis*, and shade-tolerant *P. jezoensis* and *A. nephrolepis* are the dominant species. From 1300 to 1700 m, a zone of evergreen coniferous forest develops with *L. olgensis*, *P. jezoensis*, and *A. nephrolepis* as the most common species. Between 1700 and 2000 m, alpine birch forest with dwarf birch (*Betula ermanii* Cham.) is the dominant vegetation type.

The forests of Changbai Mountain experienced relatively little disturbance by human activity before the 19th century due to their remoteness (Burger and Zhao, 1988; Barnes *et al.*, 1992). During the 20th century, human disturbance became more frequent and severe, and the area of primary forest decreased by 70.4% from 1950 to 1986 (Xin, 1987). Presently, old-growth primeval forests can only be found in the Changbaishan Natural Reserve. The Reserve was established in 1958 to protect the area from cutting and other forms of forest utilization such as corn picking and browsing by livestock (Wang *et al.*, 1980). Although forest vegetation in the Reserve reveals the legacy of past forest use, it remains to be largely a result of natural succession.

1.4.2 Field and laboratory methods

Our study focused on the transitional zone between 1000 and 1300 m, where *P. koraiensis* and *P. jezoensis* are close to their upper and lower altitudinal distribution limits, respectively. We hypothesized that this part of their distribution range may be sensitive to environmental changes, including changes in natural disturbance regimes (Ries *et al.*, 2004). To represent forest condition

along the altitudinal gradient, 19 sample plots ($20 \times 80 \text{ m}^2$ each, the longer side being perpendicular to the slope) were set at seven altitudes (1050, 1100, 1120, 1150, 1180, 1220, and 1250 m) in the summers of 2007 and 2008. At each altitude, we established 2 to 3 plots. In each plot, we recorded the species identity, diameter at 1.3 m (DBH), and tree height of all trees above 1cm in DBH. We also recorded height and diameter at the base of seedlings of the four dominant tree species (*L. olgensis*, *P. koraiensis*, *A. nephrolepis*, and *P. jezoensis*). We classified sampled individuals as seedlings (height < 1.3 m), small saplings (height ≥ 1.3 m with DBH < 1cm), saplings ($1\text{cm} \leq \text{DBH} < 5\text{cm}$), or adult trees (DBH $\geq 5\text{cm}$).

To estimate age of seedling for *A. nephrolepis* and *P. jezoensis*, we counted internodes between branch whorls. The primary reason for choosing this method was limitations imposed by forest use regulations in the Reserve, which prevented us from cutting trees and using ring counting for age estimation. The technique proved unreliable for *P. koraiensis* since internodes of this species are not easily distinguishable. We therefore used regression equation between age and diameter of *P. koraiensis*, developed for Changbai Mountain (Hu *et al.*, 2009) to estimate age of seedlings based on their diameter. The two variables were highly correlated and regression showed a high R^2 value ($A=9.975D^{0.675}$, $R^2=0.92$, $P<0.0001$, $n=251$). Age of seedlings for *L. olgensis* was not available since no seedlings were observed during our survey. In total, age was estimated for 1838 *P. koraiensis*, 1515 *P. jezoensis*, and 2060 *A. nephrolepis* seedlings.

In the summer of 2008, we established 19 subplots ($20 \times 20 \text{ m}^2$) within the areas of initially 19 sampled plots to evaluate the tree age structure at DBH level (1.3 m). Within the subplots, we cored all trees (one core per tree) of four dominant species (*L. olgensis*, *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis*) with DBH above 3 cm. Only samples with solid (non-rotten) central parts were used for analyses. Most of the *L. olgensis* trees were rotten in their center, making it difficult to estimate precise age. Totally, we measured 680 trees (59 *L. olgensis*, 126 *P. koraiensis*, 189 *P. jezoensis*, and

306 *A. nephrolepis*). We neither core nor cut saplings with DBH between 1 and 3 cm since destructive sampling is not allowed within the Reserve. We considered the error associated with age estimation to be relatively minor due to the fact that the proportion of saplings with DBH between 1 and 5 cm for all four species was relatively small (for *P. koraiensis*, *L. olgensis*, *P. jezoensis*, and *A. nephrolepis* - 1.4%, 0%, 16.1%, and 17.1%, respectively, Table 1.1).

All the samples were dried, mounted, and sanded using up to 600 mm grit sandpaper until ring boundaries were clearly visible. Cores were visually cross-dated by using the pointer year technique (Stokes and Smiley, 1968). The ring widths were measured to the nearest 0.01 mm by the LinTab measuring stage and statistically verified by the software COFECHA (Holmes, 1983). If a core had missing pith, the age was determined by using the pith locator (Norton *et al.*, 1987; Duncan, 1989). We corrected age estimate of cored trees (126 trees of *P. koraiensis*, 189 trees of *P. jezoensis*, and 306 trees of *A. nephrolepis*) to represent tree ages at the base of the tree, using regression equations between the age and the height of seedlings.

1.4.3 Data analysis

To represent contribution of each tree species to forest canopy, we calculated Importance Values (IV, Cottam and Curtis, 1956) as the average of relative density (% of the number of trees) and relative dominance (% of basal area) of a tree species in each plot, and then produced an average for the whole study area. To facilitate across-species comparisons, we presented age distributions as number of trees of a particular age class per hectare. A species age structure was presented at 10-year intervals to better reflect the actual dating accuracy affected by a possible error in counting branch whorls in seedlings, regressions used to estimate age in saplings, and in estimating of the pith years in adult trees.

For the analyses of growth releases, we used trees under main forest canopy and part of the chronologies of the modern canopy trees, representing the period when these trees were under canopy. Rationale for this protocol was an assumption that growth of understory trees is more light-limited and they show more pronounced response to increased light condition, as compared to canopy trees. To classify a tree as an understory tree, we used the height threshold of 25 m (Xu, 2001). The use of this method was complicated by the fact that the height of the cored trees could not be measured retrospectively. To address this problem, we used our knowledge of DBH - height relationships obtained for the respective species in the study area and established 25 m as a height threshold for a tree of any species, indicating its presence in the main forest canopy. We then associated 25 m height threshold to corresponding DBH thresholds to identify understory segment of tree's lifespan in modern canopy trees. Following this strategy, we combined chronologies representing understory trees and modern canopy trees during their stay under the canopy.

We utilized standard method of percent growth change (GC) to detect canopy disturbance events (Lorimer and Frelich, 1989; Nowacki and Abrams, 1997; Abrams *et al.*, 1999). The method involves determination of (a) the length of the time frame to calculate moving average of the tree ring increment and (b) the minimum GC threshold to be used as an indicator of a disturbance event. For this study, we used 10-year time spans to avoid problems with short-term climatically-induced variations in growth (Nowacki and Abrams, 1997) and, at the same time, to reflect high frequency of wind-induced canopy disturbances in the study area. We defined increase in growth, later referred to as growth release, as 100% increase as compared to the previous growth. Specifically, the percent growth change (GC) was calculated as $GC = (M2 - M1)/M1 \times 100$ where GC was percentage growth change for a single year, M1 and M2 were the preceding and subsequent 10-year ring-width mean, respectively.

A drawback of the selected method of release identification was its inability to evaluate growth conditions, and subsequently-canopy openness during the period corresponding to the beginning of tree chronologies. First, the very first decade in each chronology couldn't be compared with the previous decade. Secondly, the initial growth of the tree might have been already large and indicative of the gap conditions, making following increases in growth unlikely to qualify for "growth release" according to selected criteria.

To identify gap and close-canopy conditions at the beginning of trees' lifespan, we used two alternative approaches. First, we compared cumulative basal area increments (BAI) of the first ten years of tree growth with BAI of cumulative 10-year increments during the identified release periods. Since BAI of young trees is generally smaller than the one of the adult trees, our analyses were very conservative in the way they detected gap episodes. We used Wilcoxon matched-pairs test (Gehan, 1965) to check for significant differences in means of respective increment distributions, arranged in 2 cm² classes.

Secondly, we compared initial growth rates with thresholds, indicative of the open conditions (canopy gaps). To the best of our knowledge, no published studies provide direct estimates of such growth thresholds for the studied region. Therefore we estimated the thresholds based on their average growth rates available elsewhere. In the study of Yu *et al.* (2006, 2011), the mean radial growth at radii level and respective SD have been estimated to be 1.57 ± 0.38 , 1.63 ± 0.55 , and 1.43 ± 0.38 mm for *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis*, respectively. In the studies of Deng *et al.* (1999) and Gao *et al.* (2011), the mean growth rate during the first 10 years were 1.5 (*P. koraiensis*), 0.8 (*P. jezoensis*), and 0.9 mm yr⁻¹ (*A. nephrolepis*). Based on these studies and our own experience with analyzing the growth of the studied species in the region, we defined growth threshold, indicative of gap conditions, as respective mean growth rate increased by one SD, i.e. 1.95 mm yr⁻¹ for *P. koraiensis*, 2.18 mm yr⁻¹ for *P. jezoensis*, and 1.81 mm yr⁻¹ for *A. nephrolepis*. We considered this

approach to be more opportunistic, as compared to the first method. *L. olgensis* was not available for these analyses due to rotten center of many cored trees (84% of all sampled trees).

1.5 RESULTS

1.5.1 Stand structure

The forest was dominated by four conifer species: *A. nephrolepis*, *P. koraiensis*, *L. olgensis*, and *P. jezoensis* (Table 1.1). In canopy layer, both *P. koraiensis* and *L. olgensis* had the largest basal area, but it was *P. jezoensis* which had the highest tree density. *A. nephrolepis* dominated in sub-canopy layer, mostly due to its high density. The other two sub-canopy species, Ukurundu maple (*Acer ukurunduense* Trautv. et Mey.) and bearded maple (*Acer barbinerve* Maxim.) had a high stem density but a small basal area. Among all species, *A. nephrolepis* showed the highest abundance in both seedling and sapling strata. *P. jezoensis* was abundant as seedlings and saplings, while *P. koraiensis* was common in seedling stratum but was rare as saplings. *L. olgensis* didn't regenerate in the studied sites (Table 1.1).

Combined diameter distribution of all four species revealed an inverse J pattern, typical of an uneven-aged forest (Fig. 1.2a), although distributions of single species differed considerably. Excluding seedling classes, *P. koraiensis* showed a broadly normal distribution throughout the range of diameter classes, and dominated the large diameter class (> 50 cm) across the stands (Fig. 1.2b). *L. olgensis* exhibited a bell-shape pattern dominated by the diameter class from 30 to 50 cm and had no trees in small DBH classes (< 5 cm) (Fig. 1.2c). *P. jezoensis* was well represented from small to intermediate classes (1-40 cm) and reached large classes up to 75 cm DBH (Fig. 1.2d). *A. nephrolepis* dominated DBH classes below 20 cm (Fig. 1.2e).

DBH (x, cm) and height (y, m) were highly correlated in the four dominant species with high R²

values: *L. olgensis* ($y=0.5953x+8.3889$, $R^2=0.61$, $p<0.0001$), *P. koraiensis* ($y=5.5872+0.4427x$, $R^2=0.71$, $p<0.0001$), *P. jezoensis* ($y = 1.2908+0.6151x$, $R^2=0.88$, $p<0.0001$), *A. nephrolepis* ($y = 1.5392+0.64x$, $R^2 = 0.82$, $p < 0.0001$). On average, *L. olgensis*, *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis* reached the height of the main canopy (25 m) at DBH of 27.9 cm, 43.9 cm, 38.5 cm, and 36.7 cm, respectively. The average canopy height was similar across plots and elevations (Appendix, Table 1.1), and correlation coefficients between DBH and height didn't significantly differ across plots and species (Appendix, Fig. 1.1). This allowed us to set the same height threshold (25 m) attained forest canopy for all plots and species studied.

1.5.2 Age structure

To estimate establishment dates of *P. koraiensis*, we used the same regression equation ($A=9.975D^{0.675}$) to correct years needed to reach 1.3 m (see section of method in seedling age estimation). On average, it took 11 years for a *P. koraiensis* seedling to reach 1.3 m. For *P. jezoensis* and *A. nephrolepis*, we developed regression equations between age and height from our seedling data. The correlation between age (x, year) and height (y, cm) was statistically significant for both species and showed high R^2 values: *P. jezoensis* ($y = -16.2802+4.0956x$, $R^2 = 0.74$, $P < 0.0001$, $n = 1454$) and *A. nephrolepis* ($y = -16.9840+4.0284x$, $R^2 = 0.66$, $P < 0.0001$, $n = 1692$). It took, on average, 36 and 35 years for spruce and fir, respectively, to reach 1.3 m. We could not make similar correction for *L. olgensis* since no seedling were observed during our surveys and inability to approximate age of the adult larch trees due to rotten pith.

Combined age distribution of the four species showed a multimodal pattern (Fig. 1.3a), with several regeneration waves of moderate intensity (1810-1830s, 1850-1870s, 1900s, 1930s, and 1990s). Age structure of *P. koraiensis* presented a multimodal pattern with five periods of increased recruitment: 1820s, 1850s, 1870-1880s, 1930s, and 1990-2000s (Fig. 1.3b). *P. jezoensis* also presented a

multimodal pattern in age distribution and showed similar increased recruitment periods as *P. koraiensis* (1820s, 1850s, 1930s, and 1990s, Fig. 1.3c). *A. nephrolepis* showed increased recruitment from the 1900s to the 1930s and the 1990s (Fig. 1.3d). For *L. olgensis*, projected pith ages indicated that trees recruited mainly between the 1800s and 1860s (Fig. 1.3e). Low densities of *P. jezoensis* and *A. nephrolepis* seedlings regenerated after 2000 were in line with low frequencies of growth releases (Fig. 1.4) suggesting below average disturbance rate during the 1990s. Estimates of the low densities, however, may be partly due to a sampling artifact error reflecting seedlings' small size and difficulties in their identification in the field.

1.5.3 Growth releases and initial growth of *P. koraiensis*

One third (34.6%) of sampled *P. koraiensis* trees experienced one or more releases. Growth release analyses indicated frequent small-scale disturbances and infrequent moderate disturbances over the last 200 years (Fig. 1.4). The percentage of trees showing releases was generally low (< 6%) in each decade, except the two most pronounced release periods which were observed in the 1920s and 1980s, when the release frequency reached 19% and 13%, respectively.

In *P. koraiensis*, the initial 10-year BAI was significantly larger than the BAI during the release periods ($Z=-2.81$, $p=0.005$, Fig. 1.5). Whereas the initial 10-year growth was significantly smaller than growth in the releases periods for *A. nephrolepis* ($Z=-2.12$, $p=0.034$, Fig. 1.5) and *P. jezoensis* ($Z=-2.12$, $p=0.034$, Fig. 1.5). 31% of *P. koraiensis* trees, 0% of *P. jezoensis*, and 1% of *A. nephrolepis* showed initial growth increment which was larger than respective growth threshold, indicative of canopy gap conditions.

1.6 DISCUSSION

1.6.1 Disturbance regime

The history of mixed Korean pine dominated forest revealed no large-scale and stand replacing disturbances since the 1770s, as suggested by the lack of regeneration of pioneer *L. olgensis* as well as continuous regeneration and presence in the canopy of shade-tolerant *P. jezoensis* and *A. nephrolepis* (Table 1.1, Figs. 3c, d, and e). However, the dominance of *L. olgensis* in the current forest canopy (Table 1.1) indicated a major disturbance event that took place outside the time frame covered by this study. The most recent volcanic eruption, which occurred in 1702 and was associated with forest fires (Manchida *et al.*, 1987; Okitsu *et al.*, 1995), was a likely candidate for such an event. Despite intensive field inventories, we didn't find evidence of past fires (such as fire scars and charred stumps) in our sites, although stand replacing fires have been previously described as the main factor for the dynamics of mixed forest in Northeastern China (Chang *et al.*, 2008). High humidity in the study area and fire suppression policy (Wang *et al.*, 1980) in the Reserve might effectively limit possibilities for effective ignitions and fire spread in the area.

Two medium-scale disturbance events likely occurred in the 1920s and 1980s. Increased number of growth releases during these decades (Fig. 1.4), followed by enhanced recruitment of *P. koraiensis*, *P. jezoensis*, and *A. nephrolepis* in the 1930s and 1990s (Figs. 3b, c, and d) suggested formation of rather large canopy gaps, probably exceeding 1000 m². Although we could not exactly identify the nature of the 1920s event nor the scale of canopy disturbances occurred at that time, we considered it a wind-induced disturbance since the timing of this event coincided with a large windthrow, which was dendrochronologically reconstructed on the western slope of Changbai Mountain and dated to 1920s (Yang and Xie, 1994). The timing of the 1980s event was consistent with documentary sources reporting a hurricane on the western slope of CBM in 1986 (Yang and Xie, 1994).

The canopy disturbances were common and small-scale as suggested by frequent growth releases with low percentage of trees exhibiting the release (< 6%) in a single decade (Fig. 1.4). The wind was a likely factor causing these frequent small-scale disturbances. Two canopy dominants, *P. jezoensis* and *A. nephrolepis*, are particularly sensitive to strong winds due to their large amount of leaf biomass and shallow rooting depth (Liu, 1997), making the forests dominated by these two species especially prone to wind disturbance. Indeed, previous studies have showed regular occurrence of windthrows in our study area (Dai *et al.*, 2011; Zhou *et al.*, 2011) and reported that 40% of the gaps were formed by wind disturbances (Yu and Hao, 1998) typically smaller than 250 m² in size (Zhao *et al.*, 2006). This is similar to the mean gap size in the geographically close temperate mixed forest in Japan, which has been estimated to be 70-140 m² (Miura *et al.*, 2001; Fujita *et al.*, 2003; Kubota, 2006). Size of canopy gaps appears therefore similar across many temperate forests in Northern Hemisphere - a common size of canopy gaps has been reported to be smaller than 200 m² both in the North American deciduous forest (Runkle, 1982, 1990; Runkle and Yetter, 1987), and in the European temperate forests (Kenderes *et al.*, 2008; Motta *et al.*, 2011).

1.6.2 Forest composition response to the disturbances

Although the current study did not quantify the whole range of disturbance events known for mixed Korean pine forests, it points to a large temporal variability in frequency and severity of disturbance events, resulting in a complex forest stand structure. Regeneration dynamics of the most shade-intolerant species *L. olgensis* exemplified the difficulties in understanding the role of the larger disturbance events. Lack of recent fire disturbance was in line with absence of *L. olgensis* regeneration and its presence in the forest exclusively as a canopy dominant (Table 1.1). However, some understory trees (5 cm < DBH <15 cm, Fig. 1.2) were observed in the forest, suggesting that another important factor for regeneration of this species might have been severe windthrows which maintains presence of *L. olgensis* in the forest canopy (Okitsu *et al.*, 1995; Liu, 1997). A previous

study in the Changbai Mountain has shown that forest patches dominated by *L. olgensis* were larger than 1 km² in size (Liu *et al.*, 2004), suggesting large-scale disturbance events creating these patches. In our sites, canopy gaps were typically smaller than 250 m² (field observation), which would explain the lack of *L. olgensis* regeneration (Table 1.1). Large-scale disturbance have also been shown to be important for the regeneration of Dahurian larch (*Larix gmelini* Rupr.) in old-growth larch forests of Da Xingan Ling Mountains, located to the North of Changbai Mountain (Ban *et al.*, 1998).

Interval between reconstructed medium-scale disturbances in the studied forest was 60 years and shorter than the lifespan of all the dominant species, indicating that such events might provide important regeneration possibilities for canopy dominants. In particular, regeneration and growth of *P. koraiensis* benefited from the two medium-scale disturbance events (Figs. 3b and 4) and regular small-scale disturbances (Wang and Zhao, 2011; Dai *et al.*, 2011). We suggest that high wind episodes creating canopy gaps with improved light conditions promote establishment and growth of *P. koraiensis*. Instead, decreased frequency of canopy gaps might reduce recruitment of this species. *P. koraiensis* is a mid-tolerant species, however its seedlings are shade-tolerant during the first 30 years of their lifespan and their saplings are shade-intolerant (Ge, 1994). Limited light availability under the closed canopy of mixed forests causes high mortality of *P. koraiensis* at sapling stage, decreasing overall density of this species under the forest canopy (Table 1.1).

The majority of sampled *P. koraiensis* trees apparently took advantage of canopy opening early in their lifespan, as suggested by comparison of the initial and gap-associated growth (Fig. 1.5). Since the trees in our study were sampled at DBH (1.3 m) and not at the ground level, it was not possible to deduce light conditions for these trees at the time of establishment. About one third of the sampled *P. koraiensis* trees experienced more than one release, indicating that the species need improved light conditions to grow into canopy layer. Indeed, previous studies have indicated that trees of *P. koraiensis* typically experience several canopy gap episodes before reaching the main canopy (Wang

and Zhao, 2011), regeneration of this species benefiting from gaps as small as 250 m² (Yu and Hao, 1998; Zhao *et al.*, 2006). In a study of an old-growth mixed forest in the Russian Far East, geographically close to our study area, 30–40% for *P. koraiensis* trees regenerated in the gaps (Ishikawa *et al.*, 1999).

It was difficult to deduce exact forest dynamics due to limited precision of our age data and since more than 200 years passed since the occurrence of the last major disturbance event. However, survival of shade-tolerant *P. jezoensis* and *A. nephrolepis* under the forest canopy appeared to be less dependent on disturbances than that of light-demanding *P. koraiensis* and *L. olgensis*. Persistent recruitment of *P. jezoensis* and *A. nephrolepis* over the last 220 and 110 years (Figs. 3c and d), together with their low increments during the initial growth period (Fig. 1.5) suggested that two species might be independent of treefall gap episodes due to their high degree of shade-tolerance (Yang *et al.*, 1994; Okitsu *et al.*, 1995; Liu, 1997). Ability to withstand a prolonged period in suppressed condition with low radial growth, and fast response to improved light conditions allow them to maintain their presence in the canopy (Yang *et al.*, 1994). This strategy is similar to the ones of other shade-tolerant species like Norway spruce (*Picea abies* (L.) Karst.) and silver fir (*Abies alba* Mill.) in European boreal forests, and balsam fir (*Abies balsamea* (L.) Mill.) in North American boreal forest. Regeneration of these species takes advantage of small-scale gaps (Kneeshaw and Bergeron, 1998; Drobyshev, 1999; Nagel *et al.*, 2007; Firm *et al.*, 2009; Zielonka and Malcher, 2009).

In a short-time perspective (< 200 years), stand-replacing disturbance events were probably of limited importance as drivers of the forest dynamics in Changbai Mountain, primarily due to the fact that the interval between such disturbance events was longer than the typical maximum lifespan of dominant species. Volcanic eruptions occurred in the study region with the interval exceeding 600 yr and were likely causes of stand-replacing fires (Zhao, 1981; Manchida *et al.*, 1987). This interval was longer than the lifespan of dominant species *P. koraiensis* (~400 yr), *P. jezoensis* (~300 yr), *A.*

nephrolepis (~200 yr), and *L. olgensis* (~300 yr) (Ishikawa *et al.*, 1999; He *et al.*, 2005). The similar pattern was also found in deciduous forests of the eastern United States, where the average interval between severe disturbances was approximately 1000 years (Lorimer, 1977, 1989; Canham and Loucks, 1984; Whitney, 1986). In the absence of large-scale disturbances, forest structure and composition in such forests are largely driven by small-scale canopy disturbances due to wind-induced mortality of single trees or small group of trees (Runkle, 1985, 1991; Canham, 1989; Drobyshev, 2001; Motta *et al.*, 2011).

Since no tree mortality data was available in the current study, we were unable to evaluate actual contribution of species and time-specific mortality patterns into overall canopy composition. However, joint analysis of growth release chronologies and tree age distributions suggested that current forest composition, expressed as DBH distributions of canopy trees, is driven by regeneration events and probably not by changes in mortality rates over time.

1.6.3 Effects of future climate on forest dynamics

Future climate changes affecting intensity and frequency of stand disturbances may have implications for forest structure and composition. We speculate that changes in wind climate (Dai *et al.*, 2011) may be particularly important since they are directly connected to availability and size distribution of disturbed patches, which are important for the regeneration of canopy trees. Future climate projections suggest that China will experience more extreme events such as hurricanes and typhoons in the future (IPCC, 2007). Particularly, such storms will expand along the coast areas from south to northeast China within rising sea surface temperatures (IPCC, 2007). This may increase the frequency of medium and large-scale wind disturbances in the forest of northeast China.

Since such disturbances favor the establishment of light demanding species the trend may benefit the growth release of *P. koraiensis* and *L. olgensis* in Changbai Mountain, increasing the share of shade-intolerant species in the forest canopies.

Increase in forest fire activity could be another consequence of climate change. Significant warming trends during the fire season (by 0.36°C per 10 years in spring and by 0.22 °C per 10 years in summer) and decrease in precipitation (by 100 mm) have been observed since the 1960s in Changbai Mountain (Qian and Qin, 2006; Yu *et al.*, 2006), this climate trend may indicate an increased chance of fire occurrence in coming decades. Beside direct effect on drought frequency and severity, future climate change may also affect forest flammability through a succession towards more fire-prone vegetation. Simulation of the forest ecosystem response to climate warming in Changbai Mountain suggested that future climate would benefit *L. olgensis*, making vegetation more prone to forest fires (He *et al.*, 2005).

In general, our results suggest an important role of climate variability on dynamics of a mixed Korean pine dominated forest over last 200 years. Indirect effects of climate variability such as changes in wind intensity and fire frequency will likely be important factors affecting forest dynamics in the future. We speculate that climatically driven changes in disturbance regimes and direct effects of climate on growth may be equally important in shaping the structure and dynamics of the mixed Korean pine dominated forests.

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1.8 REFERENCES

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Table 1.1. Stand structure of the studied mixed forest on the northern slope of Changbai Mountain, North-Eastern China. Importance Values (IV) defined as the average of relative density (% of the number of trees) and relative dominance (% of basal area). Data are mean (SD). Seedlings of *Acer* species were not recorded, though they were abundant across all study sites.

Species	Basal area (m ² /ha)	Density (stems/ha)			Relative density (%)	Relative dominance (%)	IV
		seedlings	Saplings	adult trees			
Canopy species							
<i>Pinus koraiensis</i>	11.61 (3.6)	795 (418.5)	13 (10.2)	104 (27.8)	6.1 (1.8)	23.6 (6.2)	14.9 (3.2)
<i>Larix olgensis</i>	11.43 (8.0)	0	0	105 (82.8)	5.3 (5.1)	23.7 (13.9)	14.5 (9.7)
<i>Picea jezoensis</i>	6.36 (3.0)	411 (262.9)	118 (119.5)	165 (50.1)	13.3 (5.8)	12.6 (5.3)	13 (4.5)
Subcanopy and understory species							
<i>Abies nephrolepis</i>	7.20 (1.7)	845 (406.3)	321 (130.6)	576 (151.4)	45.7 (17.4)	14.6 (2.6)	30.2 (9.8)
<i>Acer mono</i>	0.70 (0.9)	/	6 (5.5)	21 (25.8)	1.7 (1.6)	1.5 (2.0)	1.6 (1.8)
<i>Acer tegmentosum</i>	0.45 (0.7)	/	76 (102.0)	34 (72.6)	4.4 (4.7)	0.9 (1.4)	2.6 (3.0)
<i>Acer ukurunduense</i>	0.41 (0.4)	/	98 (104.3)	48 (57.2)	6.9 (6.7)	0.9 (0.7)	3.9 (3.5)
<i>Acer barbinerve</i>	0.18 (0.2)	/	115 (117.5)	13 (8.3)	6.7 (7.6)	0.5 (0.5)	3.6 (3.8)

Fig. 1.1. The location of study sites on the northern slope of Changbai Mountain, North Eastern China.

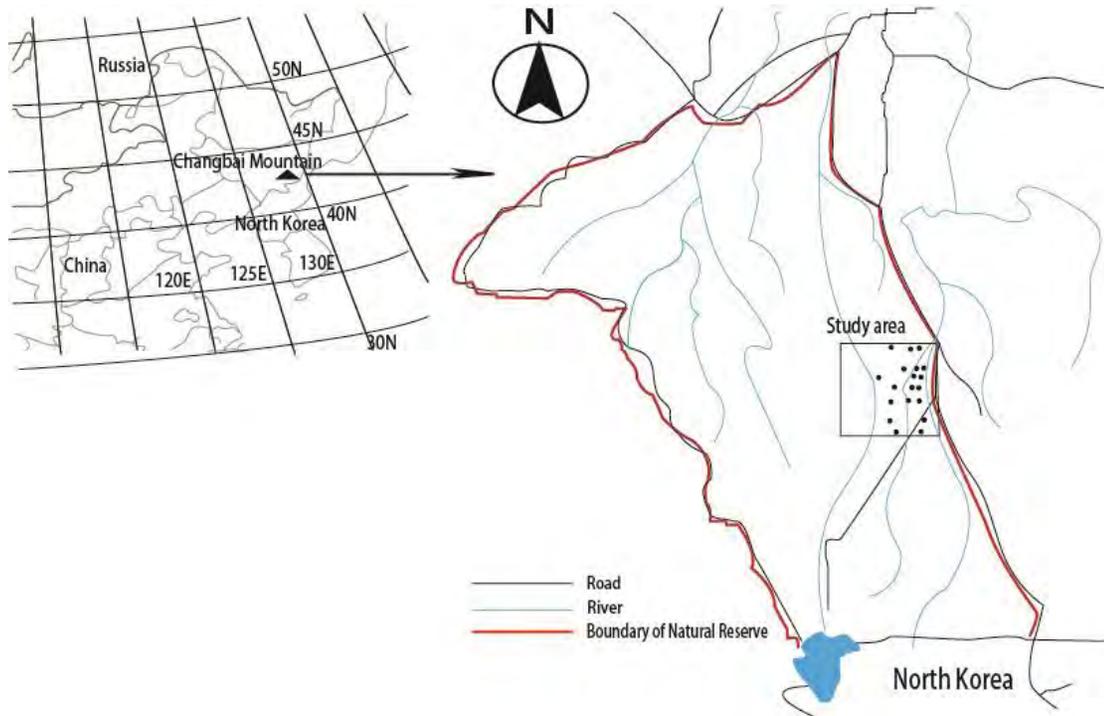


Fig. 1.2. Diameter distributions of four dominant species in a mixed Korean pine dominated forest on the northern slope of Changbai Mountain, North-Eastern China. (a) Combined data of the four species, (b) *P. koraiensis*, (c) *L. olgensis*, (d) *P. jezoensis*, (e) *A. nephrolepis*. The break at vertical axis is at 50 stems/ha.

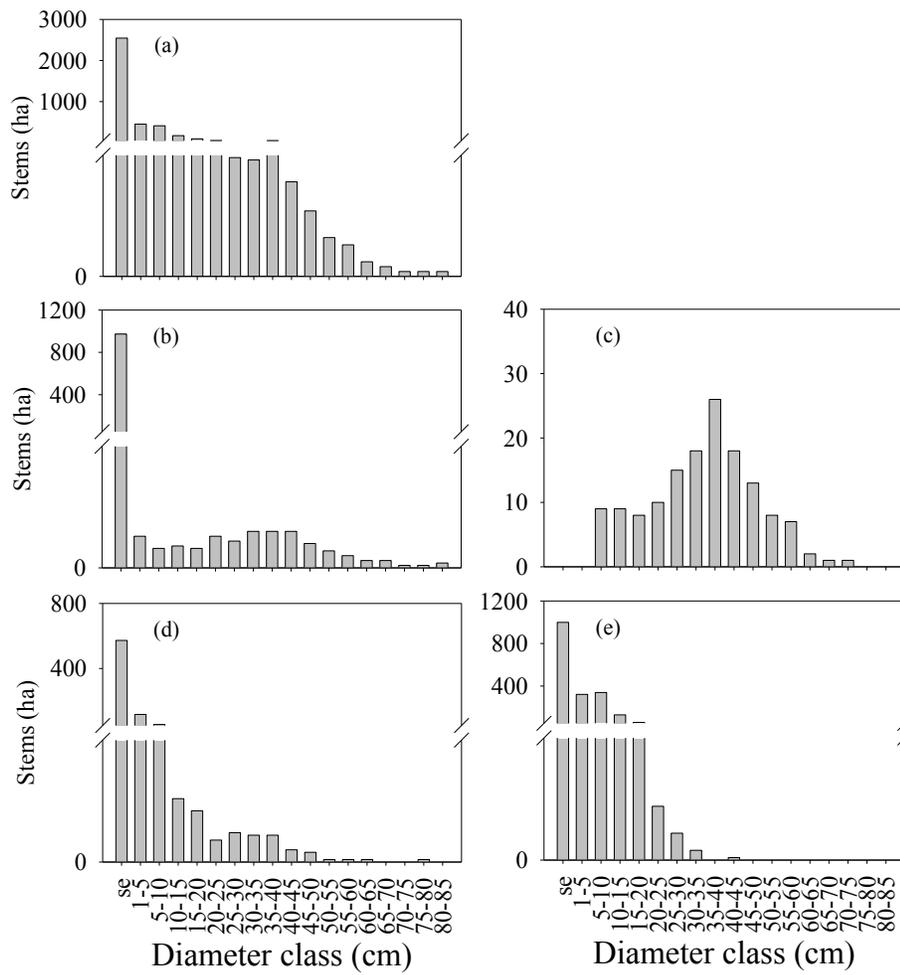


Fig. 1.3. Age structure of four dominants in a mixed Korean pine dominated forest on the northern slope of Changbai Mountain, North-Eastern China. (a) Combined data for all species, (b) *P. koraiensis*, (c) *P. jezoensis*, (d) *A. nephrolepis*, (e) *L. olgensis*. Age estimates for *L. olgensis* represent minimum ages at DBH level, since 84% (50 out of 59) samples exhibited rotten pith.

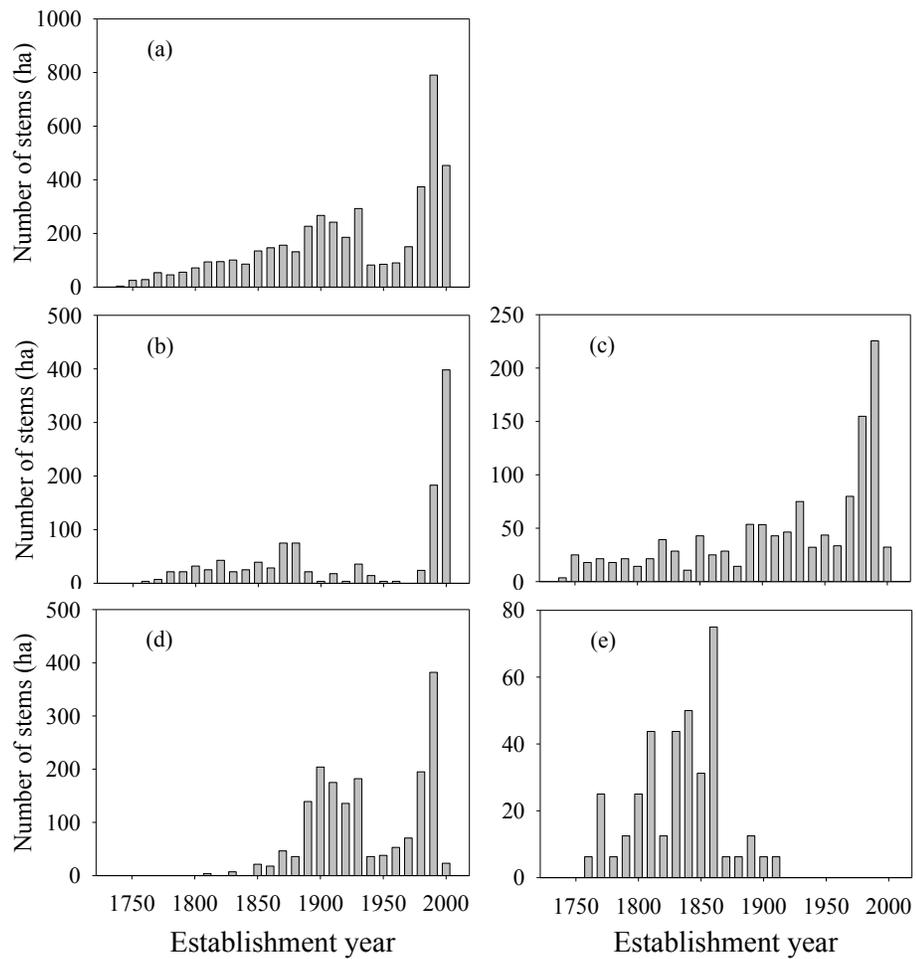


Fig. 1.4. Growth releases of four dominants in a mixed Korean pine dominated forest on the northern slope of Changbai Mountain, North-Eastern China.

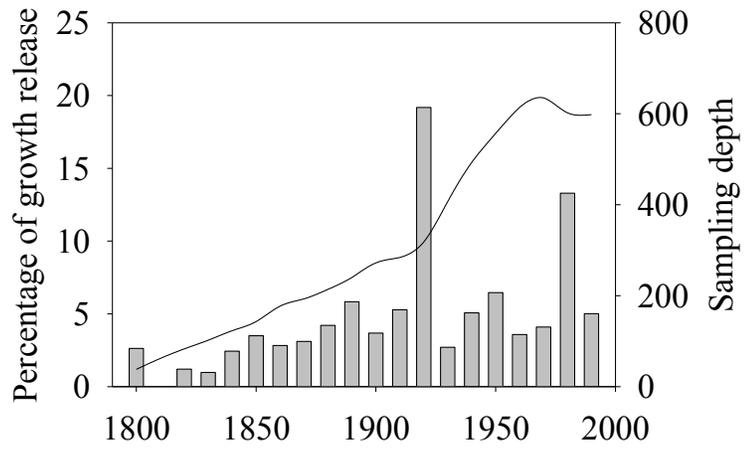
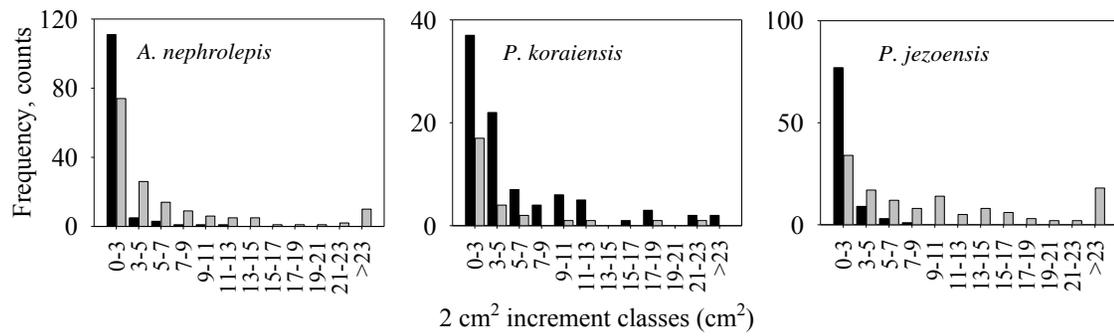


Fig. 1.5. Distribution of basal area 10-year cumulative increments for initial growth periods (black bars) and gap-associated (gray bars) periods in *A. nephrolepis*, *P. koraiensis*, and *P. jezoensis*.

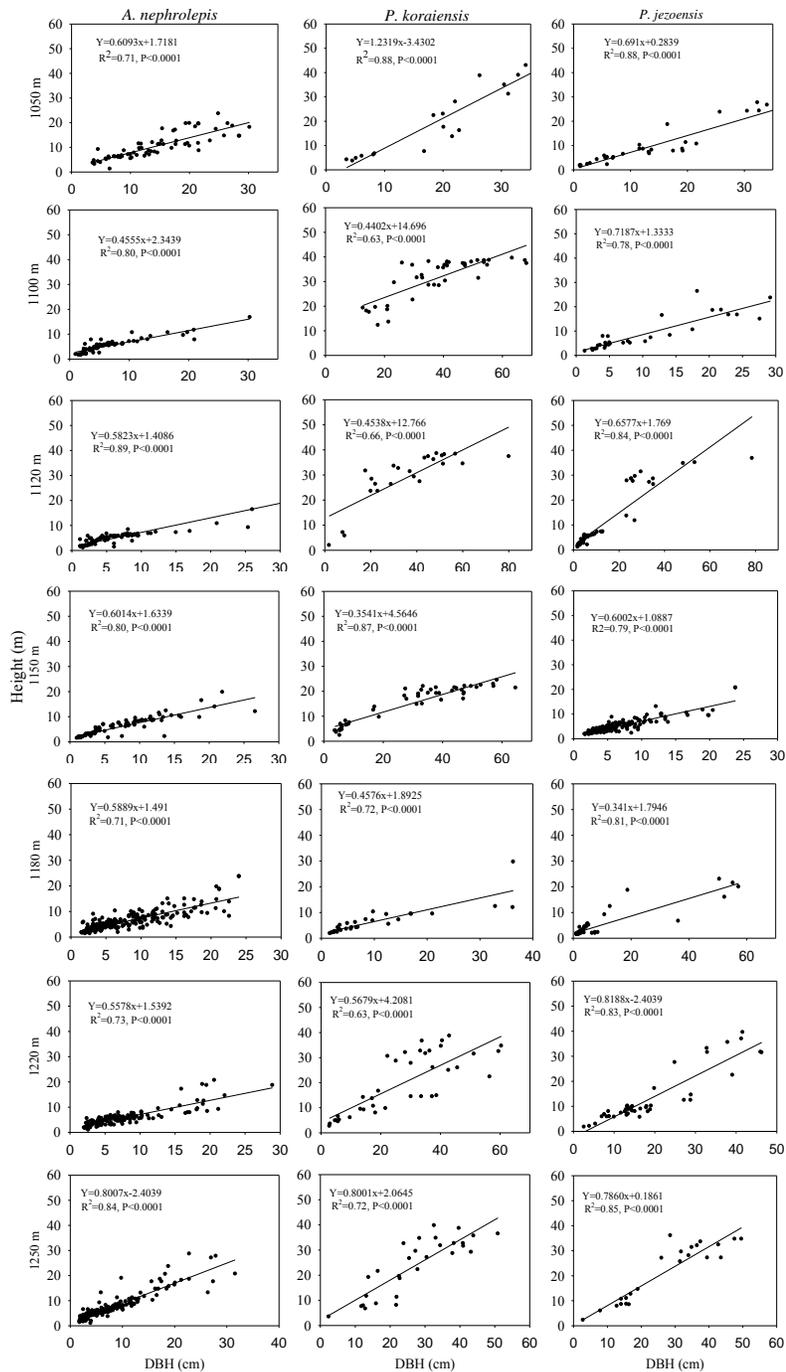


Appendix 1.1. Height information of selected sites along the altitudinal gradient on Changbai

Mountain.

Altitude (m)	Average canopy height (m)
1050	28.9
1100	29.6
1120	28.7
1150	26.5
1180	25.8
1220	29.1
1250	30.4

Appendix 1.2. DBH-height relationships of the three species at different sites. Correlation coefficients showed no significant differences between *A. nephrolepis* and *P. koraiensis* ($t=0.89$, $p=0.41$), *A. nephrolepis* and *P. jezoensis* ($t=-1.4$, $p=0.21$), and *P. koraiensis* and *P. jezoensis* ($t=-2.4$, $p=0.06$).



CHAPTER II

CLIMATE CONTROLS ECOTONE POSITION BETWEEN BROADLEAVED-KOREAN PINE AND CONIFEROUS FORESTS BY INFLUENCING GROWTH OF DOMINANT CONIFERS IN THE CHANGBAI MOUNTAIN, NORTHEASTERN CHINA

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2.1 RÉSUMÉ

Pour améliorer notre compréhension de la dynamique à long terme induite par le climat de forêts de montagne de l'Asie de l'Est, nous avons utilisé des relevés de terrain et des techniques dendrochronologiques pour examiner la densité de la régénération, l'accumulation de la biomasse, et la sensibilité de la croissance au climat de trois espèces de conifères communs à leurs limites respectives de répartition altitudinale dans la montagne Changbai du nord-est de la Chine. Les espèces étudiées sont le sapin de Mandchourie (*Abies nephrolepis* (Trautv.) Maxim., répartis entre 780 et 1750 m d'altitude), le pin de Corée (*Pinus koraiensis* Siebold et Zuccarini, entre 780 et 1300 m d'altitude), et l'épinette de Jezo (*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu, entre 1000 et 1750 m d'altitude). Les densités de la régénération ne diffèrent pas significativement entre les élévations, sauf pour la l'épinette Jezo, qui a montré une densité nettement plus faible à 1000 m d'altitude, par rapport à 1300 et 1750 m d'altitude. Les trois espèces ont une surface terrière significativement plus élevée (BAI) à la partie médiane du gradient altitudinal qu'aux limites inférieure et supérieure du gradient. La croissance du sapin de Mandchourie et de l'épinette Jezo a montré une plus grande sensibilité aux précipitations qu'à la température à leurs limites inférieures de distribution et la tendance inverse a été observée à leurs limites supérieures. Dans tous les cas, les corrélations entre la croissance et la variable respective de climat ont été positives, à l'exception de la réponse de la croissance de l'épinette Jezo à la précipitation. La croissance du pin de Corée a été positivement corrélée avec la température printanière et avec l'humidité estivale à la limite inférieure de sa distribution, et avec la température estivale à sa limite supérieure. Les communautés forestières à la limite inférieure de répartition du pin/épicéa - sapin écotone feuillus-coréen (1000-1300 m d'altitude) ont montré une plus grande diversité et une structure plus complexe de la canopée et du sous étage qu'à la limite supérieure. Notre étude suggère que les limites d'élévation de la végétation forestière sont limitées par des facteurs climatiques qui affectent la croissance des espèces dominantes plutôt qu'à des facteurs qui contrôlent la densité de régénération. Les changements climatiques pourraient décaler les positions d'élévation de l'optimum climatique pour la croissance des espèces dominants la canopée conduisant à des changements dans la composition en espèces et la position de l'écotone. Ces changements entraîneront probablement des modifications de la structure et de la dynamique naturelle de la couverture végétale.

2.2 ABSTRACT

To improve our understanding of climate-driven long-term dynamics of eastern Asian mountain forests, we used field surveys and dendrochronological techniques to examine regeneration density, growth rate of mature trees, and growth sensitivity to climate of three common coniferous tree species at their respective altitudinal distribution limits in Changbai Mountain, Northeastern China. The studied species were Manchurian fir (*Abies nephrolepis* (Trautv.) Maxim., distributed between 780 and 1750 m a.s.l.), Korean pine (*Pinus koraiensis* Siebold et Zuccarini, 780 and 1300 m a.s.l.), and Jezo spruce (*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu, 1000 and 1750 m a.s.l.). Regeneration densities did not differ significantly among the elevations except for the Jezo spruce, which showed a significantly lower regeneration density at 1000 m a.s.l., as compared to 1300 and 1750 m a.s.l. All three species showed a significantly higher basal area increment (BAI) at the middle part of their distribution ranges than at their limits. The growth of Manchurian fir and Jezo spruce exhibited a higher sensitivity to precipitation than to temperature at their lower distribution limits and the inverse pattern was observed at the upper limit. In all cases the correlations between the growth and the respective climate variable were positive, except for the correlation between Jezo spruce growth and precipitation. Growth of Korean pine was positively correlated with spring temperature and summer moisture at its lower distribution limit, and with summer temperature at its upper limit. Forest communities at the lower limit of broadleaved-Korean pine/spruce-fir ecotone (1000-1300 m a.s.l.) showed a higher diversity and a more complex structure of canopy and sub-canopy strata than at its upper limit. Our study suggested that elevational limits of forest vegetation were constrained by climate factors affecting growth of dominant species rather than those controlling regeneration density. Climate change would likely change the elevational positions of the climate optima for the growth of canopy dominants, leading to changes in the species and ecotone ranges, and natural dynamics of vegetation cover.

Keywords: dendrochronology, climate change, ecotone, mountain forests, Asian temperate forests

2.3 INTRODUCTION

Climate warming may have a major impact on forest ecosystems (Boisvenue *et al.*, 2006) by affecting physiological processes (Way & Oren, 2010), tree sensitivity to environmental variability (Allen *et al.*, 2010), and natural disturbance regimes (Bergeron *et al.*, 2010). In the Northern hemisphere, the average annual temperature in the mid- and high-latitudes has increased by 0.74 °C from 1906 to 2005, and climate models predict an additional increase by 1.6-6.4 °C by 2100 (IPCC, 2007). Changes in climate have already affected growth, establishment, and distribution of species in many boreal and temperate forests (Peñuelas & Boada, 2003; Gamache & Payette, 2005; Jump *et al.*, 2006). In mountain ecosystems, trees respond to climate change by shifting position of their elevational ranges (Grace *et al.*, 2002; Mieszkowska *et al.*, 2006; Yu *et al.*, 2011), however there are factors that limit possibilities for such migration. These include seed dispersal limitations, competition pressure from resident species in new habitats, and local soil conditions (Brubaker, 1986; Stephenson, 1990; Peterson & Peterson, 1994; Korner & Paulsen, 2004).

The climate of Northeastern China has become warmer and drier over the last century (Qian & Zhu, 2001; Qian & Qin, 2006). Climate records have shown an increase in the annual mean temperature by 2 °C between the 1900s and 1990s (Qian & Zhu, 2001) and a decrease in the summer precipitation by -0.81 mm yr⁻¹ between the 1960s and 2000s (Liang *et al.*, 2011). Climate models predict a further increase in annual mean temperature by 4.6 °C towards the end of the 21st century (He *et al.*, 2005), which may result in a northward or an elevational extension of distribution limits for dominant coniferous species (Xu & Yan, 2001; He *et al.*, 2005).

Recruitment and tree growth are particularly sensitive to climate change at species' distribution limits due to an increased frequency of sub-optimal environmental conditions causing seedling and sapling mortality, growth declines, and tree mortality (Brubaker, 1986; Lescop-Sinclair & Payette, 1995; Wang *et al.*, 2006). Responses of recruitment and growth to climate vary along the elevational

gradient. Temperature regime tends to be critically important for seedling establishment and tree growth at species' upper elevational limits (Tranquillini, 1979). Trees at upper limits often responds to climate warming with an increase in regeneration density (Szeicz & MacDonald, 1995) and radial growth (Frank & Esper, 2005). Water availability and biotic interactions tend to control the recruitment and growth at middle to lower limits (Stephenson, 1990). Drought stress and increase in competition at lower limits may therefore lead to low regeneration density and decline in the radial growth (Gworek *et al.*, 2007; Peng *et al.*, 2008; Rigling *et al.*, 2013). Elevational zones separating different bioclimatic domains (termed ecotones, Odum, 1983) provide numerous examples of strong climate control of regeneration and tree growth (Peñuelas & Boada, 2003; Peng *et al.*, 2008; Takahashi *et al.*, 2011).

The northern slope of Changbai Mountain hosts major forest types of Northeastern China, including broadleaved-Korean pine (*Pinus koraiensis* Siebold et Zuccarini) forests and spruce-fir (*Picea jezoensis* Carr. var. *komarovii* (V.Vassil.) Cheng et L.K.Fu-*Abies nephrolepis* (Trautv.) Maxim.) forests. These communities remained largely undisturbed by human activities (Wang *et al.*, 1980; Barnes *et al.*, 1992). As in other mountain ecosystems, numerous distribution limits are observed along the elevational gradient of the Changbai Mountain (Yu *et al.*, 2011), providing suitable sites for the studies of climate-growth relationships.

Most dendrochronological studies in this region have been conducted on a single tree species (Yu *et al.*, 2006; 2013) or at a single elevation (Gao *et al.*, 2010; 2011) and only one has focused on the growth response of multiple species to climate change along the entire elevational gradient (Yu *et al.*, 2011). All these studies have suggested that temperature, precipitation, and soil moisture limited tree growth in the Changbai Mountain, and that climate change may affect forest structure in this mountain region. However, growth data alone are inadequate to identify factors behind changes in a species distribution or forest composition (Brubaker, 1986; Wang *et al.*, 2006), since such dynamics

may also be related to the recruitment patterns (Silva *et al.*, 2012; Fisichelli *et al.*, 2013) and natural disturbance regimes (Flannigan & Bergeron, 1998; Vila-Cabrera *et al.*, 2012).

The aim of this study was to advance our understanding of the factors controlling the vegetation of broadleaved-Korean pine/spruce-fir forest ecotone (BKSFE) in the Changbai Mountain, and to discuss its dynamics under the future climate. We evaluated recruitment and growth of the Korean pine, Jezo spruce, and Manchurian fir at their elevational distribution limits and upscaled these results to discuss forest composition at the upper and lower edges of BKSFE. Although the selected species were the main canopy dominants along the BKSFE, they possessed different life strategies. Korean pine is a shade-intolerant canopy species (as tree older than 40-50 years), Jezo spruce is a shade-tolerant canopy species, and Manchurian fir is a shade-tolerant species typically dominating sub-canopy. We hypothesize that:

- (1) regeneration density declined at the tree distribution limits, as compared to the central part of tree distribution, suggesting a regeneration-level control of these limits,
- (2) growth rate of mature trees declined at their distribution limits, as compared to the central part of their distributions, suggesting that prohibitively low growth rate at the distribution limits controlled their position,
- (3) tree species become more temperature sensitive at higher elevations and more precipitation sensitive at lower elevations.

To test these hypotheses, we studied regeneration density (hypothesis 1), basal area increment of the canopy trees (BAI, hypothesis 2), and used dendroclimatic analyses to study the trees' growth sensitivity to climate (hypothesis 3) across their distributions. Finally, we combined our knowledge of climate effects on regeneration and growth with data on forest composition to discuss potential effects of climate change on the dynamics of the BKSFE.

2.4 METHODS

2.4.1 STUDY AREA

The study was conducted in the Northeastern China, on the northern slope of the Changbai Mountain and within the territory of the Changbaishan Natural Reserve (41°31'-42°28' N, 127°9'-128°55' E, Figure 2.1). The area has a temperate continental climate, with long, cold winters and wet summers. Mean annual temperature varies from 2.8 °C in the lower reaches (700 m a.s.l.) to -7.3 °C at the top of the mountain (2691 m a.s.l.). Variation in mean annual precipitation along this gradient is from 750 mm to 1340 mm (Zhao, 1981). About 70% of the annual precipitation falls between June and September (Appendix 2.1). Below 1700 m a.s.l., the topography of the area is gentle with slope inclinations below 5°. Above 1700 m a.s.l., the slopes are relatively steep with an average angle exceeding 20°. Volcanic soils overlaying a deep layer of volcanic ash are common across the study area (Shao, 1996). Soil type varies from moderately deep mountain brown forest soil (~50 cm) at the 750-1100 m a.s.l. to more shallow (~20 cm deep) mountain brown coniferous forest soil at 1100-1700 m a.s.l. (ECJF, 1988).

Forest vegetation is composed of broadleaved-Korean pine forest at 750-1100 m a.s.l., spruce-fir forests at 1100-1700 m a.s.l., and of Erman's birch (*Betula ermanii* Cham.) forests from 1700 to 2000 m a.s.l. (Wang *et al.*, 1980). Each forest type possesses a unique assemblage of sub-canopy trees and shrubs (Table 2.1). The tree distribution of Manchurian fir is limited to 700-1800 m a.s.l., of Korean pine to 700-1300 m a.s.l., and of Jezo spruce to 900-1800 m a.s.l. (Figure 2.1). Two forest ecotones are formed along this elevational gradient. The BKSFE ranges from 1000 to 1300 m a.s.l., with the canopy dominated by Korean pine and Jezo spruce and the sub-canopy - by Manchurian fir. The spruce-fir/alpine dwarf birch forest ecotone is located between 1700 and 1800 m a.s.l. with Jezo spruce and Erman's birch dominating the canopy layer and Manchurian fir dominating the sub-canopy layer.

2.4.2 CLIMATE DATA

The closest meteorological stations to the sampling sites are the Open Research Station of Changbai Mountains Forest Ecosystems (ORS, 740 m a.s.l.), the Tianchi meteorological station (TC, 2623 m a.s.l.), and Songjiang town (SJ, 601 m a.s.l.) meteorological station (Figure 2.1). Comparison of climate records (mean and maximum monthly temperatures, and total monthly precipitation) among the three stations showed significant correlations ($p < 0.05$). A check for homogeneity in the climate data from the three stations, using Mann-Kendell and Double-Mass tests, found no indications of abrupt changes in climate records, indicating that data from any of these stations could represent the climate of the study area. In the analyses, we used data produced by the SJ station since it had the longest record (1958-2007) as compared to the other stations (ORS, 1982-2007; TC 1959-1988) and showed a generally higher correlation with growth than data from the ORS and TC stations.

2.4.3 FIELD SAMPLING AND CHRONOLOGY DEVELOPMENT

We selected sampling plots at four elevations - 780, 1000, 1300, and 1750 m a.s.l., which corresponded to the middle and marginal parts of the species distributions (Figure 2.1). At each elevation we established two 20×80 m² plots, separated by approximately 500 m. Due to a high variability in topographic conditions in the studied area and a rough terrain commonly separating our plots located on the same elevation, the plots were considered independent in respect to all growing conditions, except climate. The longer side of the plots was perpendicular to the slope and divided each plot into four subplots (20×20 m²).

Field sampling was carried out in 2012 (for elevation 780 m), 2008 (1000 and 1300 m), and 2009 (1750 m). Although we could find trees of three studied species at elevations above their present upper distribution limits, we established plots only below these limits, since those trees were sparsely distributed, making it impossible to obtain sufficient replication for the dendrochronological analyses.

In each plot, we recorded the species identity and diameter at breast height (DBH, 1.3 m) of all trees with DBH greater than 1 cm. In the four corners of each subplot, we established one 5×5 m² and one 2×2 m² plot to record presence of the shrub and herb species, respectively. To assess contribution of tree species to the canopy, we calculated Importance Values (IV, Cottam & Curtis, 1956) as the average of relative density and relative dominance of a species in each plot. Relative density is number of individuals of a species represented as a percentage of the total number of individuals of all species, while relative dominance is total basal area of a species calculated as a percentage of the total basal area of all species. To clearly show the variation of forest structure along the altitudinal gradient, we compiled our own investigation of forest composition together with data from the published study (not a copy of a table but a summary) to exhibit forest composition in three strata (Table 2.1).

One 20×20 m² subplot was selected randomly within each plot to count the amount of regeneration (seedlings > 1 cm in diameter at the stem base and < 1.3 m in height). Regeneration density of each species in the selected subplot was expressed as number of stems per hectare, and then was converted into a species- and elevation-specific average.

In each plot, we cored 12 to 17 dominant trees of each studied species at DBH. One core per tree was taken at elevation 1000 and 1300 m, while two cores were extracted at elevation 780 and 1750 m (Appendix 2.2). Tree-ring samples were dried, mounted, and sanded until ring boundaries were clearly visible. Cores were visually cross-dated using the pointer year technique (Stokes & Smiley, 1968). Ring widths were measured to the nearest 0.01 mm by LinTab measuring stage and the data quality was verified by COFECHA program (Holmes, 1983). Totally, 92 cores of Manchurian fir, 103 cores of Korean pine, and 115 cores of Jezo spruce were dated and used for dendrochronological analyses. Since the two plots located at the same elevation were ecologically similar and within 200-500 m of each other, we combined data for each altitude to produce nine altitude- and

species-specific chronologies (Appendix 2.2).

We collected soil samples from the mineral layer (20-30 cm) to characterize soil texture and pH in each plot. One pit was dug in the central part of each subplot and four soil samples were collected from each plot. The soil samples from the same plot were mixed together, air dried at 20 °C during one week, and sieved through a 2-mm grid. Soil texture was quantified by the hydrometer method (Sheldrick & Wang, 1993), and pH was measured in 0.01 M CaCl₂ at a 1:5 soil solution ratio.

2.4.4 STATISTICAL ANALYSES

To test hypothesis 1, we checked differences between regeneration density among the elevations for each species by using ANOVA with type III sum of squares and LSD post-hoc tests, using elevation and species identity as independent factors. In this and the following ANOVAs, we considered only direct effects of independent factors, ignoring any additive effects. Since we sampled two plots per elevation, our replication for each contrast in the analysis was two, that exceeded the theoretically required minimum replication for this type of ANOVA, which is one (Maxwell and Delaney 2003).

To test hypothesis 2, we analyzed variability of growth rate for each species along the elevational gradient. We averaged all single-tree chronologies into a mean chronology for each species at each elevation. We converted tree-ring width increment into basal area increment (BAI) to obtain average BAI over 1996-2005, since the value of BAI was a better representation of the tree's growth rate than diameter increment (Pedersen, 1998). ANOVA with LSD post-hoc tests (similar with regeneration density analysis above) was used to test for the differences between BAI among elevations for each species. The rationale to use the most recent 10 year frame in this analysis stemmed from the fact that this period covered mature phase in the trees' lifespan for all species, which allowed us to minimize age-related effects on growth. Furthermore, selecting the most recent decade minimized potential impact of differences in stand disturbance histories on the growth dynamics. The analysis was conducted using the software SPSS 13.0 at 0.05 significance level.

To test hypothesis 3, we detected climate-growth relationships of studied species by using dendroclimatical analysis. We removed the age- and size-related trends in tree growth by detrending chronologies with a cubic spline with a 50% frequency response at 60 years, using ARSTAN program (Cook & Peters, 1981). Ring width values were transformed into index values by dividing the observed chronology values by the predicted values. This detrending procedure retained high-frequency variation and filtered out low-frequency age- and disturbance-related trends. Autoregressive modeling was also performed on each detrended series to remove temporal autocorrelation. The residual chronologies (RES) were used in the analyses of climate-growth relationships.

We used response function correlations to assess associations between radial growth and climate variables. A response function is a principal component regression to solve the problem of collinearity among climatic predictors (Briffa & Cook, 1990; Morzukh & Ruark, 1991) and is often used to evaluate climate-growth relationships. Correlation coefficients of response functions were calculated by the DendroClim2002 program (Biondi & Waikul, 2004) over the common interval 1958-2007. Climate data included mean monthly temperature and total monthly precipitation from the previous year July to the current year September, as climate conditions of the previous year might have an effect on tree growth in the current year (Fritts, 1976). We also considered seasonal climate conditions based on known seasonal weather patterns in the study area (Yu *et al.*, 2013), i.e. the mean maximum temperature and the total sum of precipitation of the previous autumn (September-October), the current spring (April-May), and the current summer (June-August). We preferred maximum temperature over mean temperature since the former produced more statistically significant results and might have a stronger influence on growth processes than mean temperature (Oberhuber, 2004).

2.5 RESULTS

2.5.1 SOIL CHARACTERISTICS AND TREE-RING CHRONOLOGIES

Soil texture and pH were similar among sites and did not show a clear elevational pattern (Appendix 2.3). A majority of sites showed a high sand content (> 70%) and acid soil conditions.

Nine tree-ring chronologies ranged from 122 to 354 years in length. Jezo spruce had the longest chronology, extending back to 1654 (Appendix 2.2). Mean sensitivity (MS) of the chronologies increased with decreasing elevation. The contribution of the first principal component (PC1) in the datasets of Korean pine chronologies increased at higher elevations, while the PCs obtained on Manchurian fir and Jezo spruce datasets did not show any clear elevational pattern (Appendix 2.2). We observed high signal-to-noise ratio (SNR), expressed population signal (EPS), and the variability accounted for by the first PCs of all the residual chronologies, indicating a strong population-wide signal in the site chronologies.

2.5.2 FOREST COMPOSITION

The diversity in canopy and undercanopy, shrub, and herb strata decreased with an increase in elevation (Table 2.2). Species numbers in all three strata were much higher at the lowest (780 m) than at the highest elevation (1750 m). In the BKSFE (1000-1300 m), the differences in the number of species were higher for the canopy and undercanopy strata (15 vs. 9 species) than for both the shrub and herb strata (9 vs. 7 species, and 11 vs. 10 species, respectively). The studied coniferous trees showed their lowest Importance Values (IV) at their respective lower distribution limits (Table 2.2). Manchurian fir and Korean pine showed the highest IV at the center of their distributions, whereas Jezo spruce had the highest IV at its upper limit. A high IV of Manchurian fir was largely attributed to its high density, while a high basal area maintained high IV of both Korean pine and Jezo spruce. This was particularly true for Korean pine which showed a high relative dominance (22.7%) and a low relative density (6.7%) at its upper limit (at 1300 m). Broadleaved trees showed a decrease in IV with an increase in elevation.

2.5.3 REGENERATION DENSITY

There was no significant difference in the regeneration densities of Manchurian fir and Korean pine among the elevations (Figure 2.2; Appendix 2.4). Regeneration of Manchurian fir and Korean pine was abundant at all elevations with the density of seedlings exceeding 565 ha^{-1} (Figure 2.2A). Neither species showed a significant tendency towards a higher regeneration density at the midpoint of their distribution range (Figure 2.2B). Jezo spruce was the only species which showed significant differences in regeneration densities among the three elevations (Appendix 2.4), with the lowest regeneration density ($222 \pm 46 \text{ ha}^{-1}$) at the lower limit and the highest density ($1441 \pm 449 \text{ ha}^{-1}$) at the center of its distribution (Figure 2.2B).

2.5.4 DYNAMICS OF BAI AND CLIMATE-GROWTH RELATIONSHIPS

Korean pine had the largest 10-year mean BAI among the three species while the BAI of Manchurian fir was the lowest (Figure 2.3A). BAI was significantly different in pair-wise comparisons between species at each elevation (Appendix 2.4). All three species showed a significantly higher BAI at the central part of their distribution range (Figure 2.3B). Korean pine had the lowest BAI at its lower limit, while Manchurian fir and Jezo spruce showed the lowest BAI at their upper limits (Figure 2.3B).

All three species showed a higher sensitivity to temperature than to precipitation at their upper limits and the inverse pattern was observed at their lower limits (Table 2.3; Figures 2.4 and 2.5). At respective upper limits, the positive responses to temperature occurred during current year summer (for Korean pine and Jezo spruce) and current year spring (for Manchurian fir) (Table 2.3; Figure 2.4). At respective lower limits, the positive effect of precipitation was observed during previous year autumn (Table 2.3; Figure 2.5). Jezo spruce differed from two other species in term of its response to monthly climate variability. The growth at spruce's lower and middle distribution ranges responded negatively to precipitation of the current April (Figure 2.5).

2.6 DISCUSSION

Our study suggested the lack of a clear pattern in regeneration densities along the elevational gradient in two out of three studied species (rejecting hypothesis 1) and a decline in growth rate of mature trees towards their distribution limits (supporting hypothesis 2). We also observed a similar pattern of climate-growth relationship for three studied species along the elevational gradient, the growth being precipitation-sensitive at the respective lower distribution limits and temperature-sensitive at the upper limits, which supported hypothesis 3. Based on these findings, we conclude that climate influences on the distribution limits of the main forest dominants in the Changbai Mountain is likely realized through the control of tree growth rather than of regeneration.

2.6.1 PATTERN OF REGENERATION DENSITY ALONG THE ELEVATIONAL GRADIENT

Climate effects on regeneration density differed among the three species. Observed regeneration patterns failed to support our hypothesis suggesting the regeneration-level control of the distribution limits for Korean pine and Manchurian fir. Both species have been shown to be abundant seed producers (Wang *et al.*, 1959; Okitsu, Ito & Li, 1995), which successfully regenerate along the studied gradient. In addition, seedlings of pine and fir can tolerate lower light levels than seedlings of co-occurring broadleaved species, which likely made them competitive under conditions of high canopy closure (0.7-0.9), typically observed in these forests (Xu *et al.*, 2001). In contrast, regeneration of Jezo spruce appeared to be negatively affected by the climate conditions at its lower limit, supporting our 1st hypothesis. Although Jezo spruce is also capable of producing large seed crops and has shade-tolerant seedlings, soils with low water holding capacity may limit seedling survival and growth (Iijima *et al.*, 2006). The sites at the lower limit of this species were generally drier than those at its upper limit (Chi, Zhang & Li, 1981; Jiang *et al.*, 2003), which might disfavor spruce regeneration due to reduced water availability.

Negative effects of drought on seedlings are often caused by poor root development and associated decline in nutrient assimilation, effects which have been reported in Jezo (Iijima *et al.*, 2006) and in other spruces (Karlsson *et al.*, 1997; Chhin & Wang, 2008; Slugeňová *et al.*, 2011).

2.6.2 GROWTH RATES AND ABUNDANCE ALONG THE ELEVATIONAL GRADIENT AND DIVERSITY OF THE BKSFE

All three species showed the highest BAI at the middle of their respective distribution ranges, which supported our second hypothesis and suggested that current species distributions were centered in the area with climatic optima for the biomass accumulation rates. Two of the three studied species (Manchurian fir and Korean pine) also showed the highest Importance Values here, likely indicative of their competitive advantage in the middle of their distribution ranges.

IV of studied canopy dominants varied between their respective lower and upper limits, suggesting that the forest composition might be controlled by different factors. At their lower limits, both competition with broadleaved species (Table 2.1) and the climate (see next subsection) might be limiting canopy abundance of the coniferous species and their range expansion towards lower elevations. In contrast, the high IV of the three studied species at their upper limits may be caused by the lack of broadleaved trees at high elevation (above 1100 m). This suggests a direct climate effect on forest structure through limiting distribution of broadleaved species towards higher elevations. Indeed, the annual average temperature for the upper limits of all three species was below $-0.75\text{ }^{\circ}\text{C}$ (Jiang *et al.*, 2003), supporting a view on the low temperature as a limiting factor for an upward expansion of broadleaved trees.

Variation in community diversity of the BKSFE, pointed to the important role of climatic conditions controlling the structure of the studied ecotone. An increase in elevation was associated with a decline in the diversity across all forest strata. Canopy dominants and the undercanopy trees appeared to be moderately sensitive to the changes in the environmental conditions along the BKSFE. In both groups

the number of species which were common across the whole BKSFE was slightly above 50% (55 and 57%, respectively). Importantly, no new species (i.e. species absent at the lower limit of the ecotone) were recorded in either canopy or undercanopy strata at the upper limit of the BKSFE (Table 2.1). The pattern was likely related to the gradient in trees tolerance to low temperatures, hardwood species gradually disappearing from the canopy with increase in elevation (Table 2.2). In contrast, shrubs and herbs were more sensitive to environment variations, as indicated by a low commonness of species in both shrub (36%) and herb (22%) strata between two limits of the BKSFE. The ground vegetation at the lower limit of the BKSFE has been shown to contain more shade-intolerant species as compared to the one at the upper limit (Xu *et al.*, 2004). Variation in the species composition of these strata might, therefore, be partly due to changes in the degree of canopy openness along the BKSFE.

2.6.3 GROWTH SENSITIVITY TO CLIMATE

Tree growth was more sensitive to climate at the lower limits than at the upper limits, as indicated by (a) the pattern of mean sensitivity of tree-ring chronologies (Appendix 2.2) and (b) more frequently observed significant correlations between climate data and chronologies at lower elevations, as compared to other parts of the distribution ranges (Table 2.3; Figures 2.4 and 2.5). Adequate soil water reserves at the end of the previous growing season might be important for tree growth at the respective lower limits. An increase in precipitation of the previous autumn (September through October) (Table 2.3; Figure 2.5) likely facilitated accumulation and storage of carbohydrates used for the next year growth (Ettl & Peterson, 1995; Liang *et al.*, 2001). The soils in the Changbai Mountain are rich in volcanic float stone with low water holding capacity (Yu *et al.*, 2011), which might make soil moisture limiting for the growth. Earlier dendrochronological studies have pointed to the summer water deficit as an important factor limiting the growth of Korean pine at its lower distribution limit (Yu *et al.*, 2011; 2013). In our study, we demonstrated that moisture conditions of both the current summer and the previous autumn affected Korean pine growth at its lower limit. In contrast,

Manchurian fir at the same elevation did not show response to water stress, probably due to its lower evapotranspiration demand as a shade-tolerant sub-canopy tree. Positive effects of precipitation in the previous autumn on trees growth at the species' lower distribution limits have previously been shown for subalpine conifers in the Northern China (Gao *et al.*, 2013), and specifically - for Korean pine in the Changbai Mountain (Yu *et al.*, 2011; Wang *et al.*, 2013).

At the species upper limits, summer (June through August) temperature positively affected growth of Korean pine and Jezo spruce, and showed a similar though non-significant effect on Manchurian fir (Figure 2.5). Higher temperature during the growing period would increase activity of the cambial tissue and the radial growth (Kozłowski, 1962) and may prolong growing season. As compared to the middle parts of respective distributions, the growing season at the upper limits decreased by 27 days for both Manchurian fir and Jezo spruce, and by 28 days for Korean pine (Chi, Zhang & Li, 1981). For Manchurian fir and Jezo spruce at their upper elevations (1750 and 1300 m, respectively), a positive effect of spring temperatures on the growth (Table 2.3; Figure 2.4) was apparently related to the thawing rate of snowpack and the onset of the physiologically active period (Tranquillini, 1979; Peterson & Peterson, 2001; Deslauriers, Morin & Begin, 2003).

In Jezo spruce, the growth was strongly and negatively correlated with spring precipitation both at its lower limit and at the middle of its distribution range (Table 2.3; Figure 2.5). Two mechanisms would explain this relationship. Firstly, higher input of water during snow melting could cause waterlogging, a decrease in soil oxygen content, and an increase in carbon dioxide concentration, reducing soil redox potential and subsequently limiting root and photosynthetic activity (Armstrong, Jackson & Brändle, 1994; Jackson & Armstrong, 1999; Stokes, 2008). Jezo spruce requires a higher soil drainage levels and has a lower tolerance to waterlogged conditions as compared to Korean pine and Manchurian fir (Andersson, 2005). Secondly, the pattern might be due to the fact that precipitation in April fell as snow and heavier snowfalls would imply delayed onset of both the budburst (Worrall,

1983; Hansen-Bristow, 1986) and the growing period (Kramer & Kozlowski, 1979). In general, our results were consistent with previous studies that showed the negative relationship between spring precipitation and Jezo spruce growth at its middle and low distribution ranges in the Changbai Mountain (Yu *et al.*, 2006; Gao, Wang & Zhao, 2011).

2.6.4 EFFECTS OF CLIMATE CHANGE ON DISTRIBUTION OF CANOPY DOMINANTS AND POSITION OF THE BKSFE

Future climate conditions will likely become warmer in Northeastern China. Regional climate model PRECIS has predicted increases in temperatures of spring (3.1°C), summer (4.7°C), and autumn (3.6°C), and minor increases in precipitation during these seasons (2, 1, and 0%, respectively, Xu *et al.*, 2006). Climate changes would inevitably lead to shifts in the elevational positions of the climate optima for the tree growth, leading to changes in species and ecotone ranges. At the respective upper limits, the growth of Manchurian fir may benefit from warming during autumn and spring, while warmer summers would likely enhance the growth of Korean pine and Jezo spruce. At their lower limits, autumn climate may become less favorable for the growth of the studied trees, since an increase in temperature and little change in precipitation would make this period drier, causing a more severe drought stress in their growth.

The effects of future climate on regeneration may be differed among species. Future drier summer may be important in limiting regeneration of Jezo spruce at its lower distribution limit. It is still unclear how changing climate would affect regeneration of Korean pine and Manchurian fir at their lower limits. Relatively high regeneration densities of these two species across the studied gradient (Figure 2A) suggested that their recruitment may be more resilient than growth to future climate variability.

The climate-driven shifts of distribution range of dominants in the BKSFE (Korean pine and Jezo spruce) would result in the upward shift of the BKSFE. Our results provided empirical support of the

simulation studies, which have suggested migration of the dominant conifer species in the Changbai Mountain to higher elevations (Shao, 1996; He *et al.*, 2005). We speculate that in the future the elevational gradient currently covered by BKSFE would likely contain a higher proportion of broadleaved species such as Amur linden (*Tilia amurensis* Rupr.) in the main canopy and maples in the subcanopy (e.g. *Acer barbinerve* and *Acer tegmentosum*), which are generally limited by low temperatures (Xu *et al.*, 2004).

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2.9 SUPPORTING INFORMATION

Appendix 2.1. Long-term pattern of climate variables over 1958-2007 in the Changbai Mountain.

Appendix 2.2. Statistics for residual chronologies of studied species on the north slope of Changbai Mountain.

Appendix 2.3. Soil conditions at the studied sites of the Changbai Mountain.

Appendix 2.4. Post-hoc comparisons of regeneration density and mean basal area increment of the three species among three elevations in the Changbai Mountain

TABLE 2.1. Community structure of major forest types along the elevational gradient on the northern slope of the Changbai Mountain, based on the data from Xu *et al.*, 2004.

Forest zone	Elevation, m	Canopy species	Understory species	Shrub species
Erman's birch forest	1700 - 2000	<i>Betula ermanii</i> <i>Larix olgensis</i>	<i>Sorbus pohuashanensis</i> <i>Alnus mandshurica</i>	<i>Rhododendron chrysanthum</i>
Spruce-fir/alpine dwarf birch forest ecotone	1700 - 1800	<i>Picea jezoensis</i> <i>Betula ermanii</i> <i>Larix olgensis</i>	<i>Sorbus pohuashanensis</i> <i>Abies nephrolepis</i> <i>Acer ukurunduense</i>	<i>Rhododendron chrysanthum</i> <i>Vaccinium uliginosum</i> <i>Lonicera caerulea</i>
Spruce-fir forest	1100 – 1700	<i>Picea jezoensis</i> <i>Abies nephrolepis</i>	<i>Betulla costata</i> <i>Acer barbinerve</i> <i>Acer tegmentosum</i> <i>Acer ukrunduense</i> <i>Sorbus pohuashanensis</i>	<i>Rosa acicularis</i> <i>Ribes maximowiczianum</i> <i>Lonicera maximowiczii</i>
Broadleaved-Korean pine/spruce-fir forest ecotone	1000 - 1300	<i>Pinus koraiensis</i> <i>Picea jezoensis</i> <i>Larix olgensis</i>	<i>Abies nephrolepis</i> <i>Acer barbinerve</i> <i>Acer tegmentosum</i> <i>Acer ukrunduense</i>	<i>Lonicera chrysantha</i> <i>Lonicera maximowiczii</i>
Broadleaved-Korean pine forest	750 – 1100	<i>Pinus koraiensis</i> <i>Tilia amurensis</i> <i>Fraxinus mandshurica</i> <i>Quercus mongolica</i> <i>Phellodendron amurense</i> <i>Ulmus japonica</i> <i>Betulla costata</i> <i>Betula platyphylla</i> <i>Populus ussuriensis</i> <i>Populus davidiana</i>	<i>Acer barbinerve</i> <i>Acer tegmentosum</i> <i>Acer ukrunduense</i> <i>Acer pseudosieboldianum</i> <i>Acer mono</i> <i>Prunus padus</i> <i>Tilia mandshurica</i> <i>Syringa amurensis</i> <i>Malus baccata</i> <i>Maackia amurensis</i>	<i>Philadelphus schrenkii</i> <i>Corylus mandshurica</i> <i>Ribes mandshuricum</i> <i>Drutzis parviflora</i> <i>Evonymus pauciflora</i> <i>Berberis amurensis</i> <i>Viburnum burejaeticum</i> <i>Viburnum opulus</i> <i>Lonicera praeflorens</i> <i>Lonicera chrysantha</i>

TABLE 2.2. Total species numbers and Importance Value (IV) of canopy trees along the elevation gradient on the northern slope of Changbai Mountain. Broadleaved species include canopy dominants *T. amurensis*, *Q. mongolica*, *F. mandshurica*, *A. mono*, *B. platyphylla*, and *P. davidiana*. Standard deviation (SD) of the respective mean values is indicated in brackets. Values of Relative Density (Rel.dens.) and Relative Dominance (Rel. dom.) are in percents.

Elevation, m	Species numbers			Broadleaved species			<i>A. nephrolepis</i>			<i>P. koraiensis</i>			<i>P. jezoensis</i>		
	Trees	Shrub	Herbs	Rel. dens.	Rel. dom.	IV	Rel. dens.	Rel. dom.	IV	Rel. dens.	Rel. dom.	IV	Rel. dens.	Rel. dom.	IV
780	18	13	15	25.6 (2.4)	37.8 (3.1)	31.7 (2.9)	3.8 (0.6)	8.0 (1.8)	5.9 (0.9)	4.3 (1.5)	6.2 (2.8)	5.3 (1.9)	-	-	-
1000	15	9	11	18.2 (3.1)	24.5 (5.3)	21.4 (4.3)	35.8 (6.2)	17.2 (2.7)	26.5 (5.1)	5.1 (2.3)	26.5 (5.7)	15.8 (4.1)	5.8 (1.2)	5.0 (3.7)	5.4 (2.7)
1300	9	7	10	0.4 (0.1)	0.6 (0.2)	0.5 (0.2)	71.9 (2.9)	15.5 (4.2)	43.7 (3.3)	6.7 (1.7)	22.7 (3.1)	14.7 (2.3)	10.3 (4.7)	16.5 (5.8)	13.4 (5.1)
1750	5	3	8	-	-	-	23.0 (4.6)	14.5 (3.9)	18.8 (4.0)	-	-	-	27.9 (2.7)	36.0 (3.5)	31.9 (3.8)

TABLE 2.3. Correlation coefficients of the response function analyses between tree growth and seasonal climate variables. Asterisk indicates significant correlations (0.05 level). Maximum temperature refers to the mean maximum temperature of respective season.

Climate variable	Season	<i>A. nephrolepis</i>			<i>P. koraiensis</i>			<i>P. jezoensis</i>		
		780 m	1300 m	1750 m	780 m	1000 m	1300 m	1000 m	1300 m	1750 m
Precipitation	PE Sept-Aug	0.38*	0.24	0.12	0.37*	0.15	0.15	0.30*	-0.17	0.07
	CY April-May	-0.11	-0.04	-0.25	-0.01	0.04	-0.04	-0.32*	-0.06	-0.18
	Current year (June-Aug)	0.10	0.12	0.10	0.36*	0.10	0.21	-0.01	0.16	0.17
Maximum temperature	Previous year (Sept-Aug)	-0.06	-0.04	0.20	0.09	-0.05	0.23	-0.06	0.03	0.08
	Current year (April-May)	-0.06	0.03	0.25*	0.09	0.05	0.17	0.13	0.12	0.13
	Current year (June-Aug)	0.03	-0.10	0.09	-0.21*	0.09	0.04	0.12	0.14	0.13

FIGURE 2.1. Location of the Changbai Mountain Natural Reserve in the Northeastern China (a), distribution of species by elevation (b), and location of the meteorological stations and study sites (c).

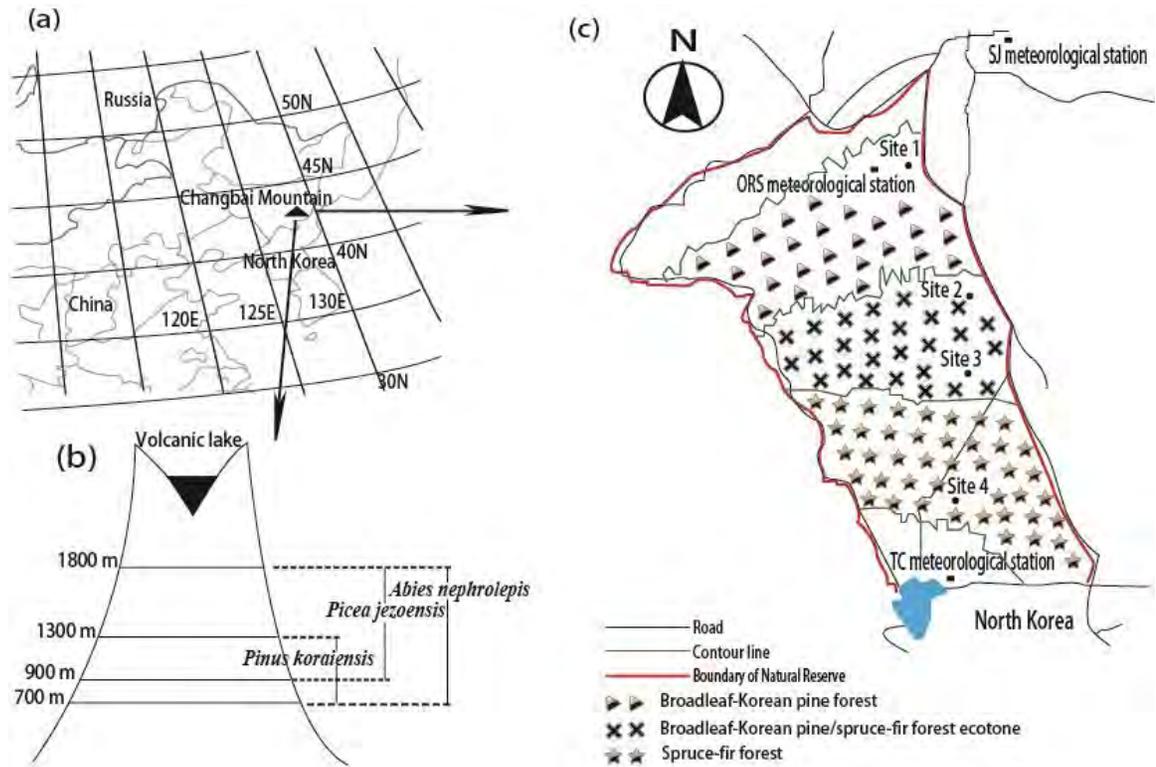


FIGURE 2.2. Regeneration density of three tree species along the elevational gradient in the Changbai Mountain. In A, x-axis represents the real elevation of the species distribution, while x-axis of B shows the relative position along the elevational gradient.

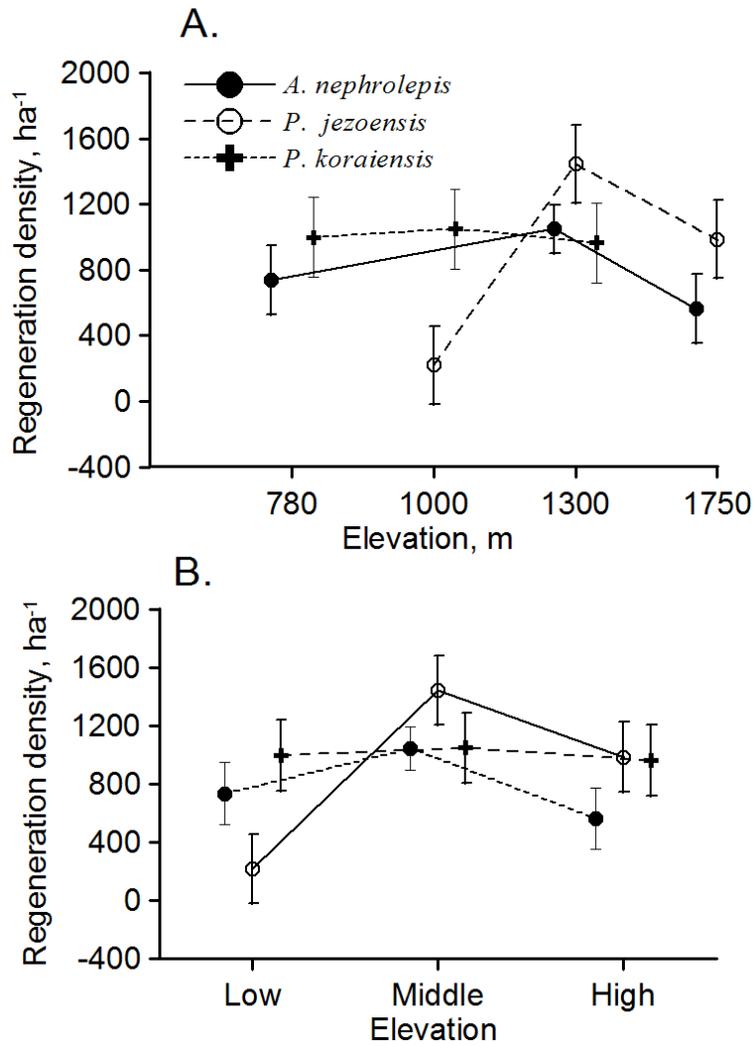


FIGURE 2.3. Basal area increment (BAI) for the three dominant species at different elevations over 1995-2006. The differences of x-axis between A and B are the same as illustrated by FIGURE 2.2.

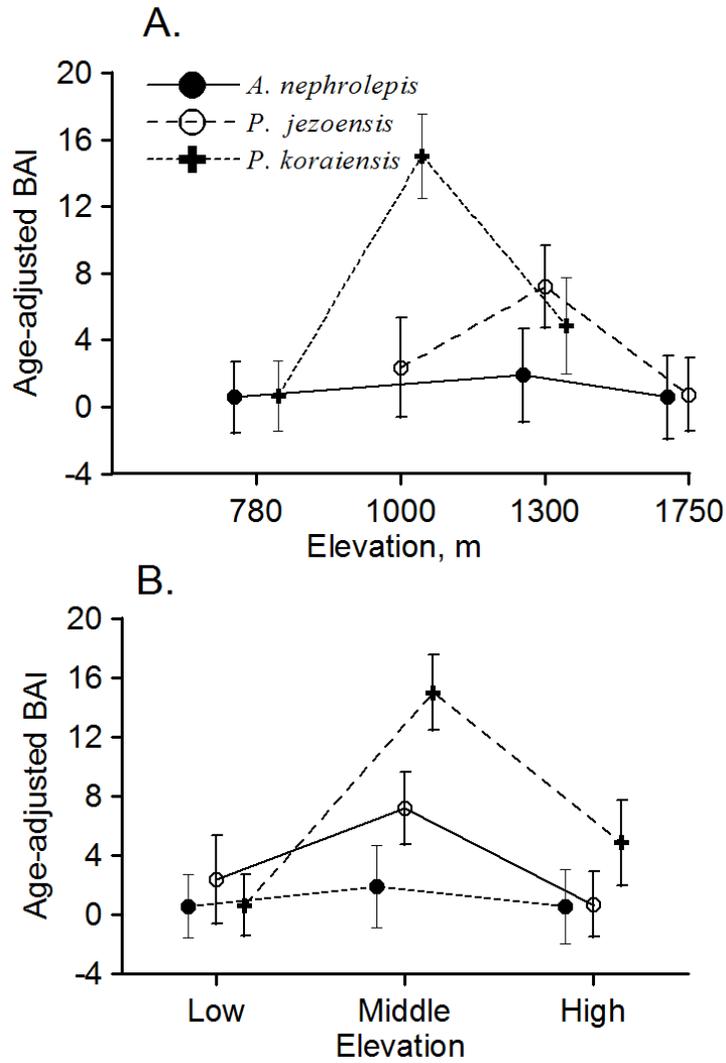
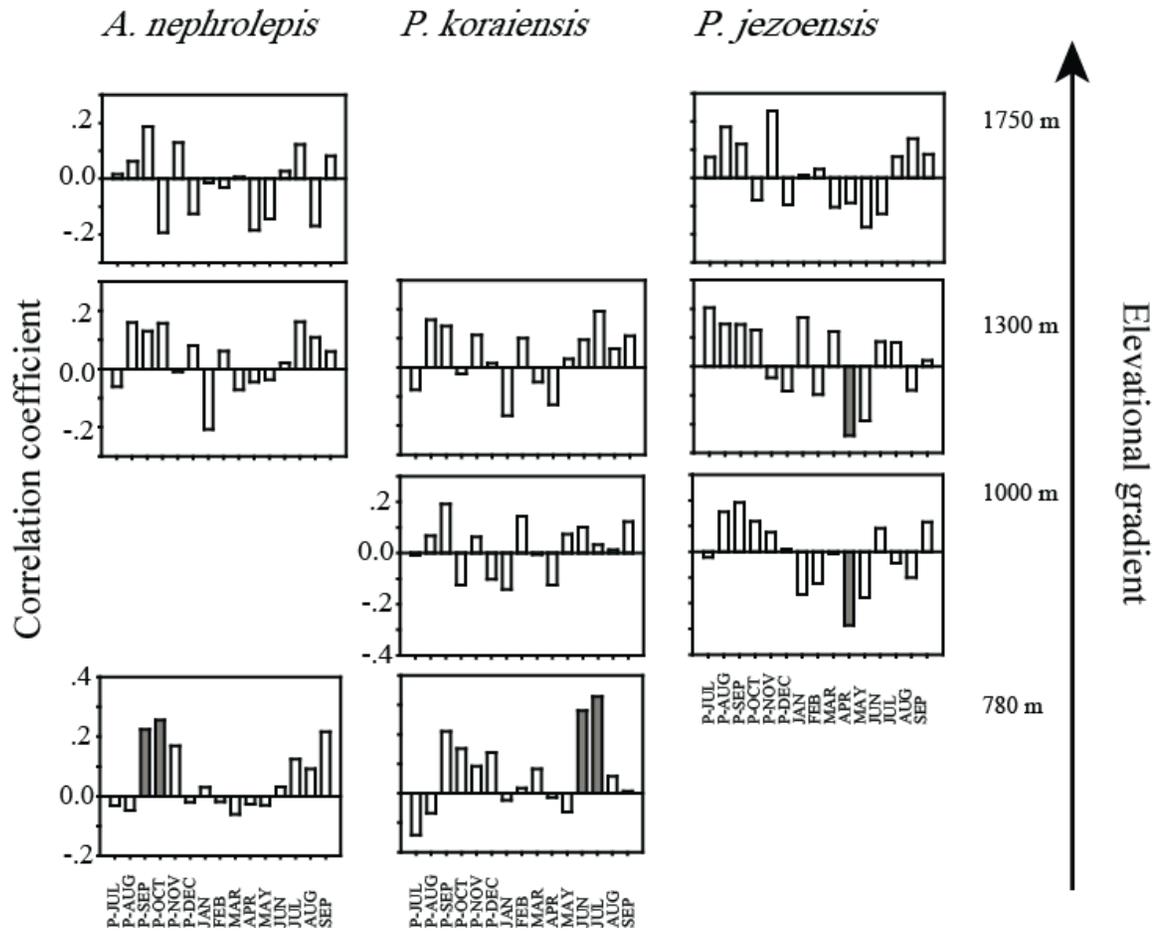
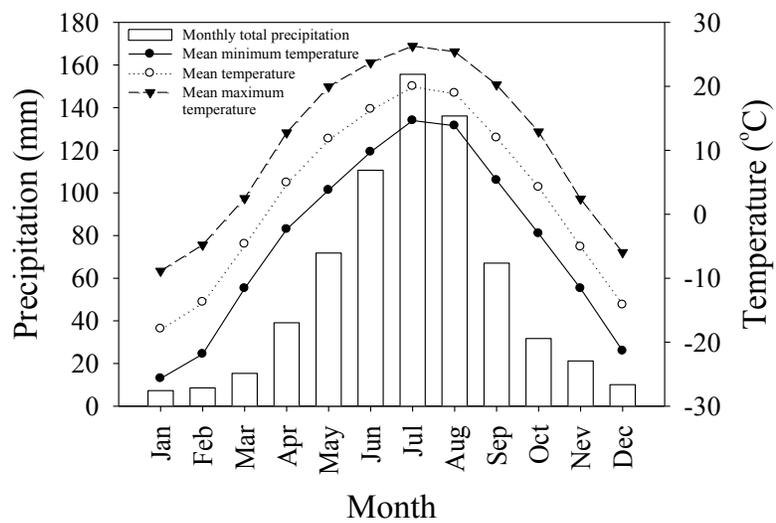


FIGURE 2.5. Response function analyses between residual chronologies of *A. nephrolepis*, *P. koraiensis*, and *P. jezoensis* and precipitation from the previous year July (P-JUL) to the current year September (SEP) on the northern slope of the Changbai Mountain for the period 1958-2007. Grey bars indicate significant relationships ($p < 0.05$).



Appendix 2.1

APPENDIX 2.1. FIGURE 2.1. Long-term (1958-2007) pattern of climate variables at the Songjiang station in the Changbai Mountain, Northeastern China.



Appendix 2.2

APPENDIX 2.2, TABLE 2.1. Chronology statistics for the studied species on the northern slope of the Changbai Mountain. Statistics refer to residual chronologies and include mean ring width (MRW), mean sensitivity (MS), standard deviation (SD), signal-to-noise ratio (SNR), express population signal (EPS), and variance explained by the first principal component (PC1, %).

Site No.	Species	Cores /trees	Chronology length	MRW (mm)	MS	SD	Period with EPS \geq 0.85	Common interval analyses for the period 1958-2007				
								Mean correlation	Core/Stem	SNR	EPS	PC1
1	<i>A.nephrolepis</i>	37/20	1889-2011	0.31	0.22	0.21	1936-2011	0.349	33/18	17.68	0.95	37.72
3	<i>A.nephrolepis</i>	33	1850-2007	0.48	0.22	0.23	1890-2007	0.480	28	25.80	0.96	40.38
4	<i>A.nephrolepis</i>	22/14	1884-2008	0.32	0.14	0.12	1922-2009	0.258	18/12	6.25	0.86	30.18
1	<i>P.koraiensis</i>	40/21	1810-2011	0.36	0.20	0.18	1929-2011	0.277	40/21	15.34	0.94	30.96
2	<i>P.koraiensis</i>	33	1795-2007	1.18	0.20	0.27	1814-2007	0.311	33	13.99	0.93	34.39
3	<i>P.koraiensis</i>	30	1788-2007	0.70	0.15	0.13	1829-2007	0.357	30	16.62	0.94	38.80
2	<i>P.jezoensis</i>	30	1780-2007	0.61	0.22	0.19	1796-2007	0.384	25	15.55	0.94	41.00
3	<i>P.jezoensis</i>	34	1865-2007	1.05	0.21	0.29	1917-2007	0.294	34	14.99	0.94	32.70
4	<i>P.jezoensis</i>	51/27	1654-2008	0.30	0.18	0.17	1780-2009	0.318	45/24	20.95	0.95	34.40

Appendix 2.3

APPENDIX 2.3, TABLE 2.1. Soil gravimetric composition is given for two plots and in percentages at the studied sites.

Site No.	Survey year	Elevation (m)	Soil (plot 1/2)			
			sand	clay	Silt	pH
1	2012	780	78/54	10/22	12/24	4.3/4.1
2	2008	1000	72/76	14/13	14/11	4.0/4.8
3	2008	1300	70/74	16/12	14/16	3.1/3.4
4	2009	1750	74/70	16/14	10/16	3.8/3.8

Appendix 2.4

APPENDIX 2.4, TABLE 2.1. Post-hoc comparisons of regeneration density and mean basal area increment (BAI) of the three species among three elevations. For each species, contrasts marked with the same letters (a-c) are not significantly different (LSD test for post hoc pairwise comparisons, $p \geq 0.05$).

Variable	<i>A. nephrolepis</i>			<i>P. koraiensis</i>			<i>P. jezoensis</i>		
	780 m	1300 m	1750 m	780 m	1000 m	1300 m	1000 m	1300 m	1750 m
Regeneration density, trees/ha	737 ± 441a	1048 ± 197a	565 ± 176a	1000 ± 530a	1050 ± 234a	965 ± 231a	221 ± 46a	1446 ± 449a	987 ± 109a
BAI, m ²	0.59a	1.90b	0.58c	0.65a	15.03b	4.87c	2.37a	7.22b	0.73c

CHAPTER III

STAND HISTORY IS MORE IMPORTANT THAN CLIMATE IN CONTROLLING RED MAPLE (*ACER RUBRUM* L.) GROWTH AT ITS NORTHERN DISTRIBUTION LIMIT IN WESTERN QUEBEC, CANADA

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3.1 RÉSUMÉ

Nous avons examiné la croissance de l'érable rouge (*Acer rubrum* L.) à sa limite nord de répartition dans l'Est de l'Amérique du Nord afin d'évaluer sa relation au climat et sa possible réponse suite aux changements climatiques futurs. Nous avons analysé les données dendrochronologiques de neuf sites situés le long d'un transect latitudinal de 300 km (47-49 °N) couvrant trois domaines bioclimatiques dans l'ouest du Québec. Les trois variables de croissance étudiées étaient les taux de croissance au cours des 30 premières années de la vie de l'érable, la croissance cumulative de la surface terrière au cours de la dernière décennie (2000-2009) et le taux de croissance annuelle pendant toute la durée de vie de l'érable. Les trois mesures étaient positivement corrélées à la latitude. Sur l'ensemble du transect, la variation annuelle de la croissance de l'érable était positivement affectée par les températures de septembre de l'année précédente. Les températures de juillet de l'année en cours et les précipitations de décembre de l'année précédente ont eu un effet positif sur la croissance dans la partie nord du transect (48-49 °N). La croissance était limitée au milieu de l'été (juillet) par la sécheresse à l'extrémité sud du transect (47-48 °N). La contradiction apparente entre les résultats de la croissance absolue et ceux de la fonction de réponse a été interprétée par l'effet de l'histoire du peuplement sur le modèle de croissance de l'érable rouge. Plus précisément, les érables recrutés après de fortes perturbations, comme à la suite d'un feu, dans le nord, pourraient profiter des niveaux de luminosité plus élevés, nécessaires à la croissance, par rapport aux peuplements plus au sud qui se sont probablement développés dans des trouées. Dans l'avenir, la croissance de l'érable rouge répondrait négativement par l'augmentation de la sécheresse de l'été dans la partie sud de la zone d'étude (la sapinière à bouleau à papier) et répondrait positivement par la hausse des températures dans le nord (le domaine de l'érablière à bouleau jaune). Cependant, les régimes de perturbations naturelles et anthropiques qui affectent les conditions de croissance à l'échelle du site semblent contrôlés plus que le climat la productivité de la biomasse de l'érable rouge au sein de son aire de répartition actuel.

3.2 ABSTRACT

We examined growth of red maple (*Acer rubrum* L.) to evaluate environmental controls of its northern distributional limit in Eastern North America and its potential response to future climate change. We collected growth data from nine sites located along a 300 km transect (47-49° N), which included frontier population of red maple and covered three bioclimatic domains in western Quebec. We analyzed three growth variables: growth rates during the first 30 years of maple lifespan, cumulative basal area increment (BAI) over the most recent decade (2000-2009), and annual growth rate over the whole tree lifespan (tree ages ranging from 58 to 112 years). We also examined growth sensitivity to climate by using response function analyses. Red maple growth was positively correlated with site latitude. Response function analyses indicated that annual growth variability was positively affected by September temperatures of the previous year, the effect being observed across the entire transect. In the northern part of transect (48-49° N) growth was positively correlated with July temperatures of the current year and December precipitation of the previous year. In the southern part of transect (47-48° N) growth was negatively correlated with July Monthly Drought Code. We interpret an apparent discrepancy between the results of BAI analyses and response function analyses by the overriding effect of stand history on the growth pattern of red maple. In particular, regeneration of maple in the southern sites likely occurred in canopy gaps, whereas its regeneration in the north was contingent upon large disturbance events such as stand-replacing fires, which facilitated maple establishment. Both stand history and climate affect red maple northern distribution limit, but stand history being much more influential on its growth. In the future, red maple growth would be negatively affected by increased summer drought in the southern part of study area (sugar maple (*Acer saccharum* Marsh.) - yellow birch (*Betula alleghaniensis* Britt.) domain) and positively affected by increased temperatures in the north (balsam fir (*Abies balsamea* (L.) Mill.) - paper birch (*Betula papyrifera* Marsh.) domain). However, the natural and human disturbance regimes affecting the growth conditions at the site level appear to be dominant controls of the actual biomass productivity of red maple at its present distribution range.

Key words: climate change, dendrochronology, ecotone, hardwoods, migration

3.3 INTRODUCTION

Climate influences forest communities by affecting species phenology and growth, and the outcomes of competitive interactions among plants (Hansen *et al.* 2001; Richardson *et al.* 2006; Tylianakis *et al.* 2008). Over the 20th century, annual mean temperature and annual total precipitation in eastern Canada have increased by 0.5-1.5 °C and 5-35%, respectively (Zhang *et al.* 2000). Temperature is expected to increase by an additional 1.5 to 4.5 °C by 2050, accompanied by 10 to 25% increases in the amount of precipitation (Boer *et al.* 2000; Plummer *et al.* 2006). Such changes in climate may have major impacts on tree growth and distribution by affecting plant physiology (Way and Oren 2010), tree sensitivity to environmental variability (Allen *et al.* 2010), and natural disturbance regimes (Bergeron *et al.* 2010). Growth responses to these changes would likely be species-specific (Ashraf *et al.* 2013).

The performance of species at their distributional limits may give clues to understand their responses to long-term climate variability (Wilmking *et al.* 2004; Zhang and Hebda 2004; Griesbauer and Green 2010; Lv and Zhang 2012). Temperature is a crucial factor for tree growth at northern latitudinal and upper altitudinal limits (Fritts 1976; Makinen *et al.* 2002; Frank and Esper 2005). Climate warming has induced a northward or an upward shift of many species at their distributional limits in different temperate biomes (Kullman 1993; Suarez *et al.* 1999; Wilmking *et al.* 2004; Pederson *et al.* 2004; Griesbauer and Green 2010). In eastern North America, temperate hardwood species are expected to migrate further north under warmer climate conditions (Goldblum and Rigg 2005; McKenney *et al.* 2007; Berteaux *et al.* 2010; Terrier *et al.* 2013).

Competition may be another factor that influences species distributional limits (Gavin and Hu 2006; Ettinger and HilleRisLambers 2013). Competition may restrict species ranges by excluding species from potentially suitable habitats (Armas *et al.* 2009), and may also enhance negative effects of sub-optimal climate conditions on tree growth (Scheller and Mladenoff 2008). Therefore, a

consideration of competitive interactions between species, together with a detailed analysis of climate-growth relationships, would help us to model accurately any potential shifts in species distributions (Davis *et al.* 1998; Guo *et al.* 2013).

Studies of the long-term forest dynamics have demonstrated that distribution ranges of hardwood species are closely linked to regional climate (Davis 1981; MacDonald 1993). For example, fossil pollen data have indicated that red maple (*Acer rubrum* L.) experienced a northward expansion in North America during the warmer period of the early to middle Holocene (from 11 000 to 7 000 years BP, Delcourt and Delcourt 1987). Dendrochronological methods have a potential to provide high resolution data to help disentangle climate-growth relationships, however there were few dendroclimatological studies on hardwood species at their northern distributional limits in eastern Canada (Tardif and Bergeron 1993; Tardif *et al.* 2006), most of them being focused on coniferous species (Drobyshev *et al.* 2010, 2013; Nishimura and Laroque 2011; Genries *et al.* 2012).

Red maple is one of the most widespread broadleaf trees in eastern North America, which also marks the border between boreal and temperate biomes in eastern Canada (Walters and Yawney 1990). In western Quebec, red maple reaches its northern distributional limit around 48° N, where its frontier populations occupy south-facing hill slopes (James and Courtin 1985; Tremblay *et al.* 2002) and coexist with other deciduous and coniferous species, forming mixedwoods. Spring frost is an important factor affecting red maple sexual regeneration in this region, with waves of maple recruitment being associated with periods of low spring frost frequency (Tremblay *et al.* 2002). However, climate effects on the growth of adult trees, which may be another factor controlling the northern distribution limit of red maple, are poorly understood. Furthermore, presence of abundant regeneration of red maple on recently disturbed sites in this region suggests importance of stand history affecting maple recruitment and abundance in the canopy.

In this study, we examined biomass accumulation rates and growth sensitivity of red maple to annual

weather along a 300 km-long latitudinal gradient (47-49° N) stretching from the southern mixed forest to the frontier maple populations in eastern Canada. We put forward two hypotheses: (1) biomass accumulation rate declines with increasing latitude, and (2) annual growth sensitivity to temperature increases with latitude while sensitivity to precipitation decreases with latitude. Both hypotheses assumed that growth was increasingly limited by temperature towards the north, reflecting a trend towards colder conditions and a shorter growing season. We also discussed the growth of red maple under projected climate change and resulting dynamics of its northern limit in eastern North America.

3.4 MATERIALS AND METHODS

3.4.1 Study area

Our study was conducted at the Quebec-Ontario border along a latitudinal gradient (47° N to 49° N) extending to the northern limit of red maple distribution (Figure 3.1). The study area covered the Abitibi-Témiscamingue region of Quebec, which is dominated by glacial deposits (Vincent and Hardy 1977; Bouchard *et al.* 2005). Regional topography is generally flat, with small hills reaching elevations of 200 to 400 m a.s.l. Stands with red maple in the canopy are usually found on till deposits or rocky outcrops (Lalonde 1991), with such habitats being more common towards the southern portion of our transect (MRNQ 1998).

Winter climate of the study area is dominated by dry polar air masses, while warm summers bring moist tropical air masses to the region. Average temperature decreases from the southern end of the study transect to its northern end, while the pattern of precipitation is reversed (Table 3.1). Annual mean temperature is about 1.7 °C at BEA (the southernmost site) and 0.8 °C at DUP (the northernmost site). January is the coldest month, with the average mean temperature ranging between -16.9 °C (BEA) and -18 °C (DUP). July is the warmest month, with the average mean temperature varying from 17.3 °C (BEA) to 16.6 °C (DUP). Total annual precipitation is between 705 mm (BEA) and 746 mm (DUP).

Nine red maple sites were selected across the three bioclimatic domains (Saucier *et al.* 2003), including two sites within the sugar maple (*Acer saccharum* Marsh.) - yellow birch (*Betula alleghaniensis* Britt.) domain in the south (sites BEA and MAR), two sites within the balsam fir (*Abies balsamea* (L.) Mill.) - yellow birch domain in the center of the study area (sites REM and KEK), and five within balsam fir-paper birch (*Betula papyrifera* Marsh.) domain in the north (sites SAB1, SAB2, SAB3, ROQ, and DUP, Figure 3.1). An ecological survey at the landscape scale across the three bioclimatic domains determined that the frequency of red maple decreased from 46% to 11%, moving northward along our latitudinal gradient (MRNQ 1998).

3.4.2 Soil sampling and analyses

To characterize soil properties, we collected two samples from the soil mineral layer (20-30 cm) at each site, which were combined to form one bulk sample. A portion of the combined sample was air-dried at 20 °C for one week and sieved to pass a 2 mm mesh screen. Soil texture was quantified by the Bouyoucos Hydrometer Method (Sheldrick and Wang 1993, Appendix 3.1). A second portion of sample was sieved through a 4 mm screen and oven-dried at 40 °C for 60 hours. We used this portion to determine soil chemical composition (Appendix 3.2), including total carbon (C, %), nitrogen (N, %), sulphur (S, %), and phosphorus, together with pH in 0.5 M CaCl₂ and cation exchange capacity (CEC). The analytical procedures followed established protocols (Laganière *et al.* 2010) at the Laurentian Forestry Centre of the Canadian Forest Service, Quebec City, Quebec, Canada.

3.4.3 Climate data

Climate data were generated in BioSIM 10.2.2.3, which is a set of spatially explicit bioclimatic models (Régnière 1996). We used BioSim to interpolate climate data that had been obtained from the five weather stations closest to each site, taking into consideration of site latitude, longitude, and elevation. We used data for the period 1964 through 2009, which was the common period across sites and had the highest quality of climate data. Analyzed climate variables included monthly mean

temperature and monthly total precipitation from July of the previous year to August of the current year. In addition, we used the Monthly Drought Code (MDC), which was calculated from May to September, to detect the effects of soil moisture on tree growth. MDC is the product of monthly maximum temperature and total precipitation (Girardin and Wotton 2009) and is considered an indicator of deep organic layer moisture content (Turner 1972).

3.4.4 Field sampling and initial data treatment

We selected study sites based on the field surveys of Lalonde (1991) and Tremblay *et al.* (2002). Stand selection was guided by the following criteria: 1) red maple should be present as large (above 10 cm in diameter at breast height) canopy or sub-canopy trees; and 2) red maple should contribute more than 20% in relative species abundance of selected stand. Identification of stand origin was based on historical records of forest fires (Lalonde 1991), data base of fire from ecoforestry maps of the Quebec Ministry of Natural Resources and Wildlife, and data of stand age available from previous studies (Lalonde 1991; Graignic *et al.* 2013). In particular, we assumed that if stand age exceeded the oldest sampled maples, the latter were recruited through canopy gaps and not through stand-initiating disturbance.

At each site, we randomly sampled 12 to 17 canopy or sub-canopy maples, measuring diameter at breast height (DBH, 1.3 m) and extracting two cores from each tree at 20 cm above the ground surface. The cores were dried, mounted, and sanded until ring boundaries were clearly visible. Cores were visually cross-dated by using the point year technique (Stokes and Smiley 1968). After cross-dating, ring widths were measured on scanned images in CDendro and CooRecorder software, ver. 7.3 (Larsson 2010). Data quality was statistically verified using the program COFECHA (Holmes 1983).

Prior to the dendroclimatic analyses, we removed age- and size-related trends in tree growth. The tree-ring series were detrended with a cubic spline using program ARSTAN (Cook and Peters, 1981).

The detrending procedure assumed a 50% frequency response over a 40-year frequency band. We then performed autoregressive modeling on detrended ring-width series to remove temporal autocorrelations and to enhance the common signal. The individual residual series were subsequently averaged together using a biweight robust mean to develop a mean standardized chronology for a site that retained high-frequency variation and which contained no low-frequency trend.

3.4.5 Dendrochronological analyses

Initial growth rates We developed cambial curves of the first 30 years of tree lifespan to evaluate the initial growth rates and regeneration conditions. To develop cambial age chronologies we calculated mean ring-width (in mm) for each year of growth from year one to year 30 using samples collected within each bioclimatic domain. Since basal area increment (BAI, m²) better represents tree biomass accumulation than does the diameter increment (Pedersen 1998), we converted the averaged ring-widths into BAI. To evaluate differences in absolute growth rates among the bioclimatic domains, we fitted BAI cambial chronology by linear regression and tested the differences among b coefficients (regression slopes) using a General Linear Model in SPSS 15.0 (Carpenter *et al.* 2004).

Environmental effects on growth of adult trees To understand environmental controls of growth for adult trees we related cumulative BAI of the most recent ten years (2000-2009) to site variables, by using multiple linear regression function `lm` and bootstrapping function `boot` of the statistical programming language R ver. 3.0.2 (Fox 2000). Similar to the analyses of initial growth, tree-ring data were converted into BAIs. To eliminate age effects on biomass accumulation, we divided BAI of each tree by tree age, and then make an average of adjusted BAI from all trees as site mean BAI. We considered latitude (representing temperature gradient, Table 3.1), soil pH value (representing soil conditions, Appendix 3.2), and an index of competition interactions, as environment factors affecting BAI.

To calculate competition interactions, we measured DBH of both cored and neighboring trees, and

recorded the distances between them. Specifically, we selected the nearest neighbor within each of the four quadrants that were located around the focal maple tree, and which were delimited by the four cardinal directions (i.e., North, South, East, and West). We then used Hegyi's (1974) single tree competition index (CI) to quantify the influence of neighboring trees on the focal trees:

$$CI = \sum_{j=1}^N \left(\frac{D_j}{D_i} \times \frac{1}{DIST_{ij}} \right)$$

where CI is the competitive load for the focal tree; D_i is for the focal tree's DBH (cm); D_j is for the competitor tree's DBH (cm); $DIST_{ij}$ is the distance (m) between focal tree i and competitor tree j ; and N is the number of competitor trees surrounding the focal tree (four in our study). According to this formula, higher CI would result from the smaller the size of the focal tree, the larger the size of the competitor, and the lower the local density (i.e., the greater the distance between trees). We averaged CI of all of the maple trees from the same site to estimate site CI.

Annual growth rate To further evaluate variability in growth rates along the transect, we calculated mean diameter growth rate of red maple by calculating a ratio between DBH and tree age for each site, and then linearly regressing it against site latitude.

Growth sensitivity to annual climate variability We used response function correlations to examine growth sensitivity to climate resolved at monthly scale. A response function is a principal component regression that is used to solve the problem of multicollinearity among climatic predictors (Briffa and Cook 1990; Morzikh and Ruark 1991), and which is usually applied when evaluating climate-growth relationships. Correlation coefficients of the response functions were calculated over the common interval 1965-2009, using the program DENDROCLIM2002 (Biondi and Waikul 2004).

3.5 RESULTS

3.5.1 Stand history and soil conditions

The majority of northern sites (ROQ, SAB1, SAB2, SAB3, and KEK) were post-fire stands according to the documentary records of fire events (Lalonde 1991) and maximum tree age of red maple in these sites (Table 3.1). At site DUP the initiation year of the stand and of the cored maples coincided (Table 3.1), and absence of recent charcoal suggested a clear-cut event. In southern sites (REG, MAR, and BEA), the maximum age of trees in the forest canopy was higher than that of sampled maples, suggesting that these maples probably regenerated in gaps or under canopy (Table 3.1).

Soils of all sites showed a high sand content ($> 73\%$, Appendix 3.1) and rather acid soil condition (pH ranging between 3.04 and 4.20, Appendix 3.2). There was no clear pattern in variation of soil nutrients (i.e. total C, N, and S) along the latitudinal gradient. Both northernmost (DUP) and southernmost (BEA) sites revealed lower nutrient concentrations as compared to more centrally located sites. Cation exchange capacity (CEC) was similar among all the sites (ranging from 17.63 to 23.79), except for the site SAB1 (5.86).

3.5.2 Chronology characteristics

The length of maple residual chronologies ranged from 58 to 112 years, with the oldest chronology dating back to 1897 (Table 3.1). Chronologies showed high expressed population signals (EPS, ranging from 0.85 to 0.91), while the variation explained by the first principal component (PC) ranged from 29.12 to 49.02%. The nine chronologies were similar in terms of their mean sensitivity (MS), which ranged from 0.24 to 0.31 (Table 3.1).

3.5.3 Growth rates

Maple growth during the first 30 years of life was significantly higher ($p < 0.001$) in the northernmost balsam fir-paper birch domain compared to the other two domains (Figure 3.2). There was no difference between balsam fir-yellow birch and sugar maple-yellow birch domains in terms of the coefficients representing the increase in growth rate with age during the first 30 years ($p = 0.54$). In

all three domains, linear regression fitted the growth patterns well, with R^2 varying between 0.95 and 0.98.

Site average BAI accumulated during 2000-2009 was significantly and positively related to site latitude ($p = 0.032$), while competitive interactions and soil pH did not show significant effects on BAI (Table 3.2). The average growth rate over whole tree lifespan was higher in the north of transect than in the south, trees on the northernmost site ROQ exhibited the highest growth rate while the trees on the southernmost site REM showed the lowest growth rate (Figure 3.3).

3.5.4 Climate-growth relationships

Temperature, precipitation, and soil moisture conditions affected red maple growth (Figure 3.4). Temperature in September of the previous year was positively related to maple growth across the whole transect, with significant correlations observed at four sites (ROQ, SAB3, MAR, and BEA). In the northern part of transect (sites DUP, ROQ, SAB1, SAB2, SAB3, and KEK), June and July temperatures of the current year, and precipitation in December of the previous year were positively correlated with maple growth. In the southern part of transect, summer water deficit appeared to limit growth, as indicated by significant and negative correlations with July MDC (sites REM and BEA), June temperature (BEA), and August temperature (REM), and by positive correlations with July precipitation (REM and BEA).

3.6 DISCUSSION

Growth rate of red maple at its northern distributional limit was not limited by temperature, which rejected Hypothesis 1. However, annual variability in growth was sensitive to temperature in the north of transect and to moisture availability in the south, supporting Hypothesis 2. The result rejected our general hypothesis assuming the dominant role of low temperature in affecting red maple growth. Initial (first 30 years of tree lifespan) and the most recent (2000-2009) growth rates, as well as rates

averaged over the whole lifespan of the trees were all higher in the northern part of transect, suggesting that stand history might be more important than direct climate variability in controlling biomass accumulation rates. Below we discuss the details of these findings and the potential effects of future climate conditions on the northern distributional limit of red maple.

3.6.1 Growth rates along the latitudinal gradient

All growth variables analyzed in this study suggested that growth of red maple increased towards the north (Table 3.2; Figures 3.2 and 3.3), which falsified our assumption about decline in growth rate towards north due to temperature limitations. We believe that differences in stand history (Table 3.1) may be important in explaining this apparent contradiction. The sites in the northern balsam fir - paper birch domain regenerated after stand-replacing fires or clear cutting, and maple establishment likely followed a stand-replacing disturbance event, thereby benefiting from high light levels during early life stages of stand development. In contrast, red maple trees in the more southerly locations (i.e., sugar maple-yellow birch and balsam fir-yellow birch domains) likely regenerated under the closed canopy and benefited from canopy gap formation. An advantage of regenerating on the open habitat would likely be due to favorable light levels over the whole lifespan of red maples, since this species is one of the most fast growing trees in the northern mixedwood on till soils (Walters and Yawney 1990).

Except stand history, local forest management may also modulate maple growth. For example, the exceptionally high growth rate of ROQ (Figure 3.3) could be attributed to selective thinning, which was applied to this stand in connection to maple syrup production in the past. A lower stand density leading to decreased competition among trees, appeared therefore to override the effects of sub-optimal climate on maple growth. Red maple has been shown to have strong and positive growth responses to decreases in stand density (Walters and Yawney 1990).

3.6.2 Climate-growth relationships

Red maple growth was sensitive to temperature in the northern part of the transect (sites DUP, ROQ, SAB1, SAB2, SAB3, KEK) and to moisture in its southern part (sites REM, MAR, BEA, Figure 3.4). Higher temperature likely enhanced photosynthetic rates during the short growing period at the northern sites, thereby favoring tree growth. A southward increase in temperature was accompanied by a decrease in precipitation (Table 3.1), which likely led to summer drought stress in the south. A recent study conducted in an area of Northern Ontario (De Silva *et al.* 2012) adjacent to our southernmost sites, likewise demonstrated a negative effect of water deficiency on red maple growth. Negative effects of drought stress on red maple growth, shown for the mixed forests of the eastern USA (He *et al.* 2005), might have caused growth declines in red maple over that region (Fekedulegn *et al.* 2003). Negative effects of summer water deficiency on hardwood species have also been observed in sugar maple, which is taxonomically and ecologically related to red maple (Tardif *et al.* 2001), as well as in other deciduous species of eastern Canada, i.e. trembling aspen (*Populus tremuloides* Michx.), paper birch (Huang *et al.* 2010), and white oak (*Quercus alba* L.; Tardif *et al.* 2006).

Red maple growth in the northern part of transect was positively correlated with precipitation in December of the previous year (Figure 3.4). We believe that deeper snow cover during December would better protect roots from the damaging effects of low temperature. Such relationship has been proposed in many studies of tree growth dynamics at distributional limits. Deep snow cover has been suggested as a factor limiting temperature-related root damage at tree lines both in northern Quebec (Payette *et al.* 1996) and in western Austria (Oberhuber 2004). Positive effects of early winter snow accumulation on tree growth have been reported for Erman's birch (*Betula ermanii* Charm.) at the upper altitudinal limit of subalpine forests in northeastern China and central Japan (Takahashi *et al.* 2005; Yu *et al.* 2007). Negative effects of a reduction in snow cover on growth of sugar maple through damaging roots have been observed in the northern hardwood forest of USA (Comerford *et al.* 2012).

Red maple responded positively to previous September temperature across the entire latitudinal gradient (Figure 3.4). Two mechanisms would explain this relationship. First, warmer autumn may lead to a longer growing season for red maple and help increases of carbohydrate reserves in roots to be used in the following growing season (Kozłowski and Pallardy 1997; Yu *et al.* 2007). It has been widely reported that root reserves during the previous year appeared to play an important role for early growth of deciduous trees in the following year (Tromp 1983; Cheng and Fuchigami 2002; Hart *et al.* 2012). Secondly, warm autumn could promote root growth by keeping soil warm (Oberhuber 2004), and increases in root biomass during previous year could facilitate early growth in the following year due to greater root mass allowing better nutrients absorption (Ettl and Peterson 1995).

3.6.3 Future responses of red maple to climate at its northern distributional limit

Our results suggested that effects of future climate on red maple distribution may be realized primarily through climatically-induced changes in the natural disturbance regimes rather than through direct effects of climate on tree growth. The data indicated a strong link between red maple growth rates and the stand histories, and absence of temperature limitation of growth within the studied transect. Both observations apparently reflected plasticity of maple life strategy at its northern distribution limit and, more generally, its ability for recruitment under different disturbance regimes (Lorimer 1984; Hart *et al.* 2012; Duchesne and Prévost 2013). An important element of this strategy appears to be a rapid response to changes in light availability, as it has been shown in the study of red maple response to budworm outbreaks (Duchesne and Prévost 2013), formation of tree fall gaps (Leithead *et al.* 2010; Hart *et al.* 2012), and timber harvesting (Abrams 1998; Duchesne and Ouimet 2008).

A projected increase in the frequency and severity of spruce budworm outbreaks (Gray 2008) and windstorms (Ouranos 2010) in the study region may favor maple colonization of new habitats, particularly - on well and moderately drained parts of landscape. Forest fire may affect northern

distributional limit of red maple in different ways depending on variations of fire severity and frequency in future. Red maple can sprout vigorously after fire disturbances (Walters and Yawney 1990) and growth rate of maple was higher at those post-fire stands than gap-initiated stands (Figure 3.3), suggesting positive effects of fire on maples. However, fire with high severity and frequency could negatively affect maple frontier populations and cause a recession of its northern limit southward. Thin bark of adult maple trees makes them susceptible to fires of even moderate intensity (Frissell 1973; Walters and Yawney 1990; Abrams 1998), and severe fire may kill roots of maples limiting vegetative regeneration. Frequent fires may reduce the amount of seed resources and lead to low levels of sexual regeneration (Tremblay *et al.* 2002), reducing possibility of colonizing newly available sites across landscape. Therefore, great increases in both fire frequency and severity may exterminate populations of red maple locally and limit capacity of maple maintenance at landscape level.

Considering direct effects of future climate on red maple in western Quebec, it is likely that general warming of the climate would benefit maple recruitment and growth. Climate models predict that temperature will rise by an additional 2.2-3.5 °C by 2050 over the entire study area, with a greater increase in winter (3.0-4.4 °C, Ouranos 2010). Models also predict little change in summer precipitation patterns, but a decrease in snow accumulation during the winter (Ouranos 2010). A large increase in the abundance of maple seedlings due to climate warming has been reported at its northern limit in northeastern Ontario (Pinto *et al.* 2008) and eastern Quebec (Duchesne and Ouimet 2008; Duchesne and Prévost 2013), two locations which were geographically close to our study area. These results imply that future warming may also enhance recruitment of red maple in western Quebec. Increasing temperatures have been expected to increase seedling abundance of other tree species at high latitudinal or altitudinal distribution limits (Camarero and Gutiérrez 2004; Gamache and Payette 2005).

In the northern part of the study area (balsam fir - paper birch domain), the warmer summer may promote radial growth of red maple. During growing period, frontier populations of red maple may also benefit from warmer soil temperatures (Houle *et al.* 2012) and, consequently, increased nitrogen availability (Butler *et al.* 2012), which may be an important factor on sites with increased thickness of soil organic layer. Maple in the southern part of the study area (sugar maple-yellow birch and balsam fir-yellow birch domains) may face more stressful summer conditions in the future. A decrease in summer water availability may have a negative influence in maple growth in the south.

To conclude, future abundance of red maple in the western Quebec appears to be largely a product of disturbance-mediated effects on its recruitment and growth. Dynamics of future precipitation, which controls levels of fire activity seems to be of immediate importance under generally warmer and longer growing seasons. We believe that better projections of future precipitation should enhance our ability to project future changes in northern distribution limit of red maple in eastern Canada.

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Table 3.1. Climatic conditions (1965-2009) and statistical characteristics of red maple residual chronologies at the study sites in western Quebec.
MDC refers to Monthly Drought Code.

Sites	DUP	ROQ	SAB1	SAB2	SAB3	KEK	REM	MAR	BEA
<i>Stand history and site location</i>									
Direct records of disturbances year	1950	1880s	1923	1923	1923	1941	-	-	-
Disturbance type	Clear-cut	Fire	Fire	Fire	Fire	Fire	-	-	-
Stand age, maple age	58, 58	112, 112	85, 85	85, 84	85, 84	65, 64	161, 88	110, 83	145, 74
Latitude, °N	48.88	48.55	48.46	48.46	48.46	48.18	47.68	47.36	47.12
Longitude, °W	79.36	79.41	79.42	79.42	79.42	79.15	79.04	79.28	79.48
Elevation, m	312	330	405	365	350	376	340	293	239
<i>Climatic conditions</i>									
Annual mean temperature, °C	0.8	1.5	1.5	1.5	1.5	1.6	1.5	1.5	1.7
Annual total precipitation, mm	895	907	899	898	898	898	897	887	846
Average summer temperature, °C	15.3	15.9	16.0	16.0	16.0	16.0	15.9	15.9	16.1
Sum of summer precipitation, mm	303	300	292	291	291	288	287	289	272
Average summer MDC	12.6	12.7	12.9	12.9	12.9	13.9	12.5	13.4	14.2
<i>Characteristics of chronologies</i>									
Number of trees (number of radii)	14 (26)	12 (23)	13 (26)	12 (24)	12 (24)	17 (32)	12 (24)	12 (23)	15 (27)
Chronology length	1951-2009	1897-2009	1924-2009	1925-2009	1925-2009	1909-2009	1921-2009	1926-2009	1937-2011
Mean ring width, mm	1.08	1.43	1.07	1.16	1.12	1.05	0.50	0.98	0.86
Mean sensitivity	0.29	0.24	0.27	0.24	0.28	0.28	0.25	0.27	0.31
Period with EPS \geq 0.85	1957-2009	1944-2009	1929-2009	1936-2009	1951-2009	1952-2009	1965-2009	1957-2009	1953-2011

Common interval analysis for 1965-2009

Express population signal (EPS)	0.91	0.85	0.90	0.88	0.87	0.90	0.86	0.89	0.91
Signal-to-noise ratio	10.57	5.53	9.05	6.6	6.50	8.71	5.99	8.47	10.65
Variance explained by the first principal component, %	36.89	29.12	49.02	44.0	44.2	28.93	30.21	36.03	39.01

Table 3.2. Multiple linear regression between cumulative BAI over 2000-2009 and site level factors. For the analysis of whole regression, coefficient R^2 (confidence interval) =0.47 (0.29, 0.56), $p=0.11$. 95% confidence intervals were obtained by bootstrapping of original dataset 1000 times and calculating distribution of the b coefficients.

Factor	Estimated coefficient, b	95 % confidence interval	Std. Error	t value	p value
Intercept	-149.5	-354.3 & -79.4	52.49	-2.849	0.036
Latitude	3.212	1.934 & 22.559	1.087	2.955	0.032
Competition	-2.291	-11.50 & 7.823	2.088	-1.097	0.323
Soil pH	0.632	-3.292 & 7.282	1.479	0.427	0.687

Figure 3.1. Site locations and distribution range of red maple.

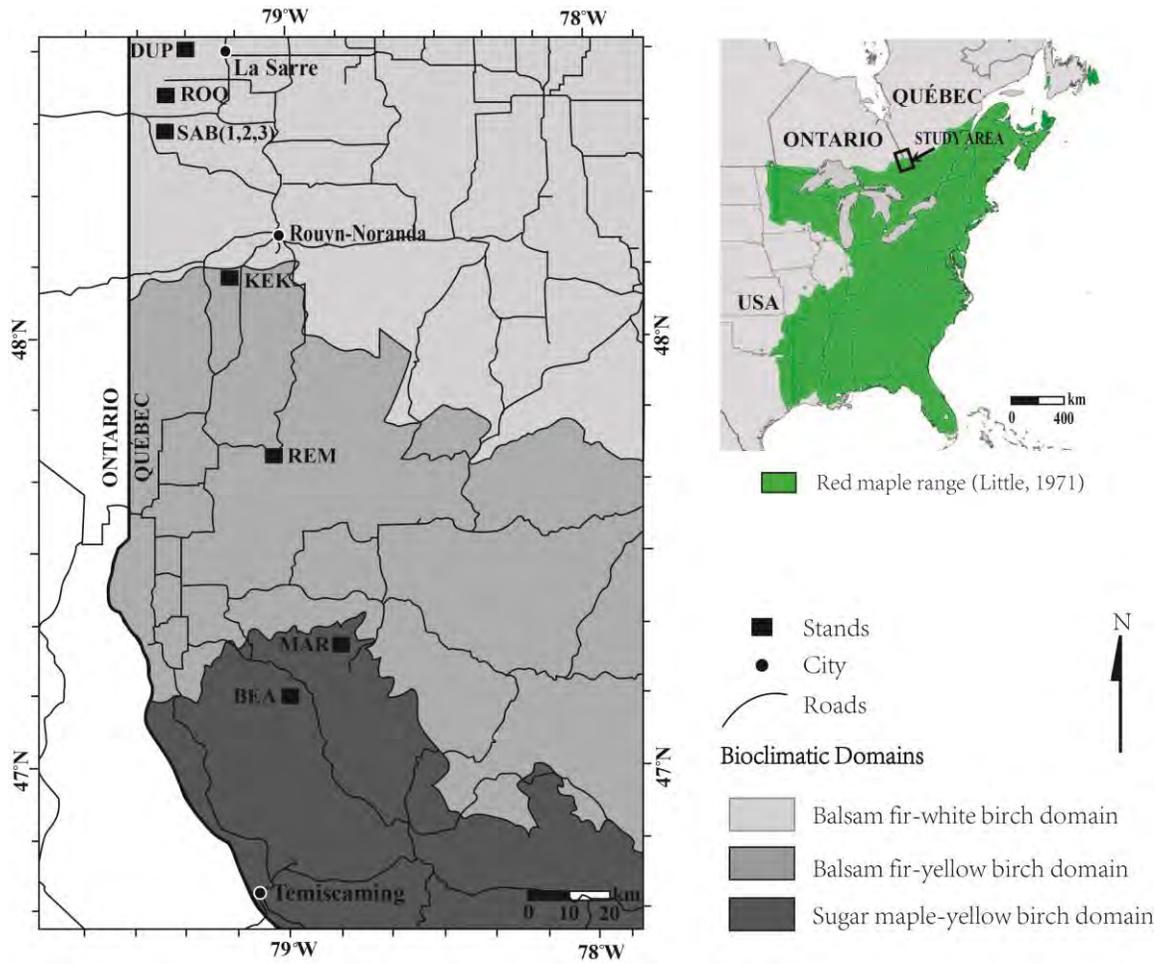


Figure 3.2. Cambial age BAI chronologies of red maple in the three bioclimatic domains at its northern distribution limit. Vertical bars represent SD (standard deviations) for a given cambial age. Data are fitted by linear regression with values of slope coefficient b and r^2 given for each domain.

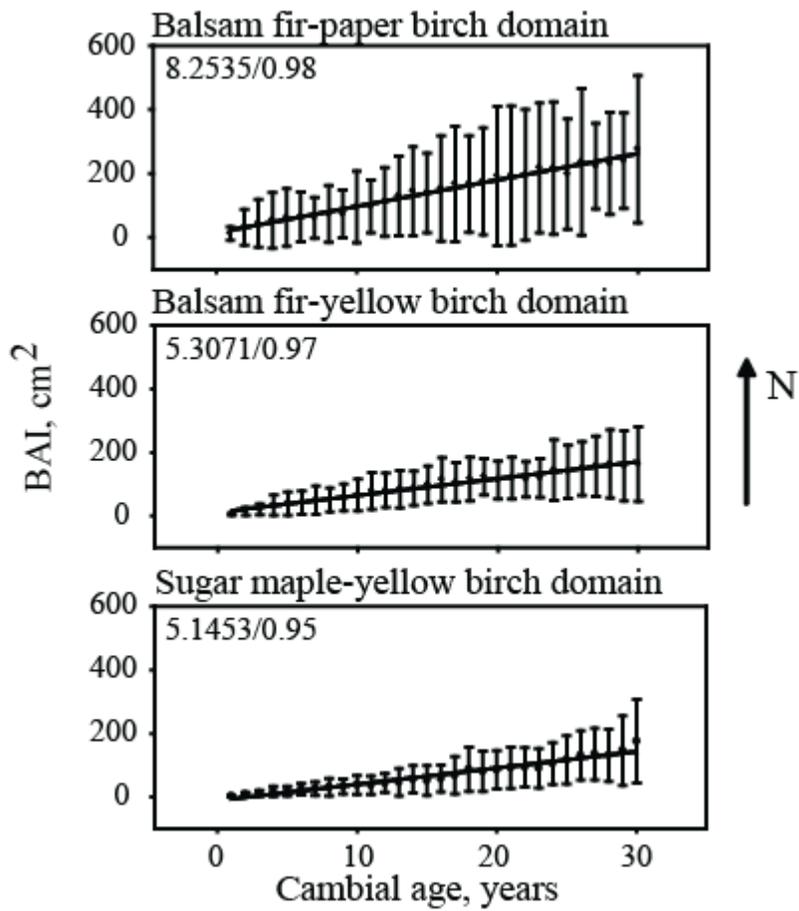


Figure 3.3. Mean diameter growth rate along the latitude and linear regression between them.

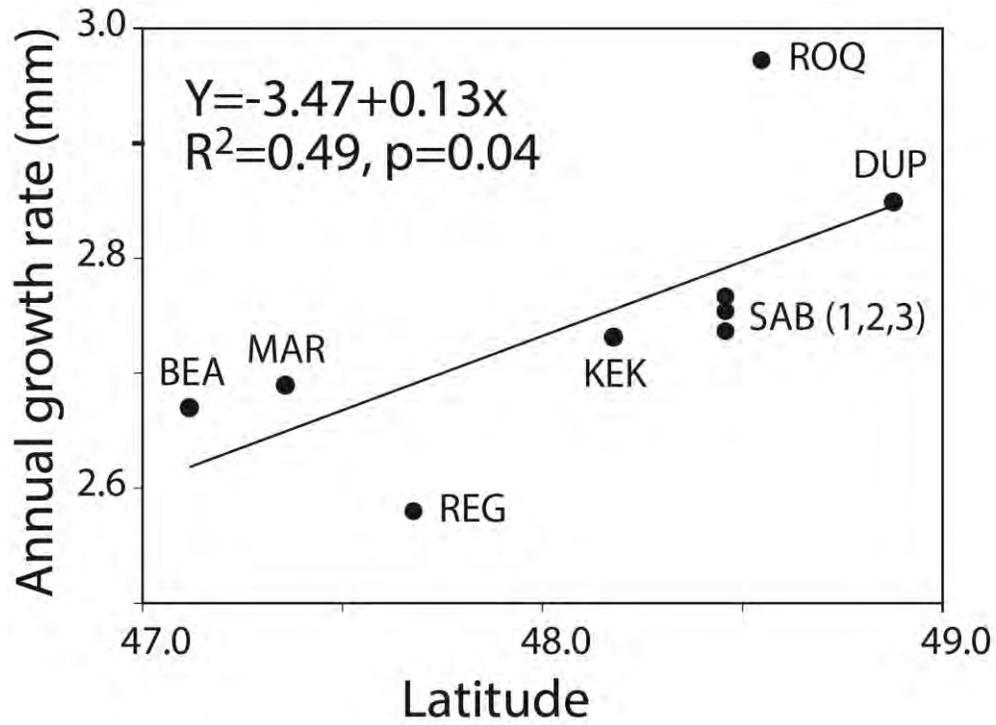
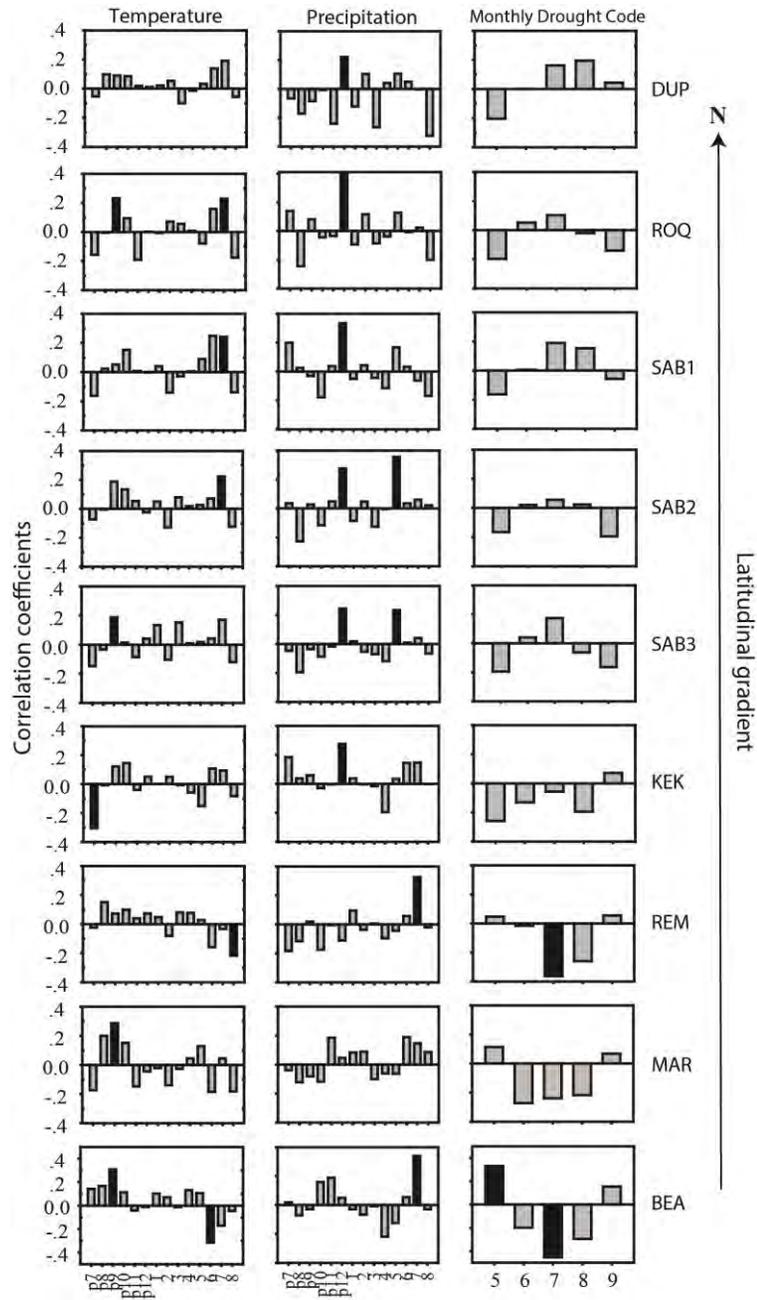


Figure 3.4. Pearson product-moment correlations (r) of the response function analysis for red maple from previous year July to current year August for the period 1965-2009 at its northern limit. A black bar indicates a significant relationship at $p = 0.05$.



3.9 APPENDICES

Appendix 3.1. Stand history and soil texture of red maple at the nine sites in western Quebec.

Site	Sand, %	Silt, %	Clay, %	Texture Class
DUP	95.5	1.0	3.5	Sand
ROQ	91.3	6.0	2.7	Sand
SAB1	92.5	4.8	2.8	Sand
SAB2	85.1	9.4	5.5	Sand
SAB3	90.3	7.0	2.7	Sand
KEK	87.5	12.2	0.2	Sand
REM	89.5	4.0	6.5	Sand
MAR	73.3	17.5	9.2	Sandy loam
BEA	95.5	1.5	3.0	Sand

Appendix 3.2. Soil chemical component of red maple at studied sites in western Quebec.

Sites	C total %	N total %	S total %	pH CaCl ₂	P mg/kg	K cmol(+)/kg	Ca cmol(+)/kg	Mg cmol(+)/kg	Mn cmol(+)/kg	Al cmol(+)/kg	Fe cmol(+)/kg	Na cmol(+)/kg	C.E.C. cmol(+)/kg
DUP	0.92	0.02	<0,01	4.08	10.86	0.06	0.42	0.11	0.02	14.34	2.66	0.03	17.63
ROQ	2.21	0.11	0.02	3.99	8.51	0.08	0.62	0.21	0.09	15.39	1.57	0.03	18.00
SAB1	1.77	0.06	0.01	3.04	16.05	0.06	0.17	0.12	0.00	4.88	0.60	0.03	5.86
SAB2	6.50	0.30	0.04	3.51	28.92	0.19	0.57	0.28	0.03	15.89	2.65	0.04	19.65
SAB3	6.38	0.34	0.06	3.87	13.05	0.18	0.28	0.21	0.02	19.51	2.14	0.04	22.39
KEK	8.15	0.45	<0,01	3.92	7.77	0.24	0.78	0.36	0.17	20.58	1.60	0.06	23.79
REM	3.53	0.18	0.04	3.82	2.84	0.10	0.73	0.36	0.01	18.15	2.11	0.03	21.51
MAR	3.82	0.21	0.03	4.01	23.35	0.16	0.78	0.33	0.05	17.08	2.22	0.06	20.69
BEA	1.50	0.05	0.01	4.20	161.73	0.17	1.49	0.48	0.11	15.00	3.01	0.03	20.30

GENERAL CONCLUSION

Climate and disturbances are major environmental controls of species distribution ranges, driving forest dynamics, and affecting forest productivity (Didier, 2001; Bergeron *et al.*, 2004; Boisvenue and Running, 2006; Laura Suarez and Kitzberger, 2010). Direct and indirect effects of recent climate warming on tree growth and recruitment have induced a profound change in forest structure (IPCC, 2007). An ecotone, as a transitional ecosystem between two biomes, may spatially exemplify the temporal changes in vegetation cover under the climate change. This observation points to the importance of understanding the response of ecotone vegetation to climate variability. This response can be partitioned as tree growth responses, changes in recruitment patterns, and finally spatial changes in ecotones positions.

The results of our studies suggest that distribution limits of studied species are affected by both direct climate control and indirect effects of climate (i.e., changes in natural disturbance regimes) on tree growth and recruitment. In this thesis, we studied an elevational gradient (750-1800 m) in northeastern China and a latitudinal gradient (46-48 °N) in western Quebec, both covering ecotones between mixed and coniferous forest, to evaluate environmental factors controlling ecotones dynamics and to project these responses over a wider temporal and geographical climate change contexts. In two study areas, both disturbances and climate were important in shaping structure and dynamics of ecotone vegetation. In the elevational ecotone of Changbai Mountain in northeastern China, gap phase dynamics driven by windthrows was the major factor maintaining coexistence of different conifers species. Our study suggested that changes in gap creation rates would induce changes in ecotone structure (Chapter I). Along the latitudinal gradient in western Quebec, fire frequency would be a crucial factor controlling red maple's northern distribution limit and, consequently, affecting forest structure in this transitional zone (Chapter III).

Following identification of the disturbance-related effects on forest ecotone, we evaluated the direct

effects of recent climate change on tree growth along the studied ecotones (Chapter II and Chapter III). All the three studied species showed temperature-sensitive at elevational upper (Changbai Mountain) or latitudinal northern limits (western Quebec), suggesting that warmer climate may favour trees growth. The results of these studies laid ground for the discussion of potential response of tree growth to future climate change and potential changes in position and structure of the studied ecotone in two study areas (Chapter I, II, and III).

CLIMATE EFFECTS ON TREE DISTRIBUTIONS AND ECOTONE POSITION

Climate affects species distributions by influencing growth rather than regeneration in Changbai Mountain (Chapter II), based on analyses of regeneration density, growth rate, and growth sensitivity. Our study showed little differences in regeneration density in two out of three studied species along the elevational gradient, but presented similar pattern of accumulative basal area increment (BAI) and growth sensitivity to climate. The observed highest BAI at the middle distribution range of respective three species, together with the high growth sensitivity to climate, indicated an important role of climate on biomass accumulation and, ultimately, on determining trees distribution limits. The three species were expected to move altitudinally upward under the current climate effects on growth, and as a consequence, the altitudinal position of broadleaf-Korean pine/spruce-fir ecotone may shift up. Our results supported conclusions of the previous studies which considered exclusively data on growth sensitivity to climate (Yu *et al.*, 2011; 2013; Wang *et al.*, 2013).

At northern margin range of red maple in western Quebec, annual variability in growth was sensitive to temperature in the north of transect and to moisture availability in the south. Mid-summer temperature (positive effects) and summer water deficiency (negative effects) were two important factors affecting maple growth in the north and south, respectively. In general, recent warming appeared to benefit frontier population of red maple. Similar results were also reported at red maple's northern limit in northeastern Ontario (Pinto *et al.*, 2008) and eastern Quebec (Duchesne and Ouimet,

2008; Duchesne and Prévost, 2013). However, if increases in precipitation no longer compensate increases in temperature, as a consequence, inducing higher fire frequency, it may offset positive influences of direct effects of climate warming on maple's northern extension.

Annual growth variability showed significant correlations with temperatures and precipitation in both study areas, suggesting that future changes in climate would have profound effects on tree growth and ecotone vegetation structure. Our study indicated that in Changbai Mountain, all the three species may benefit from a warmer climate at their respective upper limits, but more severe drought in autumn may limit the growth at their lower limits. The results suggested an upward shift of three species at their upper limits and a retreat at their lower limits in future. As a consequence, the position of studied ecotone may shift upward. In western Quebec, expected climate change would likely favor greater growth of red maple in the northern balsam fir-paper birch domain, while maple growth in balsam fir-yellow birch and sugar maple-yellow birch domains may face more stressful climate condition of summer drought.

DISTURBANCES EFFECTS ON ECOTONE STRUCTURE

In the Chapter I, the results suggested that windthrows were the major disturbances affecting the dynamics of broadleaf-Korean pine/spruce-fir ecotone in Changbai Mountain. Over the period 1770-2000, we found frequent small-scale disturbances (the size was 100-250 m²) and two medium-scale disturbance events occurred in 1920s and 1980s (1000 m²) in the studied ecotone, and canopy gap was the primary source of small- and medium-scale disturbances. An analysis of recruitment pattern and growth release showed differences in response to the disturbances among species. Our results indicated that the current disturbance regime of the studied ecotone maintained coexistence of light-demanding and shade-tolerant species.

Considering the results in a larger spatial context, we conclude that changes in wind climate may be particularly important for future forest composition not only in studied forest ecotone but also across the entire forest ecosystem in Changbai Mountain.

Similar to Changbai Mountain, disturbance (fires) was also important in affecting forest structure (Bergeron *et al.*, 1998) in boreal and mixedwood transitional zones of western Quebec. In the chapter III, the analyses of growth patterns of red maple demonstrate that stand history of local site may override the direct effects of climate on maple growth at its northern distribution limit in western Quebec. We found a consistent pattern of initial growth (first 30 years), adult tree growth (recent 10 years), and average growth of whole tree lifespan showing increased growth rates towards the north, suggesting that maples, which recruited after stand replacing fire in the north, appeared to benefit higher levels of light for growth than those of gap-origin in the south. Although our result showed a higher growth rate of red maple in post-fire stands and red maple can sprout vigorously after fire (Walters and Yawney 1990), in a long run, fires may limit red maple's maintenance at landscape scale. Even moderate fire can kill adult maples due to their thin barks (Walters and Yawney 1990), and frequent fires may cause the extinction of local population and reducing the possibility of colonizing in the new site (Tremblay *et al.*, 2002). Therefore, we believe that decreased fire frequency since the end of Little Ice Age (1850) in this mixed forest zone (Bergeron and Archambault, 1993) may positively affect red maple's development at its northern limit.

Our results pointed out the important role of disturbance regimes in influencing forest structure of ecotones through affecting species distribution, and were consistent with previous research in similar transitional areas. In deciduous-boreal transitional zone of Canada, fires and insect outbreaks were two important disturbance agents affecting forest structure. Low fire frequency and small fire area were suggested to be limiting factor for the northern expansion of Jack pine (*Pinus banksiana* Lamb.) (Asselin *et al.*, 2003). The northern distribution limits of both red pine (*Pinus resinosa* Ait.) and whit

oak (*Quercus alba*) were related to fire regime (Flannigan and Bergeron, 1998; Tardif *et al.*, 2006). Recent spruce budworm outbreak (1972–1986) favored widespread of red maple in the northern temperate zone of Quebec (Duchesne and Ouimet 2008). Another example is from mixed-boreal forest ecotones in Grand Canyon of US. Frequent and severe fires used to favor establishment and growth of shade-intolerant ponderosa pine and aspen species (Wolf and Mast, 1998; Fulé *et al.*, 2000). Subsequent cessation of the mixed-severity fires resulted in increased density and distribution of shade-tolerant conifer species, and a shift in composition from mixed conifer to encroachment of subalpine species (White and Vankat, 1993; Fulé *et al.*, 2002; Mast and Wolf, 2006).

Potential changes in disturbance regimes in two studied areas will likely affect respective forest structure. In northeastern China, frequency of extreme climate events such as windstorms will likely increase in the future (IPCC 2007). This will likely increase the frequency of medium and large-scale wind disturbances across the forest of northeast China. In Changbai Mountains, such a trend would lead to an increase in proportion of light demanding species in the canopies of broadleaf-Korean pine/spruce-fir forest ecotone, including Korean pine (*Pinus koraiensis* Siebold et Zuccarini.) and Olga Bay larch (*Larix olgensis* Henry.). In western Quebec, a predicted increase in fire frequency (Bergeron *et al.*, 2010) could restrict red maple's distribution range even a retreat at species northern limit.

IMPLICATIONS IN ANALYZING UNPUBLISHED DATA (CHAPTER IV)

Chapter I, II, and III have demonstrated the importance of both disturbance and climate effects on tree growth and forest dynamics at the transitional zones in two study areas. These results provide us a good idea to combine climate, disturbance, and other factors like topography and competition to investigate the contribution of each factor in species distribution at their distributional limits.

Understanding what drives species distributions is a fundamental goal in forest ecology (Gilbert *et al.*, 2004). Climate, topography, disturbance, and competition are all factors affecting species distributions

and forest composition (Archer and Smeins, 1991; Bergeron *et al.*, 1997; Pickering *et al.*, 2008). Climate is often considered as the main factor determining species distributions and thus climate change substantially affects dynamics of forest ecosystems (Hamann and Wang, 2006). Many studies have demonstrated shifts in species distribution range with respect to climate change (Beckage *et al.*, 2008; Leithead *et al.*, 2010). However, large-scale climate variables can not account for the spatial distribution of species at a local scale since variations of microenvironment occurs across landscape, and topography significantly affects species distributions through regulation of microclimate and soil condition (Archer and Smeins, 1991). Furthermore, disturbance and competition can also modify species distributions based on species own characteristics (Bergeron, 2000; Asselin *et al.*, 2003). Therefore, understanding relative contribution of factors affecting species distributions can help us better understand future forest dynamics in the context of global warming.

In the Chapter IV, we aim to identify respective contributions of investigated factors that may affect red maple distribution at its northern distributional limit, by 1) investigating recruitment pattern of red maple in post-fire stands; 2) examining growth rates and climate-growth relationships of red maple along a short altitudinal gradient (100 m); 3) evaluating relationship between microenvironment (topographic attributes and micro-temperature) and maple performance over a 50 ha mountain area. We hypothesize that 1) cold temperature is limiting factor for tree growth and recruitment, i.e. positive correlations between growing-season temperatures and growth as well as establishment; 2) red maple has higher abundance of seedlings and saplings at the sites with warmer temperature due to their sensitivity to frost.

POTENTIAL CHANGES IN FOREST STRUCTURE AT ECOTONES

Analyses of climate-growth relationships and disturbance effects on tree growth, combined with our discussion of effects (both direct and indirect) of future climate change on growth, may allow us to infer potential changes in forest structure of studied ecotones. In Changbai Mountain,

broadleaf-Korean pine/spruce-fir ecotone will likely be rearranged due to changes in optimal-climate and microhabitats. Direct increases of temperatures may cause an upward shift of Korean pine at upper edge of the studied ecotone and a retreat of Jezo spruce (*Picea jezoensis* Carr) at ecotone's lower edge. Furthermore, increases in wind events may create more open habitats in favouring mid-tolerant Korean pine rather than shade-tolerant Jezo spruce. Therefore, we may expect a higher abundance of Korean pine and lower abundance of Jezo spruce, accompanied with an upward shift of the elevational position of this ecotone. In western Quebec, the future northern limit of red maple seems to be a product of direct climatic and disturbance-mediated effects on its recruitment and growth. Although warmer climate would benefit frontier population of red maple, increases in fire activity may offset this positive influence due to its overriding effects on maple distribution.

Many efforts have been made to model biome-level changes at both temperate and boreal regions (Sykes *et al.*, 1996; Koca *et al.*, 2006; Xu *et al.*, 2007). Simulating upward/northward expansion of deciduous forest is complex and should consider effects of climates, disturbance regimes, seed dispersal, and soil process. A northward movement of deciduous forest into southern boreal forest has been modeled in deciduous-boreal transitional zones in Scandinavia (Prentice *et al.* 1991), East Asia (Zhang *et al.* 2009), and North America (Frelich and Reich, 2009). However, a few field-based empirical studies have been carried out (Goldblum and Rigg, 2002). Therefore, our study would certainly add contribution to improve the simulation of future forest dynamics in such transitional zones. A previous study combined gap model (linkages) and landscape model (LANDIS) to predict responses of forest ecosystem to warming climate in Changbai Mountain (He *et al.*, 2005), and they reported that Korean pine, Jezo spruce, and Manchurian fir would disappear at lower elevations and finally replaced by broadleaved species, but it would take longer time than the time periods predicted by the gap models (considering climate effects only). Our empirical data, suggesting upward shifts of major conifer species and position of the studied ecotone, agreed the simulation result in a certain degree, although we could not estimate exactly time period causing forest transition.

IMPLICATIONS FOR FOREST MANAGEMENT

Potential changes in the forest structure of ecotone may provide guidance for the management strategies, although field experiments more focused on different silvicultural options are needed to translate results of the current study into a practical context. Our results suggested that the main species of broadleaf-Korean pine/spruce-fir ecotone in Changbai Mountain coexisted due to interspecific differences in shade tolerance and growth response to canopy disturbances. In particular, the establishment of Korean pine was mainly associated with multiple-tree fall gaps, while Jezo spruce and Manchurian fir were able to recruit in single-tree fall gaps or under the canopy. Our results argue for promoting Korean pine regeneration by creation of large canopy gaps. This is in line with group-selective cutting system developed for the better conservation and utilization of this high value species and of natural forest resources in northeastern China (Yu *et al.*, 2011). We also suggest that the creation of smaller gaps may be necessary for the regeneration and growth of shade-tolerant Jezo spruce and Manchurian fir.

In Quebec, creation of canopy gaps (400-600 m²) can be viewed as a way to increase the presence of red maple in the mixed boreal landscapes. Red maple responds positively to gap opening (Fei and Steiner, 2009; Duchesne and Prévost, 2013). In addition, light-intensity burning can be used to increase the abundance of red maple due to its ability to sprout vigorously after fire (Walters and Yawney, 1990). However, frequent and intense burning strategy is not recommended to spread maple distribution, since it could limit sexual regeneration level by killing adult trees and consequently, causing longer dispersal distances and reducing possibilities of colonizing new sites (Tremblay *et al.*, 2002).

Altogether, my Ph.D. study focuses on the growth dynamics of main tree species in the deciduous forest-boreal forest ecotones, where little effort has been made to understand its successional dynamics (Goldblum and Rigg, 2010). The findings reported in this thesis should contribute to

improve our understanding in tree growth response to climate and disturbance regime at forest-forest ecotones, and vegetation dynamics under global warming. Hence our study would be a good template for exploring factors (climate and disturbance) determining trees distributions and ecotone position in other temperate-boreal regions of the Northern Hemisphere. This could aid us to quantitatively assess potential changes in forest composition across Mountain or high-latitude ecosystem of the Northern Hemisphere, which in turn may help us to make long-term strategies for the sustainable forest management in such transitional zones.

REFERENCES IN GENERAL INTRODUCTION AND CONCLUSION

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