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MODELING THE EFFECTS OF FOREST MANAGEMENT AND CLIMATE CHANGE ON CARBON DYNAMICS IN CANADA'S BOREAL FORESTS

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PREFACE

This dissertation is comprised of six chapters (four main papers) that present and discuss the effects and implications of forest management on carbon dynamics in the boreal forest under climate change. All four papers involved in the dissertation are my original contributions to my Ph.D. study in Environmental Science at Université du Québec à Montréal.

Chapters I and VI are the general introduction and general conclusion, respectively. Chapters II to V are correspondingly based on the following four publications:

1. **Wang, W.**, Peng, C., Zhang, S.Y., Zhou, X., Larocque, G.R., Kneeshaw, D.D. & Lei, X. (2011) Development of TRIPLEX-Management model for simulating the response of forest growth to pre-commercial thinning. *Ecological Modelling,* **222,** 2249-2261.
2. **Wang, W.**, Peng, C., Kneeshaw, D.D., Larocque, G.R., Lei, X., Zhu, Q., Tong, Q. & Song, X. (2011) Modeling the effects of various forest management regimes on carbon dynamics in jack pine stands under future climate., *Canadian Journal of Forest Research,* (**Accepted after revision**)
3. **Wang, W.**, Peng, C., Kneeshaw, D.D., Larocque, G.R., Song, X. & Zhou, X. (2012) Quantifying the effects of climate change and harvesting on carbon dynamics of boreal aspen and jack pine forests using the TRIPLEX-Management model. *Forest Ecology and Management,* **281**. 152-162
4. **Wang, W.**, Lei, X., Ma, Z., Kneeshaw, D.D. & Peng, C. (2011) Positive relationship between aboveground carbon stocks and structural diversity in spruce-dominated forest stands in New Brunswick, Canada. *Forest Science,* **57,** 506-515.

I developed all hypotheses with my Ph.D. supervisor, Dr. Changhui Peng. I designed the new forest management sub-model under the framework of TRIPLEX and programmed the model code with C++. After the model development, I conducted the model validation and data analysis as well as published five peer-reviewed journal papers (first author) and the dissertation. Dr. Daniel Kneeshaw and Dr. Guy Larocque constantly advised and discussed with me about my Ph.D. project, and commented on early versions of the manuscripts and this dissertation. Dr. Xiangdong Lei discussed and commented on the initial versions of the manuscripts for Chapter II, Chapter III, and Chapter V. Dr. Xiaolu Zhou helped to explain the model code and discussed the programming problems. Dr. Qiuan Zhu compiled the climate data used in Chapter II and III. Dr. S. Y. Zhang and Dr. Queju Tong provided the forest thinning data used in Chapters II and III. Dr. Xinzhang Song discussed and commented on early versions of the manuscripts in Chapters III and IV. All coauthors contributed comments and suggestions, greatly improving the quality of the papers.

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RÉSUMÉ

Les changements climatiques et ses effets potentiels sur les systèmes environnementaux renforcent la nécessité de stratégies de gestion forestière qui augmentent l'adaptabilité et la capacité de séquestration du carbone (C) forestier. Un modèle qui évalue avec précision les changements dans la productivité des forêts et des stocks de C en réponse aux changements climatiques et la gestion des forêts va nous permettre d'évaluer l'impact des changements globaux sur les forêts.

L'objectif de cette thèse était d'améliorer la compréhension de la façon dont les forêts existantes séquestrent une plus grande quantité de C à cause des changements climatiques mondiaux au moyen de stratégies d'aménagement forestier. Tout d'abord, un module de gestion des forêts incluant un modèle (TRIPLEX) basé sur les processus a été développé pour quantifier les effets des pratiques d'aménagement forestier (coupes d'éclaircie et coupes à blanc) sur la croissance des forêts, le rendement du bois et la séquestration du C en réponse à des conditions climatiques pour les forêts de pin gris (*Pinus banksiana* Lamb.). Ce modèle récemment mis au point (TRIPLEX-Management) a ensuite été utilisé pour étudier les moyens d'accroître la séquestration du C dans les forêts de pin gris en utilisant la gestion des forêts exploitées par l'industrie forestière pour la production de bois à long terme. Pour accroître la crédibilité et l'applicabilité du modèle, il a été validé par rapport à des sources de données multiples (mesures de *eddy covariance*, de stocks de C et de données de croissance d'arbres) et, par la suite, a été utilisé dans la projection des effets potentiels des changements climatiques et des coupes à blanc sur la dynamique du C de la forêt boréale (*Populus tremuloides* Michx.) et des forêts de pin gris. Finalement, les relations entre la diversité structurelle et les stocks de C dans les forêts dominées par l'épinette ont été examinées par analyse de corrélation, de régression linéaire multiple et de corrélation partielle.

Dans le développement du modèle, la validation de ce dernier a montré que le « TRIPLEX-Management » a été généralement capable de simuler la réponse de croissance aux éclaircies pré-commerciales des peuplements de pins gris. Dans l'analyse des scénarios de gestion forestière, les résultats des simulations ont montré que les rotations courtes (10-20 ans par exemple) pourraient améliorer l'absorption du C et diminuer le risque des changements climatiques sur les forêts de pin gris. Les effets positifs des forêts éclaircies sur la production de bois ont été éliminés par le réchauffement climatique. En outre, un éventuel changement climatique sur la limite sud de la forêt boréale en Amérique du Nord pourrait améliorer le taux de séquestration du C s'il n'y avait pas d'épisodes de sécheresse sévère. Dans les forêts dominées par l'épinette, l'analyse statistique pour 411 placettes-échantillons permanentes a confirmé que la diversité structurelle du peuplement a eu un effet positif significatif sur les stocks de C hors sol, même si la relation était faible dans l'ensemble (les coefficients de corrélation de Spearman sont généralement de l'ordre de 0,319–0,600, P<0,01).

En résumé, cette thèse présente une tentative d'améliorer notre compréhension du rôle de la gestion des forêts dans l'atténuation et dans l'adaptation des forêts aux changements climatiques. En conséquence, le raccourcissement de l'âge de rotation peut être nécessaire pour les forêts de trembles et de pins gris dans le but d'augmenter la séquestration du C pour une échelle donnée temporelle, et diminuer le risque des impacts des changements climatiques. Le maintien de la complexité de la composition et de la structure peut aider les forêts à s'adapter aux futures conditions environnementales et à absorber les perturbations (par exemple, les insectes, les maladies, les incendies, ou les sécheresses). Cette thèse a des implications pratiques pour l'utilisation de stratégies d'aménagement forestier pour atténuer les effets des changements climatiques futurs.

Mots-clés: distribution des diamètres, gestion des forêts, gestion du carbone, hypothèse de la complémentarité de niches, indice del Shannon-Wiener, analyse de scénarios, durée de la rotation

ABSTRACT

Climate change and its potential effects on environmental systems bolster the need for forest management strategies that increase forest carbon (C) sequestration capacity. A model that accurately evaluates changes in forest productivity and C stocks in response to climate change and forest management will permit us to assess the impact of global changes on forests.

The aim of this dissertation was to improve our understanding of how existing forests sequester a greater amount of C by means of forest management practices. Firstly, a novel forest management module within the framework of a process-based model (TRIPLEX) was developed to quantify the effects of forest management practices (thinning and harvesting) on forest growth, timber yield, and C sequestration in response to climatic conditions for jack pine (*Pinus banksiana* Lamb.) forests. This newly developed model (called TRIPLEX-Management) was then used to investigate how to increase C sequestration within jack pine forests under climate change using forest management that are also exploited by the forestry to produce wood products. To increase the model credibility and applicability, the model was validated against multiple data sources (eddy covariance data, C stocks, and forest growth data) and, subsequently, was used for the projection of potential effects of climate change and clearcuts on C dynamics of boreal trembling aspen (*Populus tremuloides* Michx.) and jack pine forests. Finally, the relationships between the structural diversity and C stocks in spruce-dominated stands were investigated using correlation analysis, multiple linear regressions and partial correlation analysis.

Model validations showed that the TRIPLEX-Management model was generally capable of simulating C dynamics and ecosystem responses to forest management and climatic conditions for aspen and jack pine forests. In the forest management scenario analysis, simulation results showed that shortening rotation length (for example, 10-20 years) could enhance C uptake and decrease the potential risk of climate change on jack pine forests. The positive effects of forest thinning on wood production were enhanced with modest warming, but eliminated with warmer climate. Moreover, potential climate change may enhance the C sequestration rate if there were no severe natural disturbances. In spruce-dominated forests, statistical analysis confirmed that stand structural diversity had a significant positive effect on aboveground C stocks even though the relationship was weak overall (Spearman's rank correlation coefficients are generally in the range of 0.319–0.600, $P<0.01$).

Altogether, this dissertation presents an attempt to improve our understanding of forest management role in forest mitigation to climate change. As a result, shortening rotation age may be necessary for aspen and jack pine forests in order to increase C sequestration for a given temporal scale and decrease the risk of climate change impacts. Maintaining complexity of composition and structure can help forests to adapt to future environmental conditions. This dissertation has practical implications in terms of using forest management strategies to mitigate potential climate change.

Keywords: clearcut logging, diameter distribution, forest management, niche complementarity hypothesis, Shannon-Wiener index, carbon management, soil organic carbon, rotation length, scenario analysis

CHAPTER I

GENERAL INTRODUCTION

1.1 Background

1.1.1 Climate change and the boreal forest

Future global warming is largely constrained by emissions of carbon (C) dioxide (CO_2) due to fossil fuel burning and land use changes (Allen *et al.*, 2009, Matthews *et al.*, 2009). The amplitude of temperature increase is largely dependent on anthropogenic emissions of CO_2 and on C sequestration by the oceans and the land biosphere (Friedlingstein *et al.*, 2001; IPCC, 2007). The world's forests have strong controls on the global C cycle (the exchange of C between the biosphere, hydrosphere, geosphere, hydrosphere, and atmosphere of the Earth) and influence the hydrological cycle and energy budgets between the atmosphere and terrestrial ecosystems (Bonan, 2008, Chapin *et al.*, 2008).

The boreal forest, the second largest biome in the world, contains 33% of the Earth's forest cover. Boreal forests are vulnerable to global warming, and have an important role in C storage and subsequently, are identified as an important "tipping point" for the Earth's climate system (Lenton *et al.*, 2008). The climate forcing of boreal forests is highly uncertain. Low surface albedo may warm global climate (Bonan, 2008), but snow-covered boreal forest with high surface albedo during long winters may offset this warming effect (Chapin *et al.*, 2008). The cooling effects (moderate C storage and weak evaporative cooling) might be large enough to result in an overall cooling effect of boreal forests on global warming. The boreal forest stores 272 Pg C in trees and in the soil (to 1m depth) and is sensitive to climate (Pan *et al.*, 2011), although its C uptake ability is low (Bonan, 2008).

The forest is under large pressure from global climate change. Under climate change, more frequent droughts, fires, and insect outbreaks may lead to regional reductions in forest productivity (Ciais *et al.*, 2005, Zhao and Running, 2010) and even large-scale boreal forest die-off (Peng *et al.*, 2011, Kurz *et al.*, 2008). As a result, regional droughts may lead to reductions of the forest C sink (e.g., Ma *et al.*, 2012, Michaelian *et al.*, 2011). Research in Canada has shown that droughts may be having caused the reduction of 7.89±3.22 Mt year^{-1} in the C biomass of Canadian boreal forests since 1963 (Ma *et al.*, 2012). With future global warming and drying, more frequent fires have been identified as a potential in most boreal forests (Bond-Lamberty *et al.*, 2007, Harden *et al.*, 2000). A modeling study conducted by Amiro et al. (2009) estimated that the emissions of greenhouse gases from Canadian wildfires would increase from 162 Tg yr^{-1} of CO_2 equivalent to 312 Tg yr^{-1} of CO_2 equivalent under future climate change. Insect outbreaks have also recently become more severe, resulting in large C losses from forests due to tree mortality (Hicke *et al.*, 2012). In western Canada, a massive outbreak of mountain pine beetle (*Dendroctonus ponderosae* Hopkins, Coleoptera: Curculionidae, Scolytinae) has killed millions of trees weakened by droughts across 130, 00 km^2 of forest in multiple years (Kurz *et al.*, 2008), and possibly moved eastwards. In eastern Canada, spruce budworm (*Choristoneura fumiferana* Clem.) –caused mortality was estimated to decrease ecosystem C stocks by 2-10% by the end of simulations (2024) (Dymond *et al.*, 2010).

Elevated atmospheric CO_2, rising temperature, and elevated nitrogen (N) deposition may enhance forest C sequestration if other growth factors such as water are not limiting (Hyvonen *et al.*, 2007, Luo *et al.*, 2006, Boisvenue and Running, 2006, Reay *et al.*, 2008, Huang *et al.*, 2007). Elevated atmospheric CO_2 could enhance photosynthetic CO_2 fixation (Huang *et al.*, 2007), even if recent studies reported that the effects of CO_2 fertilization on forest productivity might still be constrained by limited N availability and/or water limitation (Peñuelas *et al.*, 2011, Silva *et al.*, 2010, Reich *et al.*, 2006, Norby *et al.*, 2010). Furthermore, modest warming will enhance forest productivity due to a longer growing season and increased metabolic rates in boreal forests (Myneni *et al.*, 1997, Nemani *et al.*, 2003). Future increases in N deposition could also increase N availability, thus enhancing forest growth in N-limited forest ecosystems (Hyvonen *et al.*, 2007, Reay *et al.*, 2008). In addition, the interactions of these stabilizing factors are likely to increase the availability of soil moisture, decrease fire frequency, and enhance forest growth and biomass (Lenton *et al.*, 2008).

1.1.2 The roles of sustainable forest management under climate change

Climate change has resulted in potentially dangerous impacts on global boreal forests (Section 1.1.1). With the common concern surrounding the impacts of climate change on forests, there has been much debate on the role of forest management on adaptation and mitigation to climate change. The Kyoto Protocol to the United Nations Framework Convention on Climate Change (UNFCCC) provides an opportunity for some countries to claim for large C sinks from land use, land use change, and forestry (LULUCF), and use the C sinks to offset their fossil fuel emissions. Under *Article 3.4* of the Protocol, the forestry community proposed two ways for existing forests to face the challenge of changing climate (Millar *et al.*, 2007, Seidl *et al.*, 2007): (1) mitigation strategies that use forest ecosystem to reduce overall greenhouse gas (GHG) emission via enhancing forest C sequestration and reducing fossil fuel burning; and (2) adaptation strategies that help forest ecosystems accommodate new climate conditions.

1.1.2.1 Mitigation strategies

It has been proposed that forest management can be used in climate change mitigation strategies by (i) increasing C sequestration (stored both on-site and in long-lived wood products) (e.g., Thornley and Cannell, 2000, Seidl *et al.*, 2007, Lasch *et al.*, 2005); and by (ii) substituting fossil fuels with bioenergy from wood residues (e.g., Malmsheimer *et al.*, 2008, Hudiburg *et al.*, 2011).

Forest management can play a key role in climate change mitigation. Much effort has been invested in evaluating how to increase C sequestration (stored both on-sites and off-sites) (Seidl *et al.*, 2007, Thornley and Cannell, 2000, Hudiburg *et al.*, 2011), even if wood product C pools are not accounted for in the guidelines of the first commitment period under the Kyoto Protocol. Common sense dictates that any reasonable assessment of the role of the forests in global, national, or regional C cycles should include the consideration of C stored in forest products (Hennigar *et al.*, 2008), given that harvested wood products contain large amounts of C (Malmsheimer *et al.*, 2008, Chen *et al.*, 2008, Apps *et al.*, 1999). Based on the approach of life cycle analysis, the tradeoffs of various harvested wood products in global change mitigation need to be analysed (McKechnie et al. 2011).

Previous studies have demonstrated that unmanaged forests, such as old-growth forests, stored greater amounts of C in trees and in the soil (Pregitzer and Euskirchen, 2004), and that they are still continuing to capture C (Luyssaert *et al.*, 2008). In order to increase C sequestration, therefore, prolonging rotation length has been recommended as a useful way to increase C sequestration on-sites (e.g., Nunery and Keeton, 2010, Peng *et al.*, 2002, Kaipainen *et al.*, 2004, Liski *et al.*, 2001). Longer rotation lengths (> 90 years) in European boreal forests have been suggested to benefit C sequestration (Liski *et al.*, 2001, Kaipainen *et al.*, 2004). On the contrary, shortening rotation ages and replanting with robust genotypes has been proposed as management options for adaptation to climate change in Canada (Johnston *et al.*, 2009). Forest thinning has been suggested as a silvicultural intervention to enhance diameter growth and individual stem volume growth for residual trees due to relatively high resource availability (e.g., Tong *et al.*, 2005, Simard *et al.*, 2004, Lei *et al.*, 2007). On the contrary, research in Finland suggests that unthinned stands may produce higher merchantable volume than thinned stands (Mäkinen and Isomäki, 2004a, Mäkinen and Isomäki, 2004b). Therefore, many uncertainties remain concerning the effects of forest management on C sequestration.

Substitution of fossil fuel with bioenergy from forests has been recognized as a strategy to reduce CO_2 emissions from burning fossil fuel (Gustavsson *et al.*, 1995). Forest regeneration on the harvest site can help to achieve zero emissions in a given temporal scale (McKechnie *et al.* 2011, Ter-Mikaelian *et al.* 2011). The potential of bioenergy production to offset CO_2 emissions is counteracted by fossil fuel emission from the relative activities (e.g., forest harvest and biomass transportation) (Law and Harmon, 2011). There are also large uncertainties in impacts of biofuel removal on forest nutrient dynamics and growth.

1.1.2.2 Adaptation strategies

Adaptation strategies include resistance options, resilience options, and response options (Millar *et al.*, 2007). Practices designed to increase resistance (e.g., fuel breaks and intensive removal of invasive species) are likely to improve the defences of forests against the impacts of rapid environmental changes (Millar *et al.*, 2007). The forest response option is more likely to help forests to quickly accommodate or respond to environmental changes (Millar *et al.*, 2007). Improving forest resilience is the most commonly suggested adaptive option in current debates, but more focus needs to be put on improving the ability of forests to return to pre-existing conditions after disturbance (Millar *et al.*, 2007). A number of recent studies on forest adaptation have focused on maintaining a high diversity of species composition and structure to maintain a high productivity (Johnston *et al.*, 2009, D'Amato *et al.*, 2011, Malmsheimer *et al.*, 2008, Evans and Perschel, 2009). As such, forests might be able to adapt to future environmental conditions and to absorb disturbances (e.g., insects, disease, fires, or droughts).

1.2 Modeling forest management activities

Forest resource managers are facing challenges such as assessing the vulnerability of forests to climate change, evaluating forest response to natural disturbance (e.g., droughts), and quantifying the effects of various forest management strategies on net C sequestration under climate change. A new approach is to make use of forest simulation models in order to make decisions that satisfy long-term strategies for adaptation and mitigation to climate change (Peng, 2000).

The models used in simulating forest development can be classified into empirical growth and yield models and process-based models (also called physiological models that can simulate key ecosystem processes regarding C, N, and water cycling). Traditional growth and yield models used in forestry are generally based on statistical relationships. However, these models only work well as management tools for forecasting stand growth when environments do not change or change minimally. Thus such models are not suitable for long-term prediction of forest development under changing climate conditions. In comparison, process-based models are able to simulate key ecosystem processes related to C, N, and water cycles under a changing condition of climate. Therefore, process-based models have great potential in investigating impacts of forest management activities and climate change on forest C dynamics (Johnsen *et al.*, 2001, Mäkelä *et al.*, 2000, Landsberg, 2003, Pretzsch *et al.*, 2008). However, the use of most such models has been limited by the absence of flexible forest management practices.

1.2.1 Modeling forest thinning

Forest thinning has been suggested as a cost-effective and sustainable strategy to enhance diameter growth and individual stem volume growth for remaining trees due to the relatively high resource availability and the decreased risk of wildfire (Huggett *et al.*, 2008). As one of the most important silvicultural practices, thinning has been applied to hundreds of thousands stands across the world each year (Masek *et al.*, 2011). However, thinning would not necessarily increase the overall forest C stock, as the C of the increased growth of remaining trees might be less than the removed C of the thinned trees (e.g., Tong *et al.*, 2005, Lei *et al.*, 2007). Thus, it is important to quantify the effects of forest thinning on C dynamics for given forest conditions under a changing climate. This can be done by developing a thinning sub-model to evaluate how forest thinning operations affect stand development.

Within the context of climate change, two methods have been proposed for simulating stand structure for forest management consideration (Table 1.1): (i) incorporating empirical diameter distributions into process-based models (e.g., Lasch *et al.*, 2005, Bellassen *et al.*, 2010); and (ii) a cohort approach (all trees of a given species established in a given year are assumed to be identical). Much effort has focused on quantifying stand structure by incorporating typical diameter distribution model for management purposes. For example, Lasch et al. (2005) analyzed management effects on forest functions at a regional level in Germany, using a process-based model, 4C, that has a Weibull diameter distribution incorporated in the forest thinning algorithms. In addition, a forest management syb-model has been developed within a dynamic global vegetation model, ORCHIDEE (Krinner *et al.*, 2005), where forest thinning is simulated based on an initial distribution calculated from a truncated exponential law function and an allocation function to trees in each diameter class (Bellassen *et al.*, 2010).

Alternatively, the cohort method has also been investigated in simulating the effects of forest management on forest functions under climate change. Incorporated in a cohort approach, the FinnFor model (Kellomäki and Väisänen, 1997) was used to analyze the effects of thinning regimes on C sequestration (Garcia-Gonzalo *et al.*, 2007, Routa *et al.*, 2011, Ge *et al.*, 2011). The EFIMOD model also uses the cohort approach to simulate different types of thinning (Chertov *et al.*, 2009, Palosuo *et al.*, 2008, Komarov *et al.*, 2003).

Table 1.1 Forest management algorithms from a selection of the most commonly used process-based models, listed approximately in order of progressive increase in mechanistic detail.

Forest management algorithms	Description	Model	Reference
Forest thinning			
Biomass reduction	No explicit concept of stand structure. It is difficult to implement pre-commercial thinning or commercial thinning.	Biome-BGC	Petritsch *et al.*, 2007
Empirical diameter distribution	Incorporate traditional diameter distribution function. This does not affect the mechanical representation of ecological processes.	4C ORCHIDEE - FM	Lasch *et al.*, 2005 Bellassen *et al.*, 2010
Cohort	All trees of a given species established in a given year are assumed to be identical. Stand structure can be estimated by using stand age and diameter class.	FinnFor	Garcia-Gonzalo et al., 2007; Ge et al., 2011; Routa et al., 2011
		EFIMOD	Komarov *et al.*, 2003; Palosuo *et al.*, 2008; Chertov *et al.*, 2009
Harvesting e.g.			
Clearcuts	Import tree carbon in each component to corresponding litter carbon and soil carbon pools	Ecosys ORICHEED-FM	Grant *et al.*, 2010 Bellassen *et al.*, 2010

1.2.2 Modeling forest harvesting

Clearcuts, a common harvesting method in the boreal forest, remove almost all commercially sized trees (i.e. those trees greater than 9cm DBH [diameter at breast height]). This results in considerable amount of forest C loss not only by direct transfer of forest C to harvested wood C, but also by respiration losses if rates of heterotrophic respiration (litter and soil organic C decomposition) exceed net primary productivity (NPP) in the years following a clearcut. Many studies have found that negative net ecosystem productivity (NEP) may last for several years to decades in the early stages of stand development after clearcuts (e.g., Humphreys *et al.*, 2006, Zha *et al.*, 2009, Kolari *et al.*, 2004, Law *et al.*, 2001, Janisch and Harmon, 2002). The implications of harvest-related forest C loss highlight the importance of including harvesting in forest simulation to achieve a better understanding of regional and global C cycling (Liu *et al.*, 2011).

Clearcuts may occur at a prescribed rotation age or a prescribed threshold such as stand volume. Using a clearcut sub-model, it can be easily simulate in process-based models. When clearcuts occur, the merchantable portion of the trees is removed from the forests, while harvest residues are transferred to various dead organic C pools (e.g., woody debris and forest floor) (e.g., Bellassen *et al.*, 2010, Jiang *et al.*, 2002, Peng *et al.*, 2002, Shanin *et al.*, 2011). In some cases, a fraction of harvest residuals is left as slash piles, either burned or left to decay (Grant *et al.*, 2010, Jiang *et al.*, 2002, Peng *et al.*, 2002). After a clearcut, stand reestablishment has to be prescribed. In modeling, the reestablishment commonly has to meet a set default value of number of trees or initial biomass in each tree component.

In summary, process-based models can be used to investigate on how future climate change may affect forest C cycling across landscapes and forest types. With forest management sub-models, such as thinning and clearcut sub-models, the process-based models may provide insights into how current management practices can affect forest C dynamics.

1.3 General questions and hypotheses

There are two major weaknesses in the study of the role of forest management on C sequestration under future climate change. First, modeling forest thinning using the process-based models is highly uncertain due to the inaccurately prediction of stand structure. Second, there is no relatively strict model validation against multiple data sources (e.g., thinning experiment data, eddy covariance data, and C stocks).

To better understand the role of forest management on climate change mitigation, it is necessary to answer the following question:

> How should forests be managed to improve C sequestration to mitigate climate change?

In this thesis, I hypothesize that (1) climate change may enhance forest growth and C sequestration in the boreal forest, especially for pioneer tree species; (2) certain forest management strategies could favour C sequestration both on-site and off-site as well as decrease the potential climate change induced risk; (3) maintaining the complexity of species composition and structure could enhance forest C stocks.

1.4 Specific objectives and thesis structure

This dissertation is a combination of four manuscripts related to the investigation of the effects of forest management practices on forest C sequestration facing the challenge of changing climate. The main body of the thesis consists of two phases of research (Figure. 1.1.):

1) Quantifying the effects of forest management and climate change on forest C sequestration on-site and off-site using a process-based model (Chapters II, III, and IV);
2) Investigating the relationships between structural diversity and C stocks using statistical methods (Chapter V).

The specific objectives were as follows:

1) Chapter II: Develop a novel thinning sub-model to quantify the effects of pre-commercial thinning on forest growth, timber yield, and C sequestration in response to climatic conditions for jack pine (*Pinus banksiana* Lamb.) stands.

2) Chapter III: Investigate how to manage jack pine forests to increasing forest C sequestration when producing harvested woods for industrial purposes using the newly developed model (TRIPLEX-Management) in Chapter II.

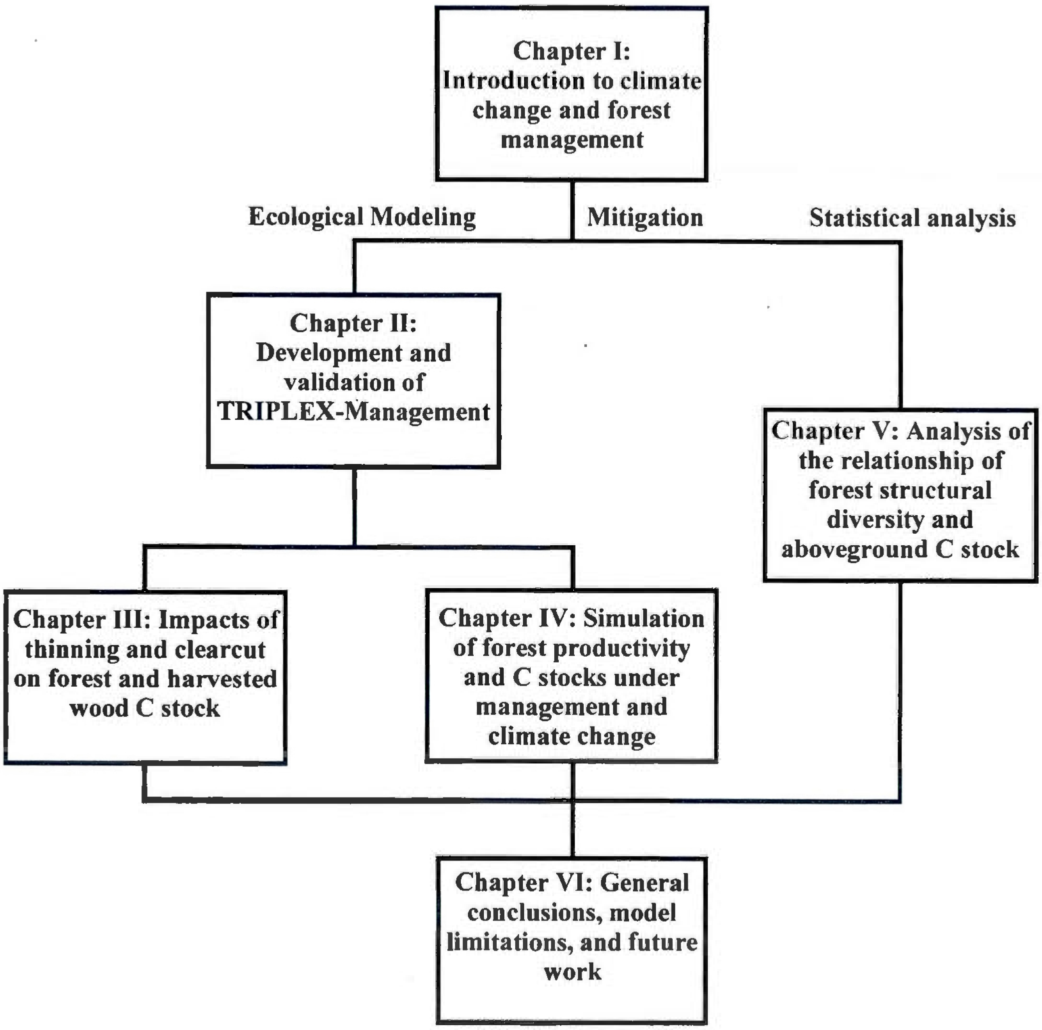

Figure 1.1 The structure of dissertation.

3) Chapter IV: Validate the TRIPLEX-Management model against multiple sources of measurement data; test whether the model is able to simulate the impacts of a drought between 2001 and 2003 on net ecosystem productivity of aspen (*Populus tremuloides* Michx.) and jack pine forests under a continental boreal climate; and predict the potential effects of future climate change and clearcut practices on net ecosystem productivity and total ecosystem C stock.

4) Chapter V: Investigate the relationship between structural diversity and C stocks in spruce-dominated stands and discusses potential management implementations of increasing C storage by enhancing stand structural diversity in such forests.

Note: This dissertation was written in the form of a collection of published or submitted peer-reviewed journal papers. Therefore, there is a little overlap in the texts between the General Introduction, General Conclusion and the main body of the Chapters.

CHAPTER II

DEVELOPMENT OF TRIPLEX-MANAGEMENT MODEL FOR SIMULATING THE RESPONSE OF FOREST GROWTH TO PRE-COMMERCIAL THINNING

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2.1 Résumé

TRIPLEX1.0, un modèle basé sur les processus et conçu pour prédire la croissance des forêts ainsi que la dynamique du carbone (C) et de l'azote (N), a été modifié et amélioré pour simuler la productivité des forêts due aux éclaircies précommerciales. Un modèle basé sur la distribution « Weibull » à trois paramètres a été intégré pour simuler des éclaircies précommerciales au sein du modèle nouvellement développé « TRIPLEX-Management ». L'intensité de l'éclaircie précommerciale est la composante du modèle qui permet à l'utilisateur de simuler des traitements d'éclaircies en appliquant la surface terrière, la densité du peuplement et le volume. La mortalité naturelle a diminué suite aux éclaircies précommerciales due à une augmentation dans l'espace pour les tiges résiduelles. Le modèle prédit également une augmentation des stocks de litière suite aux éclaircies précommerciales. Le modèle 'TRIPLEX-Management' a été testé sur des données d'observation pour des peuplements de pin gris (*Pinus banksiana* Lamb.) soumis aux éclaircies précommmerciales dans le nord-ouest de l'Ontario, Canada. Les coefficients de détermination (R^2) entre les variables prédites et observées, y compris la densité du peuplement, la moyenne du DHP (diamètre à hauteur de poitrine), la moyenne quadratique du DHP, le volume total et le volume marchand ainsi que la biomasse souterraine, aérienne et totale variaient de 0.50 à 0.88 ($n = 20$, $P < 0{,}001$), à l'exception de la hauteur moyenne des arbres ($R^2 = 0.25$, $n = 20$, $P < 0{,}05$). Globalement, l'indice Willmott de l'accord entre les variables prédites et observées variait de 0.97 à 1.00. Les résultats montrent que le modèle « TRIPLEX-Management » est généralement capable de simuler la réponse de la croissance face aux éclaircies précommerciales dans des peuplements de pin gris.

Mots-clés : biomasse, distribution des diamètres, gestion forestière, production de bois

2.2 Abstract

In order to simulate forest growth response to pre-commercial thinning (PCT), TRIPLEX1.0—a process-based model designed to predict forest growth as well as carbon (C) and nitrogen (N) dynamics—was modified and improved to also simulate managed forest ecosystem thinning practices. A three-parameter Weibull distribution model was integrated to simulate thinning treatments within the newly developed TRIPLEX-Management model. The thinning intensity component within the model allows users to simulate thinning treatments by applying basal area, stand density and volume to quantify thinning intensity. Natural mortality decreased following thinning due to an increase in growing space for residual stems. Predicted litterfall pools also increased after thinning events took place. The TRIPLEX-Management model was tested against published observational data for Jack Pine (*Pinus banksiana* Lamb.) stands subjected to PCT in northwestern Ontario, Canada. The coefficients of determination (R^2) between the predicted and observed variables including stand density, mean DBH (diameter at breast height), the quadratic mean DBH, total volume and merchantable volume as well as belowground, aboveground, and total biomass ranged from 0.50 to 0.88 ($n=20$, $P<0.001$) with the exception of mean tree height ($R^2=0.25$, $n=20$, $P<0.05$). Overall, the Willmott index of agreement between predicted and observed variables ranged from 0.97 to 1.00. Results show that the TRIPLEX-Management model is generally capable of simulating growth response to PCT for Jack Pine stands.

Keywords: biomass, diameter distribution, forest management, timber yield

2.3 Introduction

Forest management practices can influence the carbon (C) balance of forests (Thornley and Cannell, 2000, Jandl *et al.*, 2007, Brown *et al.*, 1996), and forest thinning practices are considered an effective way in which to accelerate tree growth, reduce mortality, and increase both productivity and overall timber yield (Smith *et al.*, 1997a, Nabuurs *et al.*, 2008). The Kyoto Protocol offered countries the option to include forest managerial activities within their participation in order to enhance sink potential into their Kyoto accounting during the first commitment period (2008-2012) (UNFCCC, 1997). Be that as it may, there is also a need to modify current managerial practices to optimize forest growth and C sequestration under conditions of climate change (Nuutinen *et al.*, 2006, Garcia-GonzaloPeltola *et al.*, 2007a). A new provision requires forest resource managers to make use of forest simulation models in order to be able to make decisions that satisfy long-term strategy (Peng, 2000). Henceforth, forest models must be able to simulate key ecosystem processes regarding C, nitrogen (N), and water cycling (Johnsen *et al.*, 2001, Mäkelä *et al.*, 2000, Landsberg, 2003) and the effects of forest management practices (e.g., thinning) on forest growth and yield as well as C and N cycling. Therefore, it is essential to develop a process-based model with the capacity to incorporate forest management within its scope of functionality to support decision making strategies.

Regression models based on statistical relationships are the traditional growth and yield models used in forestry. However, empirical models work well as management tools for forecasting stand growth when environments only experience inconsequential change. In contrast to empirical models, process-based models can be used as important forest management tools to explore growth and yield of forest stands to predict the effects of disturbances when environmental conditions change considerably (Landsberg, 2003, Peng *et al.*, 2002, Johnsen *et al.*, 2001, Mäkelä *et al.*, 2000). Since they are based on the representation of forest ecosystem processes such as photosynthesis, respiration, soil organic matter decomposition, and N cycling, they can contribute in the prediction of long-term impacts due to climate change. Several process-based models such as 3-PG (Landsberg and Waring, 1997, Landsberg *et al.*, 2001), 4C (Lasch et al., 2005), EFIMOD (Komarov et al., 2003), FinnFor (Kellomäki and Väisänen, 1997, Matala *et al.*, 2003), ForeSAFE (Wallman et al., 2005), PROMOD (Sands et al., 2000), TREEDYN3 (Bossel, 1996), and TRIPLEX (Peng *et al.*, 2002) are able to predict forest growth and yield. FOREST-BGC or BIOME-BGC (Running and Gower, 1991, Running and Hunt, 1993b), which were developed to simulate C and N balances, were also later modified to predict forest growth and dynamics (Korol *et al.*, 1996, Petritsch *et al.*, 2007, Tatarinov and Cienciala, 2006). Conceptually speaking, the goal of all these models is to provide forest yield estimates in the context of a changing environment.

In general, most ecosystem models assume fully stocked even-aged forests and are not designed to simulate forest management practices and impacts (Petritsch et al., 2007). Indeed, only a handful of studies have reported measures on how to take into consideration forest management practices using process-based models (Matala *et al.*, 2003, Tatarinov and Cienciala, 2006, Petritsch *et al.*, 2007, Miehle *et al.*, 2009, Battaglia *et al.*, 2004) while predicting the effects of climate change on forest functions such as C sequestration and timber yield (Lasch *et al.*, 2005, Garcia-GonzaloPeltola *et al.*, 2007b, Cienciala and Tatarinov, 2006). These models, unfortunately, have neither been widely nor well validated by way of comparing model predictions against independent field data sets. In addition, the potential effects of thinning on growth behavior and C and N cycling have not been well presented.

For this study, a forest management sub-model was added into TRIPLEX1.0 (Peng *et al.*, 2002) to incorporate thinning practices within the process-based model. The goal was to adapt TRIPLEX1.0 to be proficient in quantifying forest growth, timber yield, biomass, and C sequestration within managed forest systems. The objectives of this study were to develop a new thinning submodel (TRIPLEX-Management) to quantify the effects of pre-commercial thinning (PCT) on forest growth, timber yield, biomass, and C sequestration in response to climatic conditions, utilizing Jack Pine (*Pinus banksiana* Lamb.) stands in northwestern Ontario, Canada, to test model performance. This study hypothesized that 1) PCT may change overall diameter distribution, and 2) incorporating Weibull diameter distributions into TRIPLEX1.0 will enable the newly developed TRIPLEX-Management model to capture the response of forest growth to PCT practices.

2.4 Methods

2.4.1 Model development

TRIPLEX1.0 is a process-based model that integrates three well-established models into one: 3-PG (Landsberg and Waring, 1997), TREEDYN3.0 (Bossel, 1996), and CENTURY4.0 (Parton et al., 1993). The model can simulate key C and N cycling processes such as C allocation and N mineralization by utilizing monthly mean temperatures, precipitation, and relative humidity from a given forest stand (Peng *et al.*, 2002). This hybrid approach combines physical, biological, and biogeochemical processes that control the dynamics of C, N, and water. A unique feature of TRIPLEX1.0 is its ability to predict growth and yield of a forest stand based on ecological mechanisms and C balances (Zhou et al., 2005). TRIPLEX1.0 includes the following six submodels:

1) Photosynthetically active radiation (PAR) (Bossel, 1996). PAR is calculated as a function of the solar constant, radiation fraction, solar height, and atmospheric absorption. Forest production and C and N dynamics are primarily driven by solar radiation.

2) Gross primary production (GPP) (Landsberg and Waring, 1997). GPP is calculated as a function of the monthly mean air temperature, stand age, soil water

content, N limitation (f_N, dimensionless), and the percentage of frost days during a period of a single month as well as the leaf area index.

3) Net primary productivity (NPP) (Landsberg and Waring, 1997). NPP is the difference between autotrophic respiration and GPP. This is a modification from past usage where it acted as a constant of the ratio (C_{NPP},dimensionless) of NPP to GPP (Peng *et al.*, 2002). Autotrophic growth (GR, t ha^{-1}) and maintenance respiration (MR, t ha^{-1}) were treated separately and governed by the C factor, air temperature (T_a, °C), and component C pools such as wood (W_w,t ha^{-1}), branches (W_{Br},t ha^{-1}), foliage (W_f, t ha^{-1}), coarse roots (W_{cr}, t ha^{-1}), and fine roots (W_{fr}, t ha^{-1}), following the recent release of the TRIPLEX-Flux version (Zhou et al., 2008):

$$MR = \left(0.02\left(W_f + W_{fr}\right) + 0.01\left(W_{Br} + W_w + W_{cr}\right)\right) \times Q_{10} \tag{1}$$

$$GR = \left(0.35 - \frac{f_N}{10}\right)\left(GPP - MR\right) \tag{2}$$

$$NPP = GPP - MR - GR \tag{3}$$

$$Q_{10} = 2.3 \tag{4}$$

The N pool plays a substantial role as an output of the soil submodel and an input for the forest production submodel. In relation to TRIPLEX, C limitation is a function of available N (N_{avl}, t ha^{-1}), potential NPP (NPP_{pot}, t ha^{-1}), and the C:N response ratio ($B_{C:N}$, dimensionless) of photosynthetic products that is calculated as:

$$f_N = \min\left(1.0, \frac{N_{\mathrm{avl}} \cdot B_{C:N}}{NPP_{\mathrm{pot}}}\right) \tag{5}$$

where $NPP_{pot} = GPP_{pot} \cdot C_{NPP}$. GPP_{pot} (t ha^{-1}) is the maximum GPP without N limitation.

4) Forest growth and yield submodel (FYG) (Bossel, 1996). The primary variables in FYG are the increment of tree diameter and height, calculated using a function of the stem wood biomass increment developed by Bossel (1996).

5) Soil C and N (SCN) (Parton et al., 1993). SCN is based on the CENTURY soil decomposition submodel (Parton et al., 1993) since it provides realistic estimates of both C and N mineralization rates for Canadian boreal forest ecosystems (Peng et al., 1998). Soil C decomposition rates for each pool are calculated as functions of maximum decomposition rates, soil moisture effects, and soil temperature.

6) Soil water submodel (SW) (Parton et al., 1993). SW is a simplified water budget module that calculates monthly water loss through transpiration and evaporation as well as through soil and snow water content following the soil water module within CENTURY (Parton et al., 1993).

A more detailed description of the features, structure, mathematical algorithms, sensitivity analysis, and development strategy of TRIPLEX1.0 have been previously reported by Peng et al. (2002) and Liu et al. (2002).

2.4.1.1 Incorporating diameter distribution into TRIPLEX1.0

Diameter distribution, an important factor of stand structure, was incorporated into TRIPLEX1.0. The three-parameter Weibull distribution model was used for this study to characterize diameter distribution for a given stand since it is flexible and yields probabilities with ease and without the need for numerical integration (Cao, 2004). Certain studies have indicated that the Weibull function adequately fits diameter distribution for both unmanaged and managed forest ecosystems under a variety of thinning regimes (Zarnoch *et al.*, 1982, Cao, 2004, Álvarez González *et al.*, 2002, Nord-Larsen and Cao, 2006). The probability distribution function of the three-parameter Weibull distribution model is described as:

$$f(D)=(\frac{c}{b})(\frac{D-a}{b})^{c-1}\exp\left[-\left(\frac{D-a}{b}\right)^{c}\right] \qquad (6)$$

where a, b, and c are the location, scale, and shape parameters, respectively, of the Weibull distribution, and D is the DBH. The location parameter, such as the name implies, places the start location of the distribution along the abscissa. It stretches out the distribution while increasing the value of the scale parameter and holding the shape parameter constant. The shape parameter controls the behavior of the distribution.

The maximum likelihood method was used (R Development Core Team, 2009) to fit Eq. (6) for the DBH distribution of each plot, including stands that were thinned. When the initial estimate of a was negative, it was set to one-half of the minimum diameter in the plot after which the other two parameters were reestimated. At this point, the general form of a linear regression model was used to relate the Weibull function parameters to mean DBH ($\overline{D}$, cm), age (A, years), mean height ($\overline{H}$, m), and stand density (SD, trees ha^{-1}), which were then predicted by TRIPLEX1.0:

$$\widehat{y}=f\left(\overline{D},\overline{H},A,SD\right)=\theta_0+\theta_1\overline{D}+\theta_2\overline{H}+\theta_3A+\theta_4\ln(SD) \qquad (7)$$

where $\widehat{y}$ is the estimate of a specific Weibull parameter (a, b, and c), and θ_0 to θ_4 are the regression model parameters. Stepwise linear regression analysis (R Development Core Team, 2009) was applied to identify a set of candidate functional forms based on a 0.05 significance level.

2.4.1.2 Forest thinning considerations

Since the original version of TRIPLEX1.0 did not include a forest management sub-model, forest thinning was modeled by the inclusion of thinning time (Age_{T}„ years) and thinning intensity (I_T, %) in the newly developed TRIPLEX-Management model. Diameter distributions were estimated before the thinning treatment took place in order to quantify basic stand characteristics of the post thinning stand for future simulations. The thinning methods “thinning from above” and “thinning from below” were designed to model forest thinning practices. The following variables were considered:

1) Thinning intensity in relation to stand density (I_{SD}, %) was fixed as an input to the model by users or modelers. The lower (L_0, cm) and upper (U_0, cm) bounds of the DBH class for the residual stand was determined by Eqs. (8) and (9) while the lower (L, cm) and upper (U, cm) bounds of the DBH class for a given stand were determined by the formula $SD \cdot f(D) > 1$, which represents at least one tree in a given DBH class. The mean DBH and the quadratic mean DBH (D_g, cm) of the residual stands were then obtained by means of calculating the mathematical expectations of D and D^2 based on the diameter distribution function $f(D)$ by way of Eqs. (10) and (11). The definite integrals solution was a numerical approximation by which the area beneath the Weibull probability density function was determined by summing numerous inscribed rectangles. For model application, this study used $U_0 = U$ for “thinning from below” and $L_0 = L$ for “thinning from above.”

$$I_T = I_{SD} = \frac{N_{Removed}}{N_{Before}} \tag{8}$$

$$N_{Removed} = N_{Before} \left\{ 1 - \exp\left[-\left(\frac{L_0 - a}{b} \right)^c \right] + \exp\left[-\left(\frac{U_0 - a}{b} \right)^c \right] \right\} \tag{9}$$

$$\overline{D} = E(D) = \int_{L_0}^{U_0} D \cdot f(D) dD \tag{10}$$

$$D_g^2 = E(D^2) = \int_{L_0}^{U_0} D^2 \cdot f(D) dD \tag{11}$$

where $N_{Residual}$ and N_{before} are the number of residual trees and the number of trees, respectively, before thinning treatment takes place. Tree height (H, m) for each DBH class was estimated by the height-diameter equation (Eq. (12)) for boreal Jack

Pine forests developed by Zhang et al. (2002). Mean height was then calculated following Eq. (13).

$$H = 1.3 + 23.9313 \times (1 - e^{-0.0812 \cdot D})^{1.7149} \tag{12}$$

$$\overline{H} = \int_{L_0}^{U_0} Hf(D)dD \tag{13}$$

2) Thinning intensity in relation to basal area (I_{Ba}, %) determines the ratio of the basal area to be removed ($B_{\mathrm{Re}moved}$, m^2 ha^{-1}) to the basal area before thinning treatment takes place (B_{Before}, m^2 ha^{-1}):

$$I_T = I_{Ba} = \frac{B_{\mathrm{Re}moved}}{B_{Before}} \tag{14}$$

The lower and upper bounds of residual stands were then computed according to Eq. (15) and Eq. (16). They were used to calculate mean DBH, mean height, and the mean quadratic DBH of the residual stands through Eq. (10-13).

$$B_{Before} = \frac{\pi}{4} SD \int_{L}^{U} D^2 f(D)dD \tag{15}$$

$$B_{\mathrm{Re}moved} = B_{Before} - \frac{\pi}{4} SD \int_{L_0}^{U_0} D^2 f(D)dD \tag{16}$$

3) Thinning intensity in relation to volume (I_V, %) is another alternative way in which to describe thinning intensity. This variable represents the relative volume removal ($V_{\mathrm{Re}moved}$, m^3 ha^{-1}). Volume before thinning (V_{Before}, m^3 ha^{-1}) was calculated from stand density, tree form (φ) (Eq. (20)), and tree height for a given DBH and the Weibull function ($f(D)$) as follows:

$$I_T = I_V = \frac{V_{\mathrm{Re}moved}}{V_{Before}} \tag{17}$$

$$V_{Before} = \frac{\pi}{4} SD \int_{L}^{U} H\varphi D^2 f(D)dD \tag{18}$$

$$V_{\mathrm{Re}moved} = V_{Before} - \frac{\pi}{4} SD \int_{L_0}^{U_0} H\varphi D^2 f(D)dD \tag{19}$$

$$\varphi = 0.52 - 0.002 \cdot (\frac{H}{D} - 90) \tag{20}$$

For PCT treatments, the most important step was to obtain the lower boundary (thinning threshold) and upper boundary ($U_0 = U$) of the residual stands for all three calculation approaches.

2.4.1.3 Modifications made to the original model source code

Certain variables were recalculated for purposes of simulation. This was necessary due to the model mechanism advancement to the next time step when forest thinning occurs. Other model variables or processes that were identified as phenomenon in which full understanding remains incomplete such as tree mortality and increased litterfall due to thinning slash cannot be auto-updated. Certain necessary changes were consequently made to these related processes.

Modification in the FYG submodel

Tree mortality is separated into mortality with and without competition in TRIPLEX1.0 (Peng *et al.*, 2002). Both mortality scenarios are simply set as constant values. Given that PCT removes the majority of unhealthy trees and increases the vigor of residual stems, the mortality without competition scenario has been empirically reduced after thinning in the TRIPLEX-Management version.

Total stand volume (V_T, m^3 ha^{-1}) was estimated as a function of mean DBH, mean height, stand density, and tree form by Eq. (21) in the original TRIPLEX1.0 model. A tendency to always underestimate tree volume for young stands seems to afflict TRIPLEX1.0 (Peng *et al.*, 2002). In the current version, stand volume is the sum of all tree volume for all DBH classes (Eq. (22)). Merchantable volume (V_M, m^3 ha^{-1}) was calculated as the sum of individual trees for all trees greater than 9 cm in DBH (Eq. (23)).

$$V = SD \times \frac{\pi}{4} \varphi \overline{D}^2 \overline{H} \tag{21}$$

$$V_T = \frac{\pi}{4} SD \int_L^U H \varphi D^2 f(D) dD \tag{22}$$

$$V_M = \frac{\pi}{4} SD \int_9^U H \varphi D^2 f(D) dD \tag{23}$$

Modification in the SCN submodel

PCT is generally carried out only in even-aged forests that are approximately 15 years old. In many such forest stands, trees that are selected for removal are often too small for heavy machinery usage. The soil environment, therefore, is hardly affected by this type of thinning operation. Several studies have reported that prescribed thinning has a negligible effect on soil respiration (Vesala *et al.*, 2005, Campbell *et al.*, 2009). It was consequently assumed in the current study that thinning treatments have little effect on soil processes such as soil respiration. Nevertheless, it is assumed that thinning slash is always left on-site to enrich the soil. Litterfall pools in the SCN submodel were therefore increased by means of thinning intensity.

To quantify the biomass of residual stands and the slash that has entered into soil, biomass equations were used to estimate the change rate before and after thinning treatments occurred. The Jack Pine biomass equations used in this study were reported by Lambert et al. (2005) for aboveground biomass (Eq. (24) and Li et al. (2003) for belowground biomass (Eq. (25)).

$$Biomass_i = \beta_1 D^{\beta_2} H^{\beta_3} \tag{24}$$

$$RB = 0.222 \cdot AB \tag{25}$$

where $Biomass_i$ is the dry biomass compartment i of a living tree (kg) in which i represents wood, bark, branches, and foliage; β_1 to β_3 are the parameters of the biomass equation (Table 2.1); and RB and AB are root and aboveground biomass, respectively, obtained by adding their corresponding compartments. Biomass change rates ($I_{B,i}$, %) for each biomass component *i* of a stand were estimated as the ratio of the summed biomass in each DBH class for the before thinning and after thinning stand (Eq. (26)). Therefore, the increments of the litterfall pools ($\Delta Litter_i$, kg) were calculated by the product of the original stand C pools before thinning ($W_{Before,i}$, kg ha^{-1}) and the change rates after thinning (Eq. (27)). Furthermore, the residual stand C pools were obtained by way of the differences in stand C pools before increases in thinning and litterfall took place (Eq. (28)). All calculations in relation to root biomass (e.g., root litterfall) are based on Eq. (25).

$$I_{B,i} = 1 - \frac{\int_{L_0}^{U_0} Biomass_i f(D) dD}{\int_{L}^{U} Biomass_i f(D) dD} \tag{26}$$

$$\Delta Litter_i = W_{Before,i} I_{B,i} \tag{27}$$

$$W_{Residual,i} = W_{Before,i}(1 - I_{B,i}) \tag{28}$$

Table 2.1 Biomass equation parameters of Jack pine (from Lambert et al., 2005)

Component	β_1	β_2	β_3
Wood	0.0199	1.6883	1.2456
Bark	0.0141	1.5994	0.5979
Branches	0.0185	3.0584	–0.9816
Foliage	0.0325	1.7879	-

2.4.2 Sites

PCT may have a positive effect on individual tree volume growth for Jack Pine stands (e.g., Bella and DeFranceschi, 1974, Groot *et al.*, 1984), which in itself may lead to a shorter rotational time period (Morris et al., 1994). Published Jack Pine forest PCT data (Tong et al., 2005) in northwestern Ontario was used in this study to validate the modified model. Beginning in the 1980s or even earlier, PCT treatments were applied a single time to selected stands by way of the practice of low thinning using brush

Table 2.2. Site information based on the study by Tong et al. (2005)

Site	Stand	Age (Year)	Age_T (Year)	I_T(%)	*SD* (trees/ha)		DBH (cm)		Tree height (m)		V_T (m^3 ha^{-1})		V_M (m^3 ha^{-1})	
					Control	PCT	Control	PCT	Control	PCT	Control	PCT	Control	PCT
1	Furniss road	36	14	43	4080	2340	9.1 (3.15)	11.1 (4.90)	9.8 (3.38)	10.2 (4.46)	161.6	163.1	117.5	143.4
2	Reba road	36	15	36	2700	1720	10.9 (3.82)	13.5 (4.07)	10.1 (3.83)	13.3 (3.48)	159.1	176.7	133.2	161.0
3	Encamp	26	12	44	2840	1580	9.3 (5.35)	11.9 (4.56)	8.1 (4.00)	9.4 (3.44)	144.2	104.3	121.4	93.5
4	Mack 1	26	13	62	5740	2180	7.8 (2.74)	10.9 (2.52)	8.5 (3.29)	10.2 (1.94)	150.6	107.7	90.5	85.0
5	Mack 5	26	13	23	5260	4040	8.2 (3.08)	8.9 (3.31)	10.3 (2.27)	9.9 (2.54)	167.1	145.8	104.4	100.0
6	Graham road	34	5	21	2800	2220	11.9 (2.97)	13.7 (3.56)	14.3 (1.84)	14.3 (2.58)	222.9	235.3	188.0	213.3
7	Nelson Lake	31	11	25	2200	1640	11.9 (3.88)	13.0 (2.61)	9.0 (1.65)	9.6 (1.58)	126.1	107.5	107.6	95.0
8	Mack 2	26	12	68	4260	1360	8.4 (2.61)	14.1 (3.08)	9.3 (1.50)	11.3 (1.69)	122.1	121.0	110.5	71.6
9	Mack 3	26	12	63	5820	2180	7.8 (2.36)	11.2 (2.14)	9.8 (1.30)	10.3 (0.99)	146.8	112.7	90.0	72.0
10	Mack 4	26	12	65	4940	1740	8.5 (2.85)	12.3 (2.12)	10.1 (1.70)	10.3 (1.07)	160.5	106.0	98.9	91.0

Note: Age_T= Thinning age; I_T=Thinning intensity; *SD* = stand density; V_T and V_M are stand volume and merchantable volume, respectively.

saws. Dominant Jack Pine stands were measured in 2003 (Table 2.2) where the total volume and merchantable volume were estimated by Tong et al. (2005). A total of 10 sites containing both PCT and control stands represented the different groups of thinning intensity and thinning age. The site index was from 18 m to 20 m (the dominant height after a 50 year period of growth). At each site, 10 plots comprising of 0.01 ha each were established, five of which were control stands and five of which were PCT stands. These sites were naturally regenerated or seeded throughout a period from 1967 to 1977. The thinning summing the volumes of each segment between two cross sections as reported by time (Age_T, year) ranged from five to 15 years, and the thinning intensity in relation to stand density ranged from 21% to 68% of tree removal (Table 2.2).

Monthly air temperature, precipitation, and relative humidity were obtained from the IPCC 20th Century experiment applying the third version of the Canadian Centre for Climate Modelling and Analysis (CCCma) Coupled Global Climate Model (CGCM3.1) for the years 1850-2000 (http://www.cccma.ec.gc.ca). The average value of four corresponding grids for northwestern Ontario was used in this study.

2.4.3 Simulation experiments

2.4.3.1 Parameterization and initialization

The TRIPLEX1.0 model operates with the following sets of input data and parameters (Table 2.3):

1) An ecophysiological parameter file that characterizes the necessary eco-parameters.

2) A stand initialization file including species, regenerated year, latitude, site class, initial soil C, stocking, thinning time, and thinning intensity.

3) A form that describes species parameters such as wood C density, maximum height, etc.

Table 2.3 Parameters used in the model simulations.

Parameter	Description	Treatment		Note
		Control	PCT	
Photosynthetically active radiation				
Absorb	Atmospheric absorption factor	0.15	-	a
Cloud	Time faction of cloud days	0.4	-	a
PAR factor	Sloar radiation fraction	0.47	-	b
Gross primary productivity				
BlCond	Canopy boundary layer conductance (ml m^{-2} s^{-1})	0.2	-	c
MaxCond	Max canopy conductance (ml m^{-2} s^{-1})	0.02	-	c
StomCond	Stomata conductance (ml m^{-2} s^{-1})	0.006	-	c
ExtCoef	Radiation extinction coefficient	0.5	-	c
TaMin	Min temperature for growth (°C)	5	-	a
TaMax	Max temperature for growth (°C)	30	-	h
Topt	Optimum temperature for growth (°C)	15	-	d
N factor	N factor for tree growth	0.2	-	e
Na	Effect of age to GPP	3	-	f
Sla	Specific leaf area ($m^2 kg^{-1}$)	6		d
Net primary productivity				
GamaF	Leaves turnover per year	0.01		g
GamaR	Fine roots turnover per year	0.21		h
$B_{C:N}$	C:N response ratio	24.5		i
C_{NPP}	A constant ratio of NPP/GPP	0.39		b
Soil C and N				
Lnr	Lignin-N ratio		-	e
Ls	Lignin for leaf, fine root, coarse root, branch, and wood	0.215, 0.215, 0.255, 0.235, 0.255	-	e
Soil water				
A1, A2, A3	Soil water depth of layer 1,2, and 3 (cm)	15, 15, 15		e
AWL1, 2,and 3	Relative root density for layer 1,2, and 3	0.5,0.3,02		e
KF	Fraction of H2O flow to stream	0.5		g
KD	Fraction of H2O flow to deep storage	0.5		g
KX	Fraction of deep storage water to stream	0.3		g
AWater	Max soil water (mm)	250		g
Growth and yield				
MiuNorm	Normal mortality	0.006	0.005	This study
MiuCrowd	Competition mortality	0.02	-	g
Species parameter				
CSP	Wood C density (tC m^{-3})	0.22	-	j
CD	Crown to stem diameter ratio	25	-	a
AlphaC	Canopy quantum efficiency	0.05	-	a
MaxHeight	Max height (m)	25	-	This study
AgeMax	Max stand age (year)	150	-	This study

[a] Bossel (1996); [b] Ryan et al. (1997); [c] Coops et al. (2001); [d] Kimball et al. (1997); [e] the values are given by CENTURY (Parton et al., 1993); [f] Landsberg and Waring (1997); [g] Zhou et al. (2005); [h] Steele et al. (1997); [i] Liu and Greaver. (2009), [j] Newcomer et al. (2000); [h] Peng et al. (2002)

4) A climate data file exhibiting monthly temperature, precipitation, and relative humidity.

The TRIPLEX1.0 model has been parameterized for pure Jack Pine stands (Peng *et al.*, 2002) in Ontario as well as Jack Pine, Black Spruce (*Picea mariana* (Mill.) BSP), and Trembling Aspen (*Populus tremuloides* Michx) mixed stands in central Canada and northeastern Ontario (Zhou et al., 2004). It has also been parameterized for subtropical forest regions in southeastern China (Zhang et al., 2008) and boreal and temperate forest ecosystems in northeastern China (Peng et al., 2009). It is noteworthy that none of the previous studies mentioned considered the potential impacts of thinning on forest growth and yield.

2.4.3.2 Simulation runs

The scheme of the simulation runs is provided in Figure. 2.1. First of all, simulations began at the point of yearly regeneration for each stand. Next, if thinning occurs, the diameter distribution model parameters were estimated from the last month of the year before thinning. Residual stand characteristics (mean DBH, mean height, and stand density) were calculated and reentered as an input for the next time step in relation to the thinning intensity defined by the user. The biomass of leaf, wood, branch, and fine and coarse roots was reduced along with the change rates obtained from the biomass equations and the diameter distribution model. The model continued to simulate forest growth, C, and N dynamics for the residual stand until simulations concluded. Lastly, variables of interest such as DBH, volume, and biomass were output.

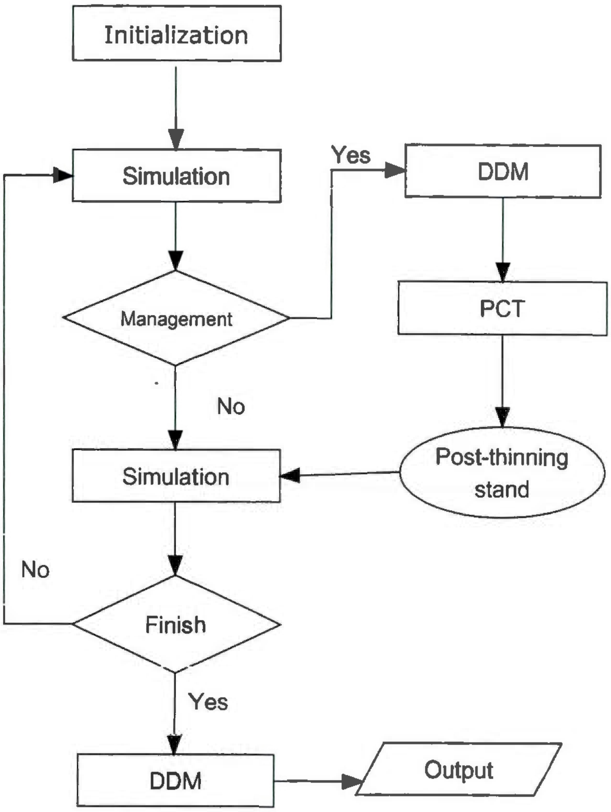

Figure 2.1 Flow diagram of a simulation run. DDM refers diameter distribution model.

2.4.3.3 Model evaluation

The one-sample Kolmogorov-Smirnov (K-S) test was used to evaluate the performance of the diameter distribution model. The statistical value of the K-S test within a plot is the largest absolute difference between the hypothesized distribution and the observed distribution from that plot. The smaller the statistical value the better the fit. The mean absolute error (MAE%, Eq. (29)) and the root mean square error (RMSE%, Eq. (30)) were used to evaluate the differences in the predicted and observed data.

$$MAE\% = 100\frac{\sum_{i=1}^{n}|P_i - O_i|}{n\bar{O}} \qquad (29)$$

$$RMSE\% = 100(\overline{O})^{-1}\left[\frac{\sum_{i=1}^{n}(P_i - O_i)^2}{n}\right]^{0.5} \tag{30}$$

where P is the predicted value and O is the observed value; $\overline{O}$ and $\overline{P}$ are the mean of the observed and predicted values, respectively; n is the number of observations.

Three criteria were calculated to evaluate the performance of the TRIPLEX-Management model. A linear regression between the observed and predicted values was used to evaluate model performance. The hypothesis is that the regression passes through the origin and has a slope of unity (45°). MAE% and RMSE% were also used to evaluate prediction errors of the TRIPLEX-Management model. The Willmott index of agreement (*d*) (Willmott, 1982) is an indicator of model performance. It carries a value from 0 to 1.0, and is expressed as:

$$d = 1 - \left[\frac{\sum_{i=1}^{n}(P_i - O_i)^2}{\sum_{i=1}^{n}(|P_i| + |O_i|)^2}\right] \tag{31}$$

where the index of 1.0 indicates perfect agreement (Willmott, 1982).

2.4.3.4 Sensitivity analysis

Sensitivity analysis was carried out in order to investigate the effects of the newly introduced diameter distribution parameters and input variables for the PCT regime on forest C dynamics in the TRIPLEX-Management model. Sensitivity scenarios involved applying a 10% increase or decrease in Weibull distribution parameters (*a, b,* and *c*), mortality without competition in residual stands, and thinning intensity. Moreover, a two year advance or extension in thinning time was also considered within the sensitivity scenarios. The model was run repeatedly under these scenarios, after which the results were compared to previous runs.

2.5 Results

2.5.1 Diameter distribution comparison

Table 2.4 provides the parameter prediction equation systems of Weibull diameter distribution within the TRIPLEX-Management model. The scale parameter had the highest R^2 (0.83) value and the lowest MAE% (9.0%) and RMSE% (13.2%) values among the three Weibull parameters while the location parameter and the shape parameter had low R^2 values and high MAE% and RMSE% values (Table 2.4). The mean and standard variations of the K-S test goodness of fit for the entire data set were 0.19 and 0.09, indicating that the diameter distribution model performs well overall.

Table 2.4 Estimated coefficients and their statistics of Eq. (7) using stepwise linear regression analysis (R Development Core Team, 2009) for Jack pine stands.

$\hat{y}$	Slope coefficient					Model statistics	
	Intercept	$\overline{D}$	$\overline{H}$	A	SD	R^2	RMSE
a	-1.149	0.471		-0.045		0.354	1.364
b	1.621	0.586		0.050		0.825	1.527
c	1.269	0.259		-0.023		0.192	1.030

Note: $\hat{y}$ is the dependent variable in $\hat{y} = f\left(\overline{D},\overline{H},A,SD\right) = \theta_0 + \theta_1\overline{D} + \theta_2\overline{H} + \theta_3 A + \theta_4 \ln(SD)$ Eq. (7); a, b, and c are the estimated location, scale and shape parameters of the three-parameter Weibull distribution, respectively; $\overline{D}$= mean diameter at breast height ; $\overline{H}$= mean tree height; A= stand age; SD = stand density; RMSE = root mean square error.

Figure 2. 2 shows that the simulated diameter distribution carried out by TRIPLEX-Management derived from stand characteristics agreed well with observed Jack Pine stand diameter distributions. PCT altered stand diameter distribution. The location parameter of the Weibull distribution within the PCT stands was larger than in the control stands (Figure 2.2 C and F) given that the PCT treatments removed lower diameter class trees. Furthermore, diameter distributions within the PCT stands were wider than in the control stands (Figure 2.2 C and F), and diameter distributions in the

PCT stands were more negatively skewed than in the control stands (Figure 2.2 C and F).

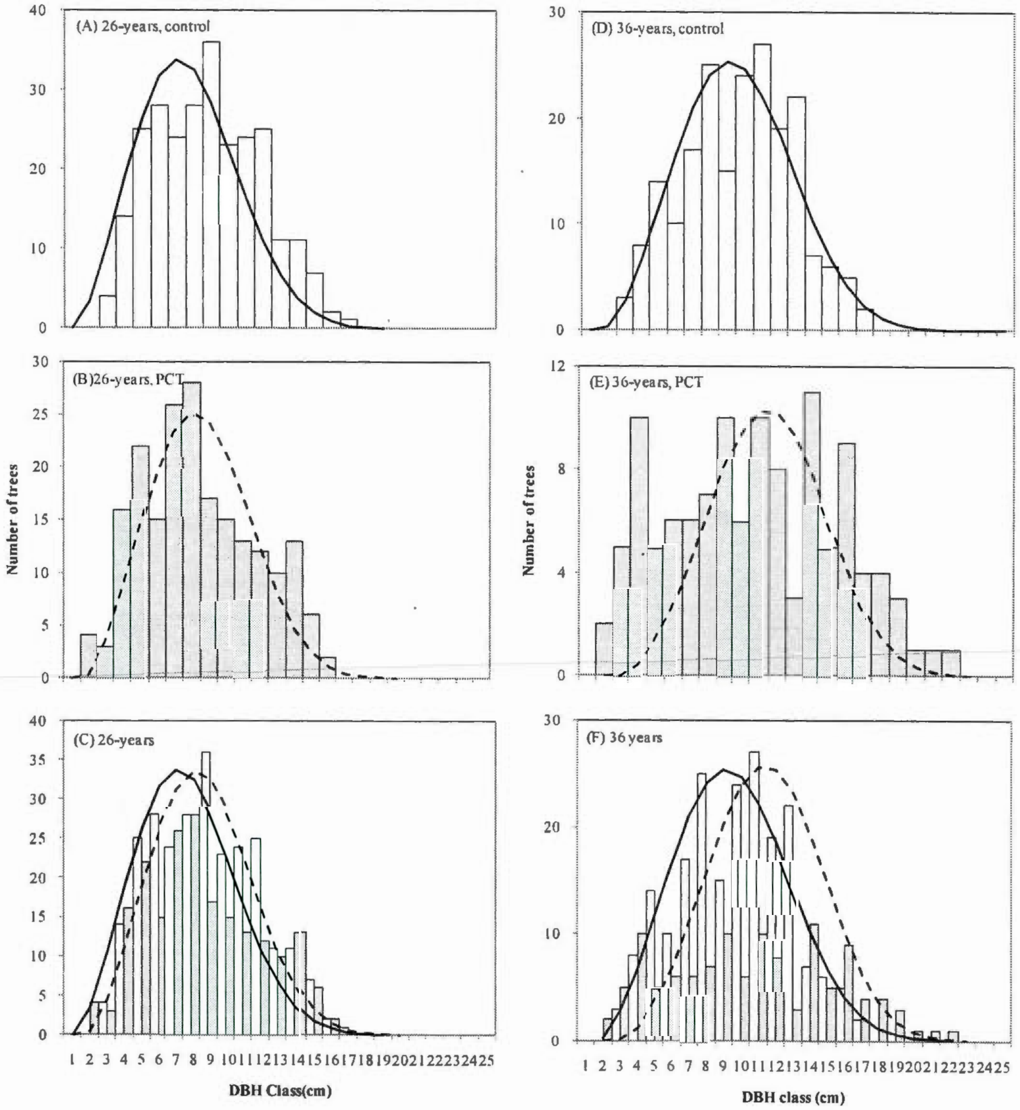

Figure 2.2 Comparison of simulated and observed diameter distributions in the unmanaged (control) and managed (PCT) Jack pine stands with different stand age (site 1, 36 years old; site 5, 26 years old) in northwestern Ontario, Canada. Solid and dash curves represent model simulated DBH distribution for control and PCT, respectively. The hollow and grey histograms represent the observed diameter distribution for control and PCT stands, respectively.

2.5.2 Stand characteristic comparison

Scatter plot results of the comparisons made between the simulated and observed data in relation to stand characteristics are provided in Figure 2.3 and Table 2.5. Both the predicted and observed data were close to the 1:1 line (Figure 2.3), although a general trend in underestimation occurred (Table 2.5). The coefficient of determination (R^2) for all stand characteristics ranged from 0.57 to 0.88 except for mean height (R^2=0.25) (Table 2.5), and the MAE% ranged from 7.3% to 16.0% for all stand variables. The RMSE% for all forest stand variables ranged from 9.4% to 20.8%. The Willmott index of agreement between the observed and simulated basic stand variables ranged from 0.97 to 1.00. Statistical analysis (Table 2.5) confirmed that TRIPLEX-Management predicted stand variables reasonably well.

Comparison results for the most essential direct measurements in forest inventory such as stand density, mean DBH, and the quadratic mean DBH showed good agreement overall (Figure 2.3 A, B, and C). Regression of the predicted versus observed stand density resulted in a high R^2 of 0.88 with a slope of 0.90 and an intercept of 234 tree ha^{-1} (n=20, $P<0.001$). The MAE%, RMSE%, and Willmott index were 11.0%, 16.6%, and 0.99, respectively. Model performance in relation to mean DBH and the quadratic mean DBH was similar to model performance of stand density (Table 2.5).

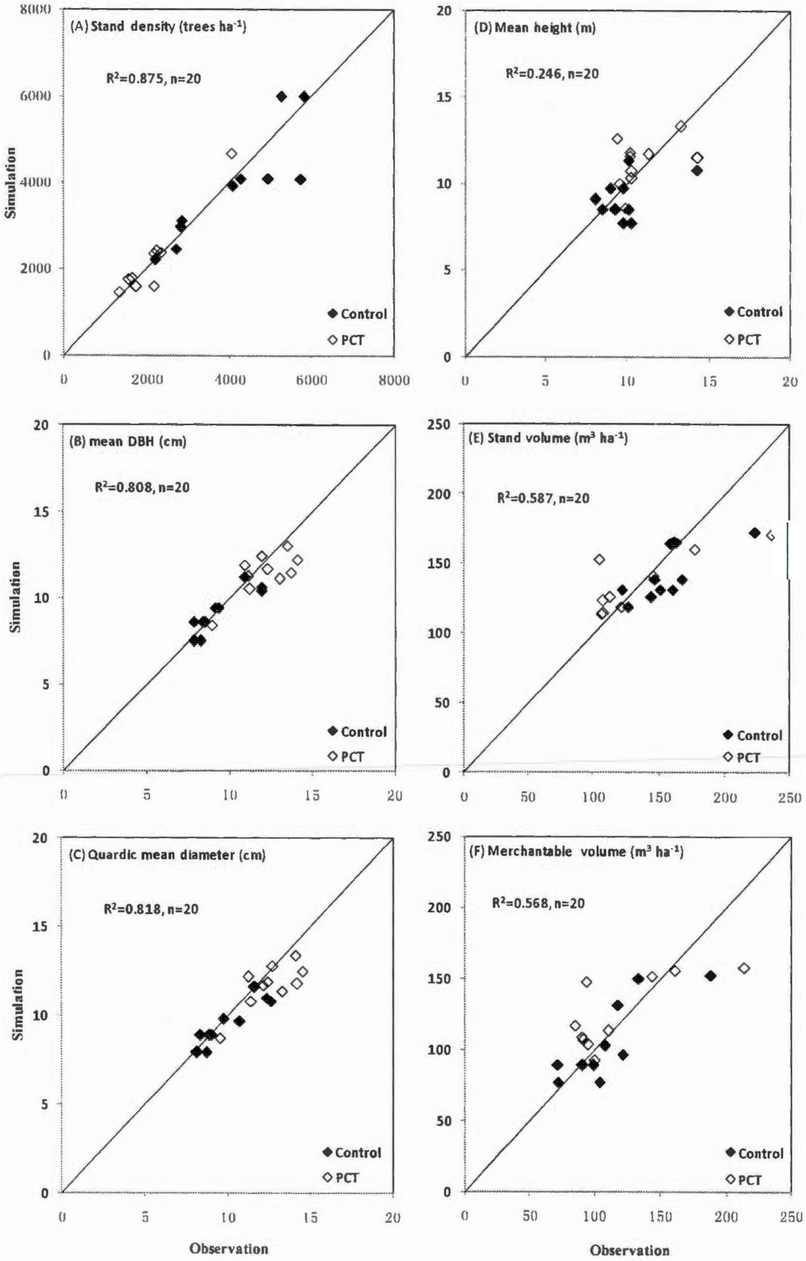

Figure 2.3 Comparisons of simulated and observed (A) stand density (trees ha^{-1}), (B) diameter at breast height (DBH) (cm), (C) quadric mean diameter (cm), (D) mean tree height (m), (E) total stand volume (m^{3}ha^{-1}), and (F) merchantable volume (DBH>9cm) (m^3 ha^{-1}) for overall 20 jack pine stands. Solid diamonds represent control plots, and hollow diamonds represent PCT plots. Solid diagonal is the 1:1 line.

Table 2.5 TRIPLEX-Management model performance

Variable	Regression analysis			MAE%	RMSE%	d^a
	R^2	slope	intercept			
Stand density (trees ha^{-1})	0.88^{***}	0.90	234.47	11.0	16.6	0.99
Mean DBH (cm)	0.81^{***}	0.73	2.51	7.3	9.4	1.00
Quadratic mean DBH (cm)	0.82^{***}	0.74	2.35	7.3	9.6	1.00
Mean height (m)	0.25^{*}	0.48	5.19	12.1	15.8	0.99
Total volume (m^3 ha^{-1})	0.59^{***}	0.42	78.14	12.3	17.0	0.99
Merchantable volume (m^3 ha^{-1})	0.57^{***}	0.57	50.24	16.0	20.8	0.99
Belowground biomass (t ha^{-1})	0.54^{***}	0.55	4.65	21.7	25.1	0.98
Aboveground biomass (t ha^{-1})	0.50^{***}	0.45	22.73	26.8	31.8	0.97
Total biomass (t ha^{-1})	0.51^{***}	0.47	27.37	25.9	30.5	0.97

*** Significant at probability levels of 0.001, *Significant at probability levels of 0.05; ^{a} Willmott index; MAE% is the mean absolute error; and RMSE% is the root mean square error.

In general, predicted and observed mean tree height was close to the 1:1 line (Figure 2.3 D). Regression of the computed versus observed mean tree height resulted in a low R^2 of 0.25 with a slope of 0.48 and an intercept of 5.19 m (n=20, $P<0.05$). The MAE%, RMSE%, and Willmott index were 12.1%, 15.8%, and 0.99, respectively. It is likely that such a low R^2 resulted from a wide range of H/D (30-285) in the natural forests under investigation and a relatively narrow mean height (8.1-14.3 m).

Overall agreements for total volume (Figure 2.3E) and merchantable volume (Figure 2. 3 F) were also generally acceptable. Regression of the computed versus observed total volume resulted in a relatively low R^2 of 0.59 with a slope of 0.42 and an intercept of 78.14 m^3 ha^{-1} (n=20, $P<0.001$). The MAE%, RMSE%, and Willmott index were 12.3%, 17.0%, and 0.99, respectively. Regression performance for the merchantable volume was similar. Such a low R^2 is partly attributable to the limited field data available such as an overall narrow age range from 26 to 36 years as well as the general tree volume calculation formula (Eqs. (24) and (25)) used for all tree species. Considerable prediction errors (relative error>25%) in relation to total volume and merchantable volume predictions were found for the PCT stands of site 6 (*SD*=2220 trees ha^{-1}, age = 34 years, see Table 2.2) where observed total volume

(235.3 m^3 ha^{-1}) and merchantable volume (213.3 m^3 ha^{-1}) were much higher compared to the PCT stands of site 2 (V_T=176.7 m^3 ha^{-1}, V_M=161.0 m^3 ha^{-1}, see Table 2.2), exhibiting similar stands age (36 years) but lower stand density (1720 trees ha^{-1}). They were even higher than those provided in site class 1 of the normal yield table developed for four primary northern Ontario tree species in the 1970s (Plonski, 1974). Similar prediction errors (relative error>20%) were found in the control stands of site 6. These results indicate that the model underestimated tree production for stands located within site classes that exhibited reasonably good conditions.

2.5.3 Stand biomass comparison

A comparison of biomass simulations for the distribution (above and belowground) of dry matter within the model relative to biomass equation estimates is provided in Figure 2.4. In general, predicted and observed biomass data pairs were close to the 1:1 line, although the model underestimated biomass production (Figure 2.4). Regression of predicted versus observed total biomass resulted in a relatively low R^2 of 0.51 with a slope of 0.47 and an intercept of 27.37 t ha^{-1} (n=20, P<0.001, Table 2.5). The MAE%, RMSE%, and Willmott index were 25.9%, 30.5%, and 0.97, respectively (Table 2.5). Regressions for above and belowground biomass were similar. TRIPLEX-Management captured the growth response to PCT treatment while a systematic negative bias was detected in the biomass simulation, especially for sites in which reasonably good conditions existed (e.g., site 6, see Table 2.3). Similar results were obtained for volume estimates. However, this study recognizes that it is possible that a bias can be produced when applying this type of national scale biomass equation (Lambert *et al.*, 2005) to a given local scale forest stand. Nevertheless, statistical analysis (Table 2.5) confirmed that TRIPLEX-Management still produces an overall acceptable agreement to biomass estimates generated from national biomass equations.

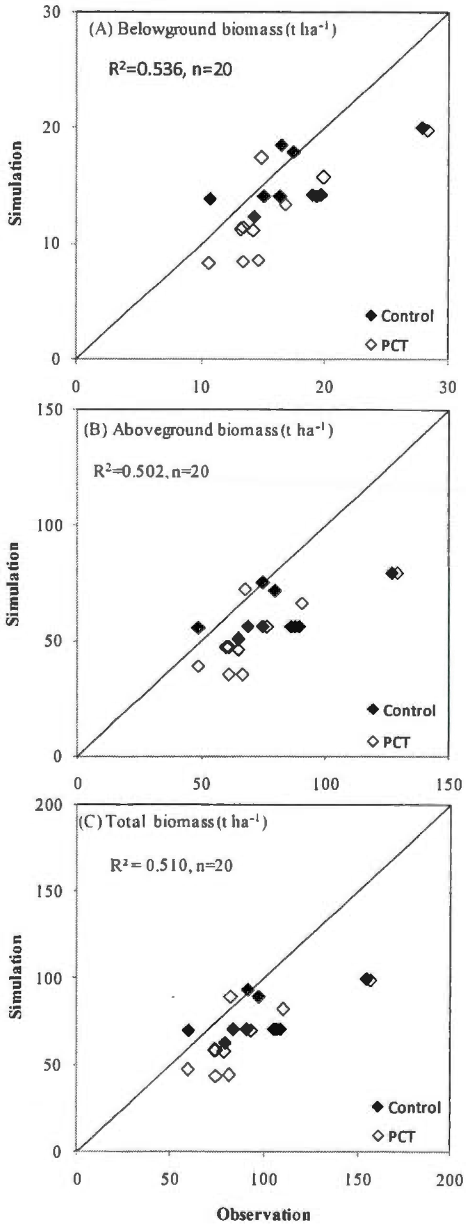

Figure 2.4 Comparisons of simulated and observed (A) belowground biomass (t ha^{-1}), (B) aboveground biomass (t ha^{-1}), and (C) total biomass (t ha^{-1}) for overall 20 Jack pine stands. Solid diamonds represent control plots, and hollow diamonds represent PCT plots. Solid diagonal is the 1:1 line.

2.5.4 Sensitivity to PCT treatment

A positive relationship was found in relation to changes in thinning intensity. For example, a 10% increase in I_T resulted in increases from 0.1% to 7.1% and from 0.1% to 7.5% for mean DBH and mean height, respectively (Table 2.6). No significant positive or negative relationships were found for total volume and merchantable volume to thinning intensity. Similarly, no significant relationships were found between variables under consideration with a two year advance or extension of thinning age and mortality adaptation for residual stands.

The three parameters of the Weibull diameter distributions had remarkably affected basic stand characteristics and total biomass, but had no significant affect on soil C for this model (Table 2.6). An apparent positive response of total volume and merchantable volume was found for location parameter (*a*) and scale parameter (*b*), especially concerning the latter. A 10% increase in the scale parameter resulted in an increase from 27.8% to 31.5% and from 33.6 to 49.6% for total volume and merchantable volume, respectively (Table 2.6), suggesting that the accurate estimation of scale parameters of the Weibull diameter distribution is critical in predicting total volume and merchantable volume. However, the shape parameter may not follow regular patterns for all related variables.

Table 2.6 Predicted sensitivity of newly introduced key variables to changes in thinning regime for three selected Jack pine stands (values are percent change).

Jack pine stands	I_T		Age_T		Mortality after PCT		a		b		c	
	+10%	-10%	+2	-2	+10%	-10%	+10%	-10%	+10%	-10%	+10%	-10%
Site 1 (Age_T=14, I_T=43%)												
$\overline{D}$	7.1	-1.8	4.4	0.9	0.0	0.0	0.0	0.0	6.2	0.0	6.2	0.9
$\overline{H}$	10.3	-0.9	8.6	1.7	-0.9	0.0	0.0	0.0	9.5	0.0	9.5	0.9
V_T	4.9	-0.4	6.1	0.4	-1.8	1.1	6.4	-5.3	31.5	-22.0	4.0	1.2
V_M	8.5	-0.8	8.6	0.9	-2.0	1.1	7.7	-6.4	38.3	-26.6	7.5	1.1
Total biomass	-4.2	-1.2	-1.9	-1.8	-1.5	1.2	0.6	0.7	-3.8	-0.6	-5.5	-1.9
Soil C	-3.4	-1.6	-3.2	-1.1	-1.3	-1.5	-1.5	-1.5	-3.4	-1.5	-2.8	-1.4
Site 5 (Age_T=13, I_T=23%)												
$\overline{D}$	0.1	-1.2	4.8	0.0	0.0	0.0	0.0	0.0	1.2	-1.2	-1.2	1.2
$\overline{H}$	0.1	0.0	8.1	0.0	0.0	0.0	0.0	0.0	1.2	-1.2	-1.2	1.2
V_T	-1.2	0.9	7.4	-1.4	-0.6	0.4	4.6	-4.7	27.8	-24.3	-4.0	4.3
V_M	-0.2	-0.2	16.0	-1.1	-0.7	0.2	7.4	-7.4	49.6	-41.4	-9.4	11.1
Total biomass	-0.1	-0.1	-5.5	-4.3	0.4	0.3	0.0	0.0	-0.9	-0.1	0.3	-1.2
Soil C	0.3	0.1	-0.7	0.0	0.0	0.0	0.0	0.0	-0.1	-0.1	0.0	-0.1
Site 10 (Age_T=12, I_T=65%)												
$\overline{D}$	5.1	-3.4	0.9	0.0	0.0	0.0	0.0	0.0	0.9	0.0	-0.9	4.3
$\overline{H}$	7.5	0.0	6.5	1.9	0.0	0.0	0.0	0.0	6.5	1.9	-0.9	12.1
V_T	-4.4	5.9	3.9	0.2	1.5	0.4	7.2	-6.7	29.1	-20.1	-0.1	8.5
V_M	-2.1	3.6	4.6	0.2	1.4	0.4	8.5	-8.2	33.5	-24.0	0.2	10.4
Total biomass	-20.6	-0.5	-13.1	-9.2	1.3	0.5	0.1	-0.1	-16.5	-4.5	1.6	-28.9
Soil C	-1.0	0.1	-0.4	-0.3	0.0	0.0	0.0	0.0	-0.6	-0.1	-0.1	-0.7

Note: Age_T= Thinning age; I_T=Thinning intensity; $\overline{D}$= mean diameter at breast height; $\overline{H}$ = mean tree height; V_T and V_M represent total and merchantable volume, respectively; a, b, and c are the location, scale and shape parameters of the three-parameter Weibull distributions, respectively.

2.6 Discussion

2.6.1 Thinning routines

This study revealed the applicability of the model with regard to forest thinning simulations. TRIPLEX-Management provides multiple ways in which to quantify thinning intensity (e.g., I_{SD}, I_{Ba}, and I_V) applying thinning methods such as "thinning from below" and "thinning from above" to calculate effects of thinning on forest growth, timber yield, biomass, and C and N dynamics. The consideration of forest management within biogeochemical-mechanistic modeling is important since it extends the applicability of the model from unmanaged to managed forests (Petritsch *et al.*, 2007). Moreover, forest models should provide the information required for ecosystem management, forest certification, and sustainable management (Landsberg, 2003). The model is capable of simulating key variables related to thinning such as mean DBH, mean height, total stand volume, merchantable volume, biomass, C pools, etc. Management practices in terms of thinning in the 4C model are defined primarily by the intensity of thinning (e.g., basal area) and the size distribution of trees that were removed (Lasch *et al.*, 2005). Thinning in the FinnFor model is first based on a reduction in basal area and then a conversion to stand density (Garcia-GonzaloPeltola *et al.*, 2007b). In addition, several adapted BGC versions (Tatarinov and Cienciala, 2006, Petritsch *et al.*, 2007) rely on a reduction of biomass before converting stem C to volume growth per hectare using conversion factors. This study, however, simply tested the thinning intensity algorithm in relation to stand density and "thinning from below." Other algorithms used to calculate thinning intensity ($I_{Ba,}$ and I_V) and "thinning from above" must therefore be further tested through a greater number of measurements in relation to both different species and different sites in the future.

2.6.2 Diameter distribution and PCT

The TRIPLEX-Management model is able to predict timber yield (DBH>9cm) and implement managerial practices through the incorporation of empirical Weibull diameter distributions. Moreover, results from this study suggest that Weibull distributions can fit well in relation to stand structure for both unthinned and thinned stands, even if stand diameter distribution is considerably altered by PCT.

Most process-based models such as TRIPLEX1.0 do not include stand structure components. Although the 4C model has been developed as a physiology-based gap model applying a cohort approach, empirical Weibull distributions are also used within the 4C model for pole-sized stands by means of a stochastic approach related to thinning (Lasch *et al.*, 2005). Cohort approaches are also used within the FinnFor model (Kellomäki and Väisänen, 1997). The difference is the diameter distribution model is directly employed to quantify diameter distributions for thinned stands in the modified TRIPLEX-Management model. The model therefore does not predict diameter distributions in the five years after thinning occurs. The empirical Weibull diameter distribution model also underestimated the number of stems in the lower range of the diameter classes for certain PCT Jack Pine stands like site 1 (Figure 2.3E). This was likely the result of the empirical diameter distribution model's inability to seize the benefit of more growth space that resulted from the thinning treatment.

2.6.3 Forest growth, yield, and PCT

TRIPLEX-Management captures mechanisms that accelerate tree growth, reduce mortality, and increase both productivity and timber production by way of adding litterfall pools and empirically decreasing residual stand mortality. Overall R^2 between the simulated and observed thinning effects were 0.69 ($n=60$, $P<0.001$) with a slope of 0.76 and an intercept of 0.07 (Figure 2. 5). Several studies pertaining to PCT in relation to Jack Pine stands have indicated that PCT has a considerable and positive effect on both DBH growth and individual stem volume growth (Tong *et al.*, 2005, Zhang *et al.*, 2006, Morris *et al.*, 1994, Tong and Zhang, 2005). Similar results were found in most preceding experimental studies that investigated other tree species (Lei *et al.*, 2007, Mäkinen and Isomaki, 2004). A thinning simulation study conducted by Petritsch et al. (2007) also indicated that thinning enhances C allocation rates to stems and increases growth efficiency as a result of higher N use efficiency. This is according to the Monte-Carlo simulations used. Overall, the TRIPLEX-Management model is capable of simulating thinning management practices by incorporating a diameter distribution model.

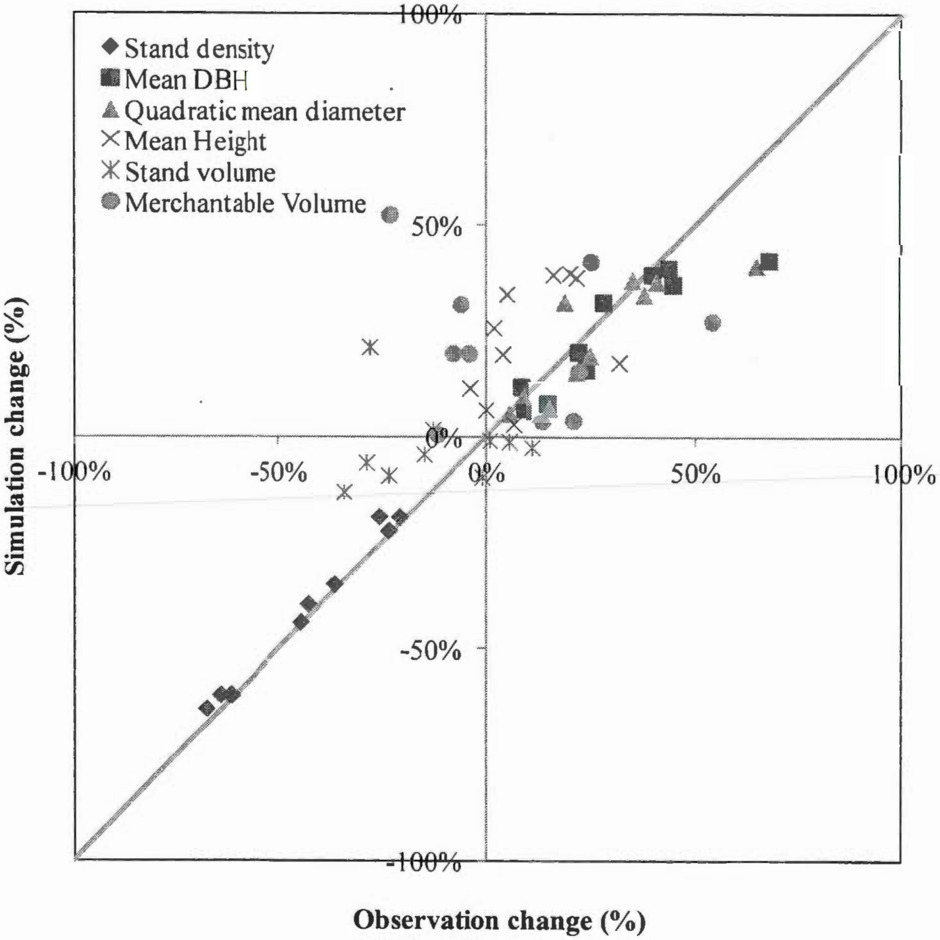

Figure 2.5 Scatter plot comparisons between the effects of PCT (=[PCT-Control]/Control) on basic stand characteristics such as stand density (trees ha^{-1}), mean diameter at breast height (DBH) (cm), the quadratic mean diameter (cm), mean tree height (m), stand volume (m^3 ha^{-1}), and merchantable volume (DBH>9cm) (m^3 ha^{-1}) for 10 sites located within northwestern Ontario in 2003. The solid diagonal representational line is the 1:1 line.

Sensitivity analysis for thinning regimes (thinning time and thinning intensity) used in this study agrees with previous thinning experimental studies where trees generally grew larger in stands in which heavy intensity thinning treatments were applied (Simard *et al.*, 2004, Lei *et al.*, 2007, Mäkinen and Isomäki, 2004b). However, results from this study indicate that PCT may not necessarily lead to high stand level total yield, especially in relation to heavy thinning treatments. Results of this study are supported by Goble and Bowling (1993), Tong et al. (2005), and Lei et al. (2007).

2.6.4 Potential application and future work

The TRIPLEX-Management model developed for this study provides a realistic tool to predict forest growth, timber yield, biomass production, and C and N dynamics. Assuming that forest management can be accurately quantified by means of forest inventory data, wide application will require continued research on three fronts.

First, stand level forest simulation studies must include a broader range of forest types and thinning prescriptions, and must be carried out for longer timeframes. The data set used in this study was limited to a relatively small range in stand age (26-36 years). Moreover, it possessed a single PCT treatment and was comprised of a single stand type within the boundaries of a single region. One of the primary goals in developing the TRIPLEX1.0 model was to scale up from stand to regional scales (Peng *et al.*, 2002). Regional application certainly depends on the composition of forest type, a broader age range, and diverse management strategies such as PCT, commercial thinning, harvesting, and N fertilization.

Second, it is critical to understand diameter distributions after forest management treatments take place for different tree species. Wood product value could be estimated based on size-dependent stem volume. For example, stand level product values were estimated using a combination of diameter distributions and individual tree product values (Newton and Amponsah, 2005). Forecasts for the stand level stem volume and merchantable volume or product value require a means to predict future diameter distributions (Liu *et al.*, 2009) and how diameter distribution is altered by forest management (e.g., thinning) decisions during forest development.

Third, forest thinning effects on soil C and N also require examination since soil C plays an important role in the global C cycle, especially in high latitude regions (Lal, 2005). Validation of the soil C pool was not possible in this study due to the lack of soil data available. Logistically speaking, PCT treatments may only result in a negligible disturbance on soil since heavy machinery is hardly used in this type of silvicultural treatment. Understanding changing processes in soil C and N dynamics under forest management practices, especially in relation to forest thinning, will prove important for model development and application.

2.7 Conclusions

TRIPLEX-Management, a new management submodel, was developed to simulate forest growth response to PCT treatments by way of incorporating diameter distribution into the TRIPLEX1.0 model. The implementation of forest thinning algorithms as reported by this study represents an important step towards improving the applicability of this process-based model for forest managers and industrial planning initiatives. Results demonstrate that the TRIPLEX-Management model is capable in capturing the growth response to PCT for Jack Pine stands in northwestern Ontario, although the model has a systemic negative bias to stands that exhibit reasonably good site conditions. It still allows for the analysis of not only impacts of forest management strategies on forest growth, timber yield, biomass, and C sequestration but also how potential climate change can affect forest management for a given forest ecosystem. Overall, the TRIPLEX-Management model is a realistic and flexible tool in which to investigate the potential effects of management strategies on forest growth and yield, biomass production, and C dynamics.

CHAPTER III

MODELING THE EFFECTS OF VARIOUS FOREST MANAGEMENT REGIMES ON CARBON DYNAMICS IN JACK PINE STANDS UNDER FUTURE CLIMATE

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3.1 Résumé

Les changements climatiques et ses effets potentiels sur les écosystèmes justifient le besoin d'implanter des stratégies d'aménagement qui augmentent la séquestration de carbone (C). Le modèle basé sur les processus TRIPLEX-Management a été utilisé pour déterminer comment augmenter la séquestration de C dans des forêts aménagées de pin gris (*Pinus banksiana* Lamb.). Les simulations ont inclus un scénario de climat constant et 2 scénarios de changement climatique générés à partir du modèle Coupled global climate Model (CGCM 3.1). Un total de 36 scénarios d'aménagement forestier (témoin sans aucun aménagement forestier, cinq régimes de longueurs différentes de rotation avant récolte, et des combinaisons de six régimes d'éclaircie et de cinq longueurs de rotation) ont été simulés sous chacun des scénarios de climat pour neuf sites caractérisés par des niveaux de densités relatives de 0.3 à 0.7. Une augmentation significative dans la séquestration de C a été obtenue sous les scénarios de changement climatique comparés aux scénarios témoins avec limat constant (($p<0.001$, n=30780, Test HSD de Tukey). La productivité moyenne nette de l'écosystème a varié avec la longueur de rotation ($p<0.001$, n=2565, ANOVA), mais n'a pas été affecté par l'éclaircie précommerciale ($p>0.94$, n=2565, ANOVA). Le réchauffement climatique peut engendrer des effets positifs limités de l'éclaircie sur la séquestration de C. Une diminution de la longueur de rotation de 70-80 années à 50 années peut accentuer la productivité nette de l'écosystème, augmenter la production de bois et diminuer le risque des impacts des changements climatiques sur les forêts de pin gris.

Mots-clés: gestion durable des forêts, âge de rotation, gestion du carbone, carbone organique du sol

3.2 Abstract

Climate change and its potential effects on ecosystems justify the need to implement forest management strategies that increase carbon (C) sequestration. A process-based model, TRIPLEX-Management, was used to investigate how to increase C sequestration within managed jack pine (*Pinus banksiana* Lamb.) forests. The simulations included a constant climate scenario and two climate change scenarios generated from the Coupled Global Climate Model (CGCM 3.1). A total of 36 forest management scenarios (a control where no forest management occurred, five varied rotation length harvesting only regimes, and combinations of six thinning regimes and five rotation lengths) were simulated under each climate scenario for nine sites characterized by stocking levels from 0.3 to 0.7. A significant increase in C sequestration was generated under the climate change scenarios compared to those under constant climate ($p<0.001$, n=30780, Tukey's HSD). Mean annual net ecosystem productivity (NEP) varied with rotation length ($p<0.001$, n=2565, ANOVA) but was not changed by pre-commercial thinning ($p>0.94$, n=2565, ANOVA). Climate warming might enhance limited positive effects of forest thinning on C sequestration. Shortening rotation length from 70-80 years to 50 years might enhance NEP, increase wood production, and decrease the risk of climate change impacts on jack pine forests.

Keywords: sustainable forest management, rotation age, carbon management, soil organic carbon, stem-only tree harvesting

3.3 Introduction

The influence of forest management practices on forest carbon (C) cycling is now widely accepted (Brown et al. 1996; Liu et al. 2011). Within the context of global climate change, this recognition has sparked the development and evolution of forest management strategies as a means of mitigating global climate change (Malmsheimer et al. 2008; D'Amato et al. 2011; Law and Harmon 2011). Two general approaches have been proposed to mitigate climate change relative to existing forests: (1) increase in C stock on-site or in harvested wood products (e.g., Seidl et al. 2007; Chen et al. 2008) and (2) substitute fossil fuels with bioenergy (e.g., Malmsheimer et al. 2008; Hudiburg et al. 2011). Nonetheless, traditional silvicultural research has focused primarily on timber production, thus leaving a knowledge gap in current efforts to develop sustainable forest management strategies that will increase C stocks on-site as well as in harvested wood C under conditions of a changing climate.

Forest management is an anthropogenic disturbance that has a great potential to affect the C cycle (Liu et al. 2011). For example, forest thinning can be used early in stand development to enhance individual-tree diameter and volume growth, but not necessarily increases the overall C stock. It is thus equivocal as to whether thinning increases the overall C stock as increased growth is offset by tree removal (e.g., Tong et al. 2005; Lei et al. 2007). Stand-replacing harvests would also lead to C losses directly or indirectly through the conversion of C stored in living trees to C stored in harvested wood as well as through the decomposition of logging debris, litterfall, and soil organic C (Amiro et al. 2010; Grant et al. 2010; Liu et al. 2011). Many studies have thus suggested that increasing rotation lengths could enhance C sequestration (Liski et al. 2001). However, a recent modeling study conducted by Wang et al.(2012b) projected growth decline in old boreal forests due to water limitations, indicating that prolonging rotation length may not increase C sequestration in boreal forests. It is thus unclear as to whether forest management could lead to increased capture of C in forest ecosystems over a long time period. In particular, the effects of treatment combinations remain to be examined in more depth.

As one of the aims of sustainable forest management is to respond to future environmental changes (Spittlehouse and Stewart 2003; Millar et al. 2007), the use of forest simulation models has become an important step in the decision making process for managed forests in a changing environment (Peng 2000). Process-based models are particularly useful in forest research and management under changing climate conditions (Mäkelä et al. 2000; Pretzsch et al. 2008), since such models can be used to analyze the potential response of forests to forest management practices and environmental change (e.g., Garcia-Gonzalo et al. 2007; Wang et al. 2011).

The objective of this study is to investigate if it is possible to increase C sequestration in forests that are harvested by the forest industry to produce wood products (timber) under changing climatic conditions. We hypothesized that future climate change can potentially increase on-site C sequestration and forest management practices could increase C sequestration over a given temporal scale under conditions of a changing climate when C stored in harvested wood is accounted for.

3.4 Methods

3.4.1 Study sites and data collection

Jack pine (*Pinus banksiana* Lamb.) is the most widely distributed pine species and a major commercial softwood species in North America. A thinning experiment for jack pine stands conducted in northwestern Ontario (Tong et al. 2005) was used to validate the model by Wang et al. (2011) and as the simulation basis of this study. In the 1970s, pre-commercial thinning, using brush saws, was applied to ten selected naturally regenerated or seeded jack pine stands. In total, ten 0.01 ha plots were established on each site, five of which were control stands and five of which were stands treated by thinning. These plots were measured once in 2003 (Table 1). Nine sites were included in this study altogether, representing the different stocking levels in the range of 0.3-0.7. The thinning time is within the range of 11-15 years, and the thinning intensity in terms of stand density is in the range of 23-68% of tree removal. More detailed site descriptions and model validation information can be obtained in the reports published by Tong et al (2005) and Wang et al. (2011).

(Table 1)

Sandy soil with good soil drainage is the typical soil condition corresponding to pure jack pine forests with high productivity (site index 18-20 m) in northwestern Ontario (OMNR 1997). Soil data in the study area were collected from the National Soil Database (NSDB) made available by the Canadian Soil Information System (CanSIS) (Siltanen et al. 1997). Soil organic C ranges from 12 to 40 t ha^{-1} in pure jack pine stands of northwestern Ontario (Siltanen et al. 1997). The mean annual temperature is 2.1 °C and the mean annual precipitation is 776.7 mm (the 30-year mean during 1981–2010 at the Sioux Lookout weather station, 50.1° N, 91.9° W, Environment Canada). Climate data including monthly mean, maximum, and minimum temperatures, as well as monthly precipitation from 1938 to 2010 were downloaded from National Climate Data and Information Archive (http://climate.weatheroffice.gc.ca, the Sioux Lookout weather station). The minimum temperature was assumed to be equal to dew point to estimate relative humidity (Running et al. 1987).

Table 3.1 Site information based on Tong et al. (2005).

Site	Stand	Age (Year)	Age_T (Year)	I_T(%)	*SD* (trees/ha)		DBH (cm)		Tree height (m)		V_M (m^3 ha^{-1})		Total living biomass (Mg ha^{-1})*	
					Control	PCT	Control	PCT	Control	PCT	Control	PCT	Control	PCT
1	Furniss road	36	14	43	4080	2340	9.1 (3.15)	11.1 (4.90)	9.8 (3.38)	10.2 (4.46)	117.5	143.4	97.0	82.5
2	Reba road	36	15	36	2700	1720	10.9 (3.82)	13.5 (4.07)	10.1 (3.83)	13.3 (3.48)	133.2	161.0	91.3	110.3
3	Encamp	26	12	44	2840	1580	9.3 (5.35)	11.9 (4.56)	8.1 (4.00)	9.4 (3.44)	121.4	93.5	59.4	58.9
4	Mack 1	26	13	62	5740	2180	7.8 (2.74)	10.9 (2.52)	8.5 (3.29)	10.2 (1.94)	90.5	85.0	90.9	74.4
5	Mack 5	26	13	23	5260	4040	8.2 (3.08)	8.9 (3.31)	10.3 (2.27)	9.9 (2.54)	104.4	100.0	109.0	93.2
6	Nelson Lake	31	11	25	2200	1640	11.9 (3.88)	13.0 (2.61)	9 (1.65)	9.6 (1.58)	107.6	95.0	79.2	73.3
7	Mack 2	26	12	68	4260	1360	8.4 (2.61)	14.1 (3.08)	9.3 (1.50)	11.3 (1.69)	110.5	71.6	83.7	81.1
8	Mack 3	26	12	63	5820	2180	7.8 (2.36)	11.2 (2.14)	9.8 (1.30)	10.3 (0.99)	90.0	72.0	105.3	78.8
9	Mack 4	26	12	65	4940	1740	8.5 (2.85)	12.3 (2.12)	10.1 (1.70)	10.3 (1.07)	98.9	91.0	107.0	74.6

Note: Age_T= Thinning age; I_T=Thinning intensity; *SD* = stand density; PCT represents pre-commercial thinning; DBH represents diameter at breast height; V_M represents merchantable volume.

* Estimated based on biometric equations provided by Lambert et al. (2005).

3.4.2 The model

This study used a process-based model, TRIPLEX-Management, originally designed by Peng et al. (2002b). It integrates functions of three well-established models, 3-PG (Landsberg and Waring 1997), TREEDYN3.0 (Bossel 1996), and CENTURY4.0 (Parton et al. 1993) to simulate forest growth, and C and nitrogen (N) cycling at a stand level. To predict the effects of thinning treatments on forest growth, timber yield, and C sequestration, a version of TRIPLEX-Management has recently been developed by Wang et al. (2011).The TRIPLEX-Management version has dutifully inherited the structure and representations of the original TRIPLEX model (Figure 3.1).

Climate driving forces include monthly mean temperature, monthly precipitation and monthly mean relative humidity. In the model, gross primary productivity (GPP) is estimated based on absorbed photosynthetically active radiation, leaf area index and a conversion constant with modifiers constrained by forest age, air temperature, soil water, nitrogen and frost duration within a month (Landsberg and Waring 1997). Maintenance respiration is calculated based on a Q_{10} function multiplied by the C content of each plant component (foliage, roots, and wood). Growth respiration is assumed to be one fifth of the remaining amount of photosynthesis production. Net primary productivity (NPP) is allocated to stems, branches, foliage, and coarse and fine roots based on allocation parameters. Soil organic C decomposition is generally based on the CENTURY soil decomposition submodel (Parton et al. 1993). Net ecosystem productivity (NEP) is the difference between GPP and total ecosystem respiration. Water balance is quantified on the difference of precipitation and water loss through evaportranspiration and drainage. Canopy transpiration is estimated using the Penman-Monteith equation. Water is drained if the soil water holding capacity of bottom layer in rooting zoon is exceeded.

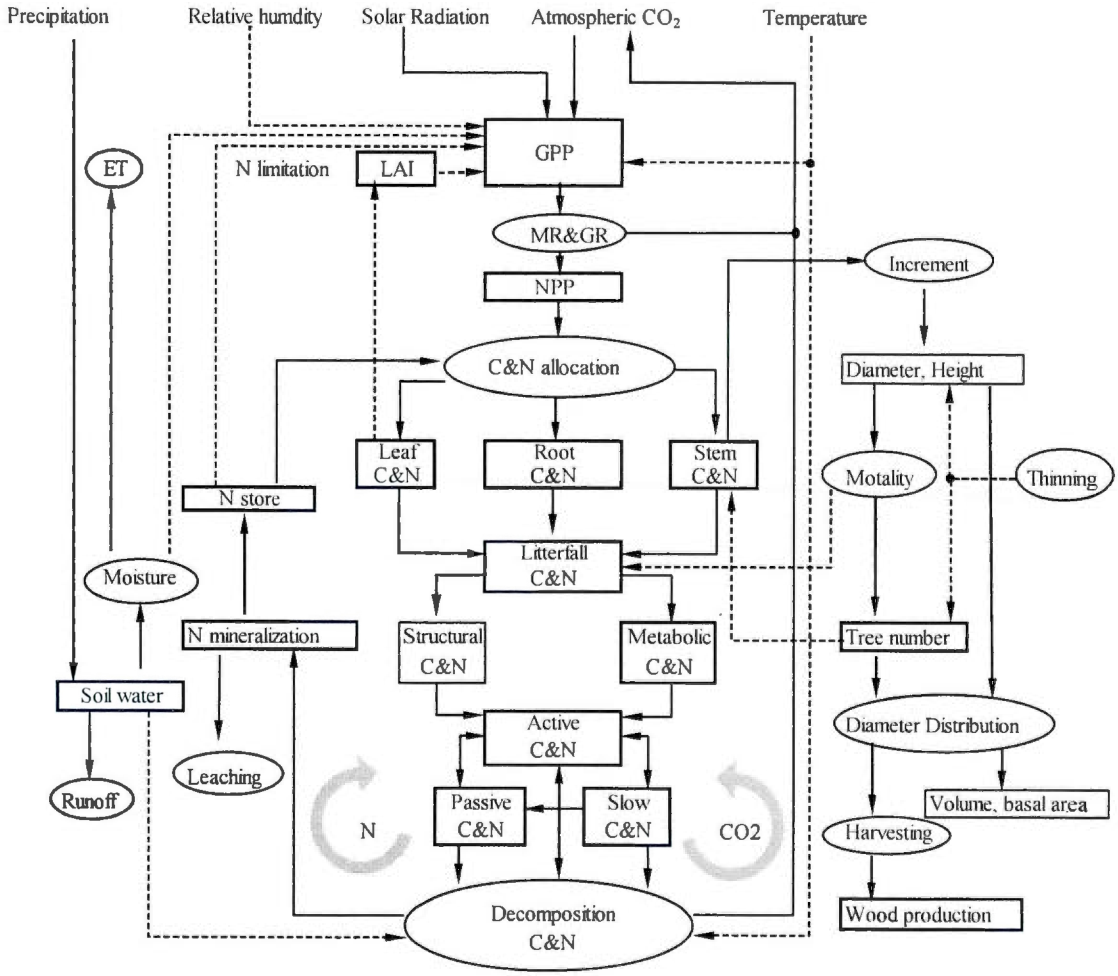

Figure 3.1 The structure of the TRIPLEX model (from Wang et al., 2012). Rectangles and ovals represent key pools or state variables and core simulation process, respectively. Dashed lines represent controls, and solid lines represent flows of C (C), nitrogen (N), water, and the fluxes between the forest ecosystem and external environment. Two arrow cycles refer to feedbacks. GPP represents gross primary productivity; MR and GR represent maintenance respiration and growth respiration, respectively; NPP represents net primary productivity; ET represents evapotranspiration.

Table 3.2 Values of key species-specific parameters used in simulations of the TRIPLEX-Management model.

Parameter	Description	Value	Reference
Gross primary productivity			
BlCond	Canopy boundary layer conductance (ml m^{-2} s^{-1})	0.2	Landsberg and Waring (1997)
MaxCond	Max canopy conductance (ml m^{-2} s^{-1})	0.02	Landsberg and Waring (1997)
StomCond	Stomata conductance (ml m^{-2} s^{-1})	0.006	Landsberg and Waring (1997)
ExtCoef	Radiation extinction coefficient	0.5	Landsberg and Waring (1997)
TaMin	Min temperature (°C) for growth	0	Data[*]
TaMax	Max temperature (°C) for growth	30	Peng et al. (2002b)
Topt	Optimum temperature (°C) for growth	15	Kimball et al. (1997)
Nitrogen factor	Nitrogen factor for tree growth	0.2	Set as 20% for growth
Na	Effect of age to GPP	3	Landsberg and Waring (1997)
Sla	Specific leaf area (m^2 kg^{-1} of C)	6	Kimball et al. (1997)
Net primary productivity			
GamaF	Leaves turnover per year	0.19	Gower et al (1997)[†]
GamaR	Fine roots turnover per year	1.55	Steele et al. (1997)[‡]
Growth and yield			
MiuNorm	Normal mortality (yearly)	0.012	Assumption
MiuCrowd	Competition mortality (yearly)	0.02	Assumption
Soil C and N			
Lnr	Lignin-nitrogen ratio	0.26	Parton et al. (1993)
Ls	Lignin for leaf, fine root, coarse root, branch, and wood	0.215, 0.215, 0.255, 0.235, 0.255	Parton et al. (1993)
Soil water			
A1, A2, A3	Soil water depth of layer 1,2, and 3 (cm)	4, 6, 28	Data[*]
S1F, S2F, and S3F	Field capacity of layer 1, 2, and 3 (m^3 m^{-3})	0.21, 0.06, 0.05	Data[*]
S1W, S2W, and S3W	Wilting point of layer 1, 2, and 3 (m^3 m^{-3})	0.07, 0.04, 0.03	Data[*]
Species parameter			
CSP	Wood C density (Mg m^{-3})	0.22	Newcomer et al. (2000)
CD	Crown to stem diameter ratio	20	Bossel (1996)
AlphaC	Canopy quantum efficiency	0.05	Landsberg and Waring (1997)
MaxHeight	Max height (m)	20	Assumption
AgeMax	Max stand age (year)	150	Assumption

* Estimated based on the old jack pine site (Fluxnet-Canada) in Saskatchewan, Canada.

†Estimated based on results (0.08-0.36 $year^{-1}$) of Gower et al (1997).

‡Estimated based on results (1.4-3.3 $year^{-1}$) of Steele et al. (1997).

Forest thinning is driven by the time of thinning, thinning type (thinning from below and from above), and thinning intensity (Wang et al. 2011). A diameter distribution model was incorporated to quantify thinning intensity for a given thinning type (Wang et al. 2011). In the model, forest thinning slash is integrated to the corresponding litter pools. The forest thinning submodel was validated against a thinning experiment for jack pine forests in northwestern Ontario (Wang et al. 2011). A more detailed description of the mathematical algorithms and sensitivity analyses of the model have been previously reported in Peng et al. (2002b) and Wang et al. (2011).

Several papers (e.g., Peng et al. 2002b; Wang et al. 2012; Zhou et al. 2005) have reported on the validation of TRIPLEX and its performance in relation to jack pine. The set of species-specific parameters used in this study (see Table 3.2) were mostly left unchanged. A more detailed description of the mathematical algorithms and sensitivity analyses of the model have been previously reported in Peng et al. (2002b) and Wang et al. (2011).

3.4.3 Harvest considerations and regeneration inputs in simulations

The implementation of harvesting scenarios included harvest type and rotation age. Two different harvesting methods that include stem-only tree harvesting (100% stem removal with branches and foliage left *in situ*) and whole tree harvesting (100% stem removal with branches and foliage removed from the harvest block) were implemented. Logging slash was estimated at 20% (Grant et al. 2010). After harvesting, total C stored in harvested wood (C_{HWC}) was calculated as:

$$C_{HWC} = C_{stem}\frac{V_M}{V_T} \qquad (1)$$

where C_{stem} is the stem C; V_M and V_T represent merchantable volume (diameter at breast height, DBH>9cm) and total volume, respectively.

Since TRIPLEX-Management does not include a tree regeneration sub-model, a uniform tree species and an initial stand density of 18,000 stems per ha (from a possible range between 10,000 and 50,000 stems per ha, Goble and Bowling 1993) were assumed for fully stocked stands in order to simulate regeneration. Initial stand density for each specific site depended on-site classes and estimated stocking levels in the model. No forest management or climate change impacts on forest regeneration were considered in the model.

3.4.4 Simulation experiments

3.4.4.1 Climate change scenarios

Three climatic scenarios were generated for the period between 2011 and 2099, i.e., one constant climate scenario where no change in climatic conditions took place and two future climate change scenarios (A2 and B1) predicted via the Coupled Global Climate Model (CGCM3.1), a General Circulation Model (GCM), under the auspice of the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A2 and B1 C dioxide emission scenarios. The constant climate scenario was compiled using a repeating cycle of the real sequence of 20-yr data (temperature, precipitation, and relative humidity) of the period 1991–2010. The IPCC SRES A2 emissions scenario assumes economic growth in a heterogeneous world, resulting in the highest temperature increases (2.0–5.4°C) by 2100 compared to 1990 (IPCC 2001) whereas the IPCC SERS B1 emissions scenario assumes lower levels of fossil fuel consumption in a globalized world, leading to lower temperature increases (1.1–2.9°C) by 2100 (IPCC 2001).

Monthly mean temperature is projected to increase by 2.5–6.7°C and 2.0–4.7°C for A2 and B1 climate scenarios, respectively (Figure 3.2). The greatest temperature increases are projected to occur during winter. CO_2 concentrations were taken as a global mean of the available IPCC SERS A2 and B1 emission scenarios. Monthly precipitation in northwestern Ontario under both A2 and B1 scenarios is projected to increase by 45% and 40%, respectively, by the end of the 21st century (Figure 3.2). However, slight decreases during growing seasons were also predicted.

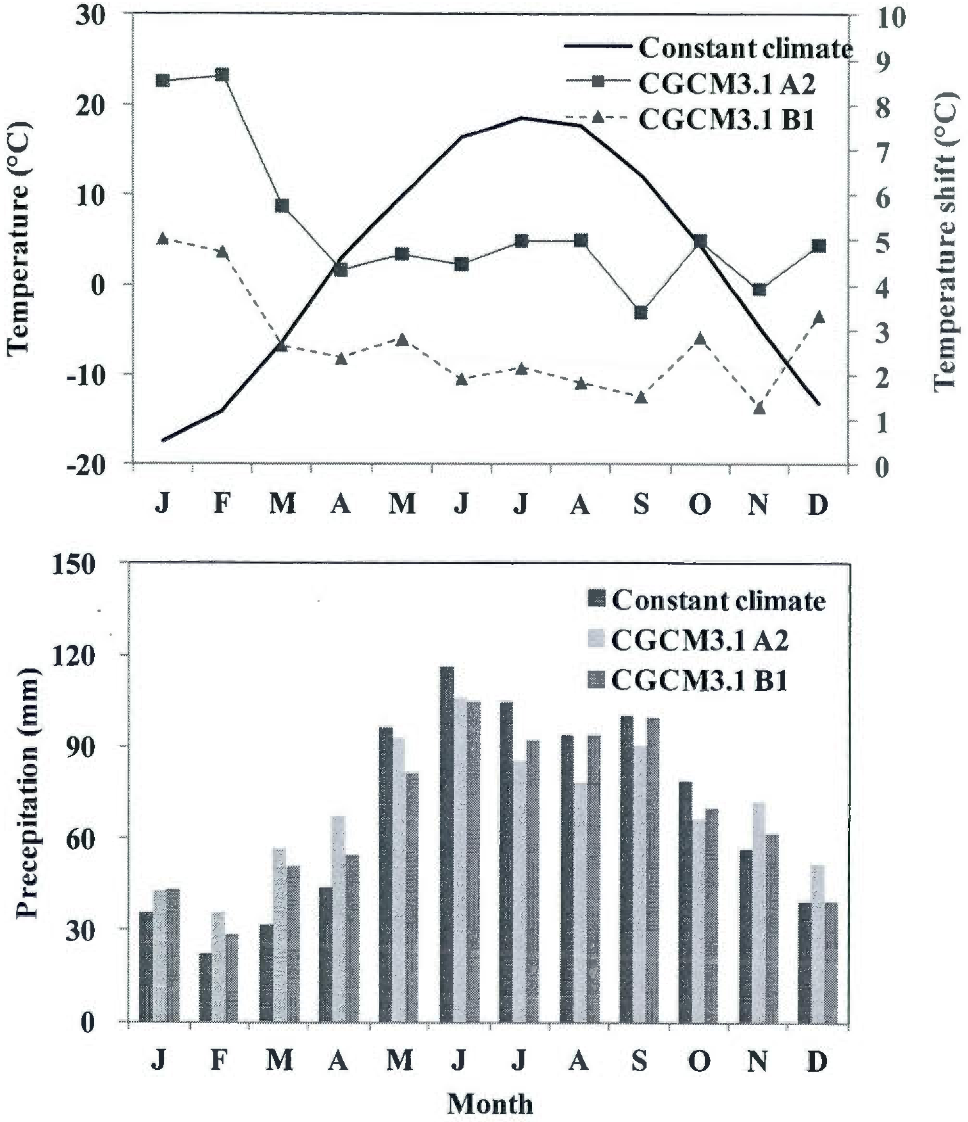

Figure 3.2 Applied scenarios of climate change from 2080-2099 (20-year monthly mean) relative to historical climate from 1981-2000: historical monthly mean temperature and shifts of mean monthly temperature under two climate change scenarios (top) and historical monthly precipitation and precipitation under two climate change scenarios (bottom).

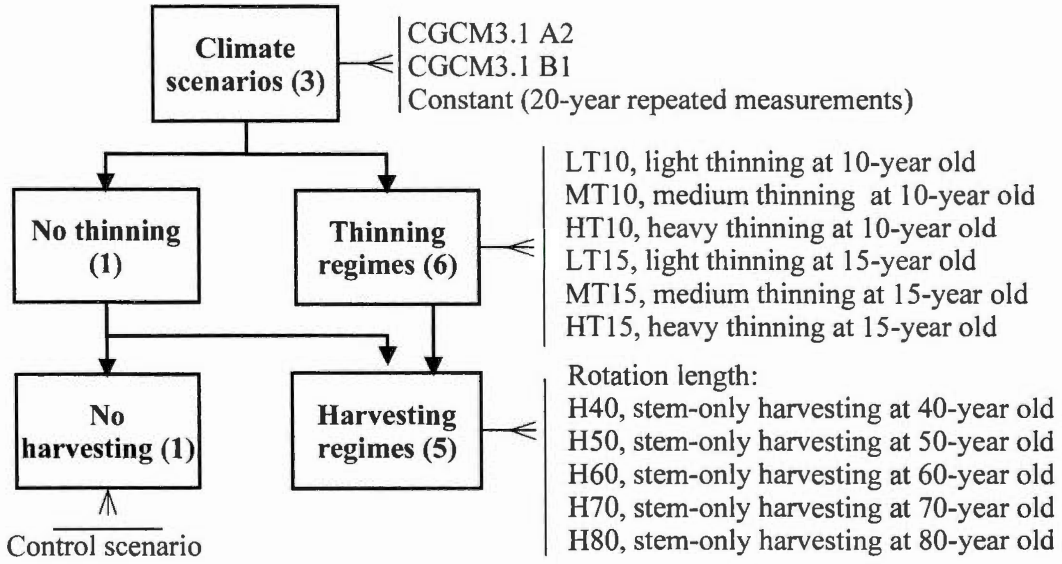

Figure 3.3 Schematic applied scenarios illustrating climate change and forest management regimes (thinning and harvesting). A simulation was assembled by one element from each step. Light, medium, and heavy thinning represent 20%, 40%, and 60%, respectively, tree removal relative to stand density.

3.4.4.2 Forest management scenarios

Procedures for forest management regimes in this study include pre-commercial thinning (thinning time and thinning intensity) and stem-only tree harvesting (rotation length) (Figure 3.3). Pre-commercial thinning in high density and young (eight to 15 years old) jack pine stands can be a cost-effective way to accelerate individual tree growth (e.g., DBH growth and stem wood production), reduce mortality, and shorten rotation length (e.g., Goble and Bowling 1993; Tong *et al.,* 2005). Six thinning regimes were developed based on a combination of three thinning intensities (light: 20% stem removal, medium: 40% stem removal, and heavy: 60% stem removal) and two thinning times (10 and 15 years after stand regeneration).

Rotation lengths of 70 to 80 years have been recommended for dense jack pine forests in northwestern Ontario (Goble and Bowling 1993). Five optional rotation ages of 40, 50, 60, 70, and 80 years were combined with different thinning regimes given that jack pine reacts well to pre-commercial thinning, which can reduce rotation age (Goble and Bowling 1993). No alternative options for harvesting, logging, and regeneration methods were considered in this study. Thus, for the grouping of the stem-only harvesting method (100% stem removal, branches and needles left *in situ*), the tree-length logging method (trees cut at the stump), and seed regeneration were simulated in this study as recommended by the Ontario Ministry of Natural Resources (OMNR 1997).

It was assumed that clearcuts was conducted in 2004 and trees started to regenerate in 2005. A full silvicultural system simulation for the scenario period (2005-2099) was grouped by choosing one element from each step shown in the forest management procedure listed above (Figure 3.3). A total of 36 forest management scenarios (including the control scenario where no management occurs) were simulated under three climate change scenarios, representing a matrix of 108 scenarios per site.

3.4.5 Indicators and statistical analysis

NEP and the C stocks from the different pools (soil organic C, litter C, belowground and aboveground C, and harvested wood C) were key simulation outputs from the nine different sites. NEP was assigned as mean values throughout the scenario simulation period (from 2005 to 2099). Harvested wood C (after harvesting treatments) was simply accumulated and ready for transferring to wood product sector. The values for ecosystem C pools were tabulated for comparisons in the last year simulated (2099). Management regimes under the same rotation length were considered as a same management group.

Climate change and management regimes effects on C uptake and C stocks in each C pool (soil organic C, living belowground C, living aboveground C, litter C, harvested wood C) were examined using two-way analysis of variance (ANOVA). Combined effects of the varied forest management regimes and climate change scenarios were also tested. For all ANOVA tests, residuals were tested for homoscedasticity and data transformed as necessary. In cases where transformation could not achieve normality, a non-parametric ANOVA was used. Differences in target variables among the different silvicultural treatments were examined using *post hoc* Tukey's tests. All statistical analyses were conducted with a significance level of 0.05, using the R programming language (R Development Core Team, 2009).

3.5 Results

3.5.1 Effects of climate change on C sequestration

Simulated annual NEP under the A2 climate scenario was the greatest among the three climate scenarios (A2, B1, and constant climate) at the beginning of stand development (e.g., Figure 3.4 A, B, and C) for all 36 management scenarios. However, the model predicted old forests (>80 years) to function as moderate C sources in the control sites (no management) under the A2 climate scenario at the end of the twenty-first century (Figure 3.4 A). Each C pool in the simulated study sites generally increased throughout the simulation period if annual NEP was positive (Figure 3.4 D).

Mean annual NEP throughout the scenario simulation period (2005-2099) for all 36 management scenarios (including the control scenario) was significantly affected by climate ($p<0.001$, n=30780, ANOVA, Table 3.3). The lowest level of mean annual NEP occurred under the constant climate scenario. Mean annual NEP under the constant climate scenario was considerably lower than those under the A2 and B1 climate scenarios ($p<0.001$, n=30780, Tukey's HSD, Figure 3.5 A). However, no significant difference in annual NEP was found between the A2 and B1 climate scenarios ($p>0.283$, n=30780, Tukey's HSD, Figure 3.5 A).

The greatest C stocks in each C pool, predicted for the harvested wood C pool in the final year (2099), generally occurred under the B1 climate scenario ($p<0.001$, n=324, Tukey's HSD, Figure 3.5 B). Significant differences in C stocks were determined for the tree C pools (aboveground and belowground C) and the litter C pools ($p<0.001$, n=324, Tukey's HSD, Figure 3.5 B) under the B1 climate scenario compared to the other two climate scenarios (A2 and the constant). However, no significant difference were determined for soil organic C ($p=0.35$, n=324, Tukey's HSD, Figure 3.5 B) under the B1 compared to the A2 climate scenario. Generally, the model predicted the lowest C stock levels in each C pool under the constant climate scenario ($p<0.001$, n=324, Tukey's HSD, Figure 3.5 B). Nevertheless, there was no significant difference in the litter C pool between the constant climate and A2 climate scenarios ($p=0.94$, n=324, Tukey's HSD, Figure 3.5 B).

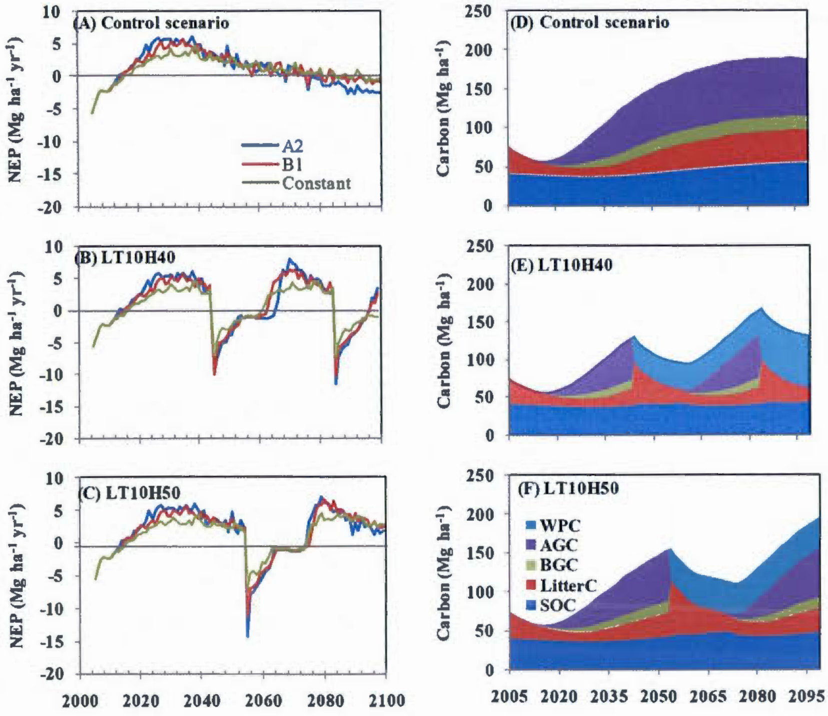

Figure 3.4 Simulation output time series of net ecosystem productivity (left) under three climate scenarios (A2, B1, and constant climate) for the control sites (A, unmanaged) and two selected management scenarios (B, the management regime of LT10H40 represents light thinning at 10-year old and harvesting at 40-year old; C, another regime of LT10H50 represents light thinning at 10-year old and harvesting at 50-year old) and carbon pools (right) under the constant climate scenario for the control site (D), LT10H40 (E), and LT10H50 (F). The values represent means of 9 sites that have different estimated stocking levels. Chronosequences start from the assumed regeneration year in 2005 and end in 2099. SOC: soil organic carbon; Litter C; AGC: aboveground living biomass carbon; BGC: belowground living biomass carbon; HWC: harvested wood carbon.

Table 3.3 Summary of ANOVAs for analyses of climate change (CC) and forest management (M) effects on net ecosystem productivity (NEP), total carbon (TC), harvested wood carbon (HWC), total ecosystem carbon (TEC), soil organic carbon (SOC), litter C, aboveground C (AGC) and belowground C (BGC). Bold font indicates that the difference is not statistically significant.

Forest management regimes	**Source**	**df**	**NEP**	**TC**	**HWC**[*]	**TEC**	**SOC**	**Litter C**	**AGC**	**BGC**
			p	*p*	*p*	*p*	*p*	*p*	*p*	*p*
All[*]	CC	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	M	34	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	CC×M	68	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Harvest only	CC	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	M	5	<0.000	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	CC×M	10	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
G-H40[†]	CC	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	M	6	**1**	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	CC×M	12	**1**	<0.001	**0.647**	<0.001	0.021	<0.001	<0.001	<0.001
G-H50[†]	CC	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	M	6	**1**	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	CC×M	12	**1**	<0.001	0.007	<0.001	0.028	0.048	<0.001	<0.001
G-H60[†]	CC	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	M	6	**0.947**	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	CC×M	12	**1**	<0.001	0.018	<0.001	**0.163**	<0.001	<0.001	<0.001
G-H70[†]	CC	2	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	M	6	**1**	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
	CC×M	12	**1**	<0.001	0.033	**0.206**	**0.519**	<0.001	<0.001	<0.001
G-H80[†]	CC	2	<0.001	<0.001	<0.001	<0.001	0.000	<0.001	<0.001	<0.001
	M	6	**0.996**	<0.001	<0.001	<0.001	0.013	0.019	<0.001	<0.001
	CC×M	12	**1**	<0.001	<0.001	<0.001	<0.001	<0.001	0.002	0.002

[*] Excludes the control scenario where no management occurred.

[†] G-H40 represents the group of management regimes with 40-year rotation length and different thinning regimes. In the same manner, G-H50, G-H60, G-H70, and G-H80 represent the similar groups.

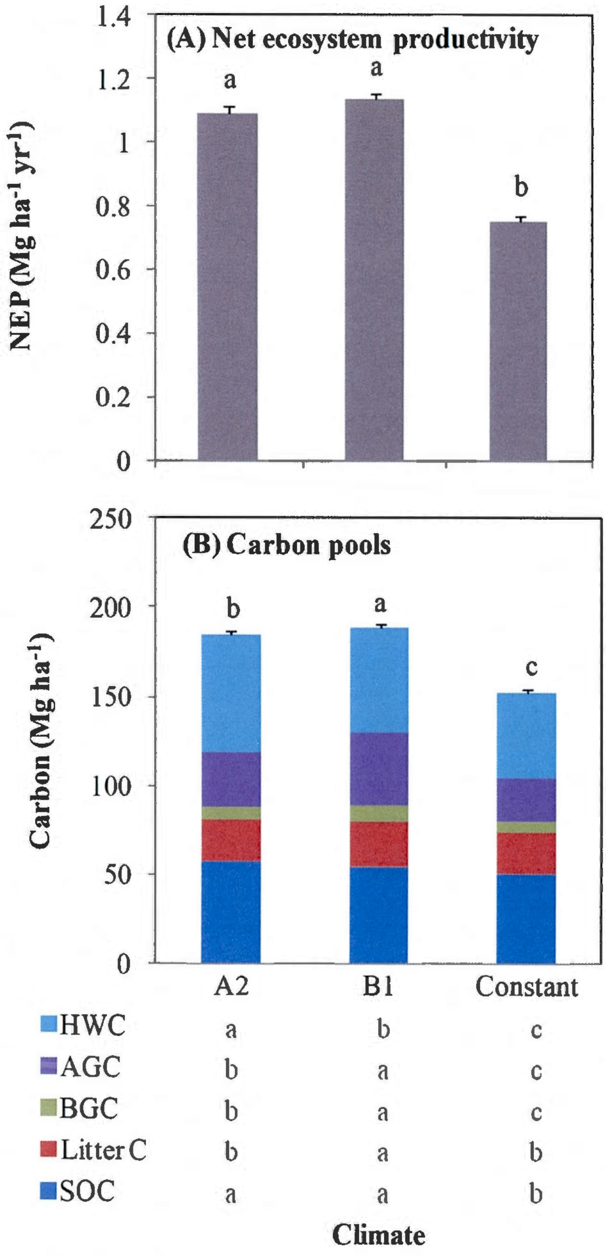

Figure 3.5 Mean (A) annual net ecosystem productivity (NEP) and (B) carbon stocks under different climate scenarios (A2, B1, and constant climate). Different letters below the graph indicate significant differences among treatments in each C pool (Tukey's HSD, $p<0.05$). Error bars represent standard errors. SOC: soil organic carbon; AGC: aboveground living biomass carbon; BGC: belowground living biomass carbon; HWC: harvested wood carbon.

3.5.2 Forest management effects on C sequestration

3.5.2.1 Model predictions

Simulated annual NEP throughout the simulation period or rotation cycle generally took the form of an inverted U shape (e.g., Figure 3.4 A, B, and C). Scheduled clearcuts resulted in C losses for several years following harvesting (e.g., Figure 3.4 B and C). Sharp declines in tree C (for both aboveground and belowground tree parts) for all 35 management scenarios were due to scheduled harvests (e.g., Figure 3.4 E and F). Living tree C after harvesting flowed directly into the C pools of the harvested wood (DBH > 9cm) and the litter C pool (harvesting residues: limbs, tops, and very small trees). Thus, sharp increases in litter C pools and the harvested wood C pools were predicted after harvesting (Figure 3.4 E and F). Litter C slowly decreased due to decomposition until inflow (fine root mortality, leaf mortality, and tree mortality) became larger than outflow (decomposition). The soil organic C pool changed little under management scenarios (Figure 3.4 E and F).

3.5.2.2 Effects of forest thinning within the same rotation length

Forest thinning regimes under the same rotation length influenced mean annual NEP throughout the entire scenario simulation period, but insignificantly (p>0.94, n=2565, ANOVA, Table 3.3). Soil organic C decreased with increased thinning intensity (Table 3.4). Moreover, total ecosystem C and total C (sum of total ecosystem C and harvested wood C) generally declined with increased thinning intensity, except for thinning regimes where thinning occurred at 10 years old under the B1 climate scenario (Table 3.4). However, harvested wood C increased with increased thinning intensity with the exception of thinning regime occurred at 15 years old under the A2 climate scenario (Table 3.4), indicating forest thinning generally enhances the growth of individual harvestable tree.

Table 3.4 The effects of thinning regimes on carbon pools under the three climate scenarios (A2, B1, and constant climate). Values are the mean percentage change rates under each thinning regime compared to the corresponding rotation length (clearcut only scenarios: the time span of 40, 50, 60, 70, and 80 years and no thinning treatments occurred). Values in parentheses are standard deviations. The letters of "LT", "MT", and "HT" represent light thinning with 20% removal of trees, medium thinning with 40% removal of trees, and heavy thinning with 60% removal of trees, respectively. The numbers after those letters represent thinning time (years). SOC: soil organic carbon; HWC: harvested wood carbon; TEC: total ecosystem carbon, and TC: total carbon.

	SOC	*WPC*	*TEC*	*TC*
A2				
LT10	1.5 (2.7)	2.2 (1.3)	1.8 (2.9)	1.5 (2.0)
MT10	0.9 (3.0)	2.5 (1.9)	1.0 (3.9)	1.1 (2.6)
HT10	0.7 (3.0)	2.7 (2.2)	−1.2 (2.9)	−0.2 (1.7)
LT15	1.1 (2.7)	1.9 (1.5)	1.7 (4.2)	1.5 (2.7)
MT15	0.6 (2.9)	1.8 (2.0)	0.3 (4.1)	0.4 (2.6)
HT15	0.0 (3.0)	1.7 (2.3)	−2.2 (5.3)	−1.1 (2.9)
B1				
LT10	0.1 (0.9)	2.1 (1.5)	0.0 (0.5)	0.0 (0.6)
MT10	−1.2 (2.8)	2.4 (1.8)	1.8 (4.3)	1.1 (3.0)
HT10	−2.9 (3.2)	2.7 (2.3)	3.6 (5.0)	1.9 (2.7)
LT15	0.1 (0.7)	2.0 (1.7)	−0.3 (0.9)	−0.2 (0.4)
MT15	−0.5 (0.3)	2.2 (2.0)	−1.2 (0.9)	−0.9 (0.6)
HT15	−1.2 (0.4)	2.4 (2.3)	−2.2 (1.4)	−1.5 (1.0)
Constant				
LT10	−0.4 (1.2)	2.0 (2.1)	0.2 (2.1)	−1.0 (2.1)
MT10	−0.6 (1.1)	3.2 (3.6)	0.2 (2.1)	−0.9 (2.1)
HT10	−1.0 (0.5)	5.0 (5.3)	−0.6 (1.3)	−0.9 (1.4)
LT15	−0.8 (1.5)	1.5 (1.8)	0.3 (3.2)	−1.1 (3.0)
MT15	−1.3 (1.4)	2.5 (2.8)	−0.5 (3.3)	−1.6 (3.1)
HT15	−1.9 (1.2)	3.7 (4.4)	−1.4 (2.2)	−1.9 (2.3)

3.5.2.3 Rotation length effects

Rotation length significantly affected mean annual NEP ($p<0.001$, n=2565) and C stocks within each C pool ($p<0.001$, n=27, Table 3.3). Predicted mean annual NEP was significantly greater under H50 (for which harvesting was conducted after a time span of 50 years and no thinning treatments occurred) than under the other four harvesting only scenarios (H40, H60, H70, and H80) as well as the control scenario ($p<0.001$, n=2565, Tukey's HSD, Figure 3.6 C). Predicted mean annual NEP under the control, H40, H60, and H80 scenarios generated the second highest levels ($p<0.05$, n=2565, Tukey's HSD, Figure 3.6 C). However, the model predicted the lowest level of mean annual NEP under H40, H70, and H80 scenarios.

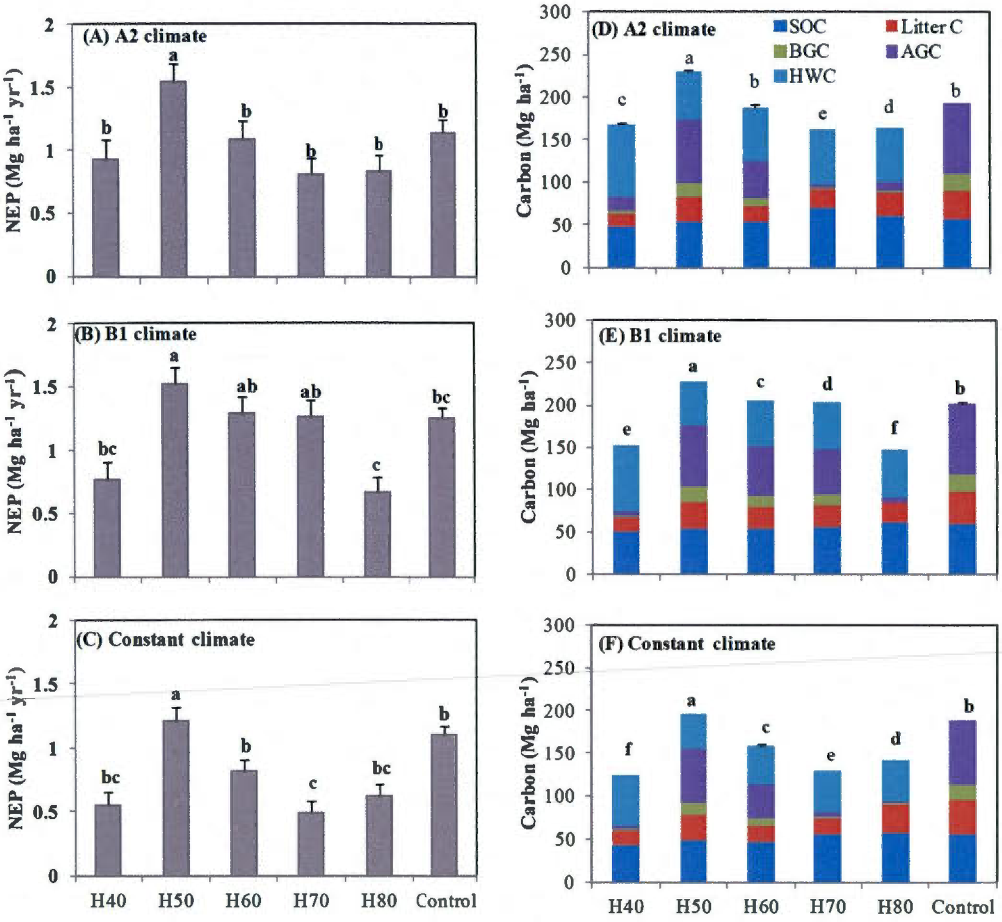

Figure 3.6 Variations of (left) net ecosystem productivity (NEP) and (right) carbon stocks under the three climate scenarios (A2, B1, and constant) for different management scenarios (The letter of "H" represent harvesting; the letters of "LT", "MT", and "HT" represent light thinning with 20% removal of trees, medium thinning with 40% removal of trees, heavy thinning with 60% removal of trees, respectively; the numbers after them represent thinning time [years]) with the same rotation length. Means with different letters are significantly different (Tukey HSD, $p<0.05$). Error bars represent standard errors. SOC: soil organic carbon. Litter C: litter carbon, BGC: belowground carbon, AGC: aboveground C, and HWC: accumulated harvested wood carbon.

Model predictions revealed that the greatest amount of C would be stored within forest stands and harvested woods under H50 ($p<0.001$, n= 27, Tukey's HSD, Figure

3.6). The second highest C stock level in each C pool occurred in the control sites ($p<0.001$, n=27, Tukey's HSD, Figure 3.6 D, E, and F). No obvious patterns related to total C stock for the other four harvesting only scenarios were apparent (H40, H60, H70, and H80).

3.5.4 Interactions between climate change and forest management

Mean annual NEP was not influenced by forest thinning when climate change and rotation length were held constant ($p=1$, n=2565, ANOVA, Table 3.3) although it did change C distribution. Climate warming generally weakened the effects of forest thinning on harvested wood C, but enhanced soil organic C and total ecosystem C under a same thinning regime (Table 3.4 and Figure 3.7).

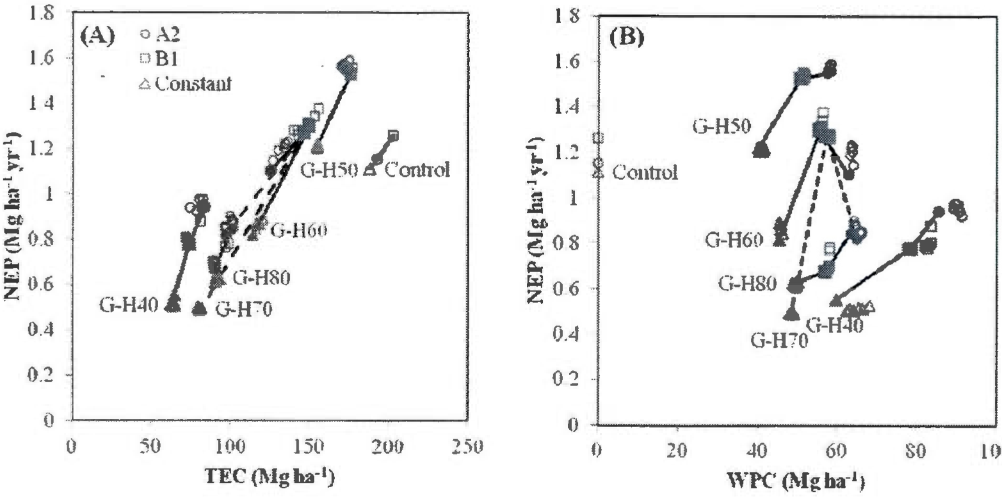

Figure 3.7 Pair-wise correlations (A) between total ecosystem carbon (TEC) and mean annual net ecosystem productivity (NEP) and (B) between harvested wood carbon (HWC) and mean annual NEP by various management scenarios under varied climate scenarios (A2, B1, and constant climate). Triangles, squares, and circles represent the constant, B1and A2 climate change scenarios, respectively. Solid symbols represent harvesting-only management regimes. Hollow symbols represent management regimes with thinning treatments. Solid and dashed lines linked the same management groups (e.g., G-H40 represents a set of management regimes with a rotation length of 40 years) under the three climate change scenarios.

Mean annual NEP throughout the scenario simulation period and C stored within each C pool in 2099 were influenced by interactions between rotation length and climate change (Table 3.3). Warmer climate conditions counteracted differences between the various treatment scenarios as per rotation length (Figure 3.6 A, B, and C). The three significant difference levels for mean annual NEP under the constant climate were reduced to two significant difference levels in the A2 climate scenario (Figure 3.6 A and C). Total C followed a similar pattern to that of mean annual NEP throughout forest management regimes under the three climate scenarios (A2, B1, and constant climate, Figure 3.6 D, E, and F). We also found that rotation length changed C distribution among the five different C pools (Figure 3.6 D, E, and F). Higher temperature increases under the A2 climate scenario reduced the ability of jack pine forests to sequester C under G-H60 (i.e. G-H60 represents a set of management regimes with the rotation length of 60 years) and G-H70 management regimes, compared to that under the B1 climate scenario (Figure 3.7).

3.6 Discussion

3.6.1 Boreal forest C sequestration through changing climate conditions

Simulation results in this study suggest that climate change (temperature and precipitation) may enhance the potential C sequestration of jack pine forests if compound natural disturbances, such as insect outbreaks, do not counteract its effects (Figures 3.5 and 3.6). Modeling research conducted in Canada (Chertov *et al.,* 2009), China (Peng *et al.,* 2009), and Finland (Kellomäki *et al.,* 2008) under climate conditions typical of boreal biomes has shown a similar increasing trend in forest productivity and tree C uptake in response to climate warming. Elevated atmospheric CO_2 and modest warming often enhance forest C sequestration (see reviews by Hyvonen *et al.,* 2007).

The model projected a decline in forest productivity (negative NEP) under the warmer climate scenarios for relative old forests (>80 years) (Figure 3.4). This finding is consistent with the recognition that the more frequent droughts in recent years have resulted in a global-scale decline in forest productivity (Zhao and Running 2010), an abnormal increase in tree mortality (Allen *et al.,* 2010; Peng *et al.,* 2011), and overall reduction of biomass (Ma *et al.,* 2012), and this is expected to continue into the future (Hartmann 2010). Boreal forest growth decline has also been predicted by other modeling studies (e.g., Grant *et al.,* 2007; Wang *et al.,* 2012b). In light of this information, it is becoming increasingly apparent that the careful management of forests is necessary under continuing and rising temperature.

3.6.2. Role of forest management under changing climate conditions

Currently, an ongoing debate is taking place about the role of forest management on C sequestration. On one hand, managed forests can produce harvested wood C (e.g., Chen et al. 2008), and bioenergy can substitute for fossil fuel (e.g., Hudiburg et al. 2011; Malmsheimer et al. 2008). Moreover, it is also widely accepted that younger forests have higher productivity than older forests. On the other hand, certain management practices (e.g., clearcuts) may result in C emissions from forest sites when older forests are replaced by very young forests (e.g., Amiro et al. 2010).

Modeling experiments conducted in this study quantified the effects of forest management and climate change on C sequestration for boreal jack pine forests. Clearcuts lead to considerable C emissions for decades after clearcutting (e.g., Figure. 3.4 B and C). However, the increase in released C was mainly caused by litter decomposition (e.g., Figure 3.4 E and F). Soil organic C did not constantly increase or decrease appreciably after clearcutting. These findings are consistent with previous studies arguing that harvesting does not significantly affect soil C (Johnson and Curtis 2001; Yanai et al. 2003). Forest management thus does not accelerate the C emission from the important forest C pool.

Many studies have suggested that extending rotation length could be an effective way in which to increase boreal forest C sequestration (e.g., Liski et al. 2001; Peng et al. 2002a). Results from this study tell a novel story that jack pine forests might capture and storage greater amounts of C under a reasonable reduction of rotation length (Figure 3.6). Slightly lower amounts of C are stored on-site since a considerable amount is transferred to harvested woods (Figure 3.4). These findings are consistent with previous studies stating that lengthening rotation length may be not useful for increasing C sequestration in boreal forests (Wang et al. 2012), since forest declines were predicted for mature boreal forests due to water limitations in old forests (e.g., Grant et al. 2007; Wang et al. 2012). The cost of increasing rotation length would be decreased revenues for landowners (Liski et al. 2001) and the reduction of C capture ability (Nunery and Keeton 2010). Multiple natural disturbances (e.g., droughts, wildfires, and insects) could also threaten the limited benefits of prolonging rotation length. Therefore, findings from our study suggest that reasonably shortening rotation length may help in the uptake of greater amounts of C due to possible forest decline induced by climate change and senescence.

Tree C enhancement in the stand level will likely occur due to increases in thinning intensity (Table 3.4), however there is no strong evidence from this study to show that forest thinning increases either NEP or total ecosystem C stocks (Table 3.4). These findings are consistent with most previous field studies that have investigated growth response to pre-commercial thinning for both boreal forests (e.g., Lei et al. 2007; Mäkinen and Isomäki 2004; Tong et al. 2005). In summary, at a given temporal scale, the results strongly support the former argument stating that certain forest management approaches may lead to a greater capture of C (Figure 3.6 C and Figure 3.7) and greater C storage if the C stored in harvested woods is accounted for (Figure 3.6 F and Figure 3.7) and its fate reliably projected.

3.6.4 Model limitations and non-simulated processes

Most process-based modeling studies are limited by antecedent assumptions and simplified ecological processes. Nevertheless, process-based modeling is trying to provide more realistic answers to scientific questions based on current knowledge and modeling ability. The authors recognize the uncertainty due to model structure and the parameters of TRIPLEX-Management. The simplification or absence of process-based forest population dynamics in the model (i.e., regeneration, recruitment, and mortality) could lead to bias in the results in this study. For example, after clearcuts, initial stand density is set as a default value (18000 stems ha^{-1}) in the model, assuming no strong impacts (density and natural selection of species) of climate change on forest regeneration. More importantly, the absence of mechanistically modeling tree mortality (e.g., carbon starvation and hydraulic failure) has limited our understanding of the impacts of climate change on forest ecosystem dynamics (McDowell et al. 2011; Wang et al. 2012a). A multi-cohort approach could provide a solution, but it is not a panacea. Future study to address the process of tree mortality and regeneration will certainly improve our interpretation on effects of adaptive forest management strategies on forest C sequestration under climate change.

3.7 Conclusions

Results from this study clearly identify the effects of forest management regimes and potential climate change on forest C sequestration and harvested wood C in northwestern Ontario, Canada. Findings suggest that boreal jack pine forests could capture a greater amount (44.7-50.8%) of C under climate change scenarios (A2 and B1) than under constant climate scenario, which supports the study's first hypothesis that climate change may enhance C sequestration of boreal jack pine forests. Results also suggest that a rotation length of 50 years plus light thinning may enhance annual NEP by 8.2-37.8%, at the same time, decrease impacts of climate change on jack pine forests. Pre-commercial thinning could enhance merchantable tree wood production by 1.7-5.0%, but may not necessarily increase total ecosystem C. Climate warming might enhance the benefits of forest thinning on merchantable wood production. These findings support the hypothesis that some forest management approaches can help increase forest C sequestration if harvested wood C is also accounted for. Therefore, in order to increase C stocks when facing potential climate change risks, forest management regimes could help forest ecosystems sequester greater amounts of C.

CHAPTER IV

QUANTIFYING THE EFFECTS OF CLIMATE CHANGE AND HARVESTING ON CARBON DYNAMICS OF BOREAL ASPEN AND JACK PINE FORESTS USING THE TRIPLEX-MANAGEMENT MODEL

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4.1 Résumé

Un modèle qui évalue avec précision les changements dans la productivité des forêts et des stocks de carbone (C) en réponse aux changements climatiques et la gestion des forêts va nous permettre d'évaluer l'impact des changements globaux. L'objectif de cette étude est de prévoir les effets potentiels des changements climatiques et des coupes à blanc sur la dynamique du C du peuplier faux-tremble (*Populus tremuloides* Michx.) et du pin gris (*Pinus banksiana* Lamb.) dans les forêts boréales méridionales de la Saskatchewan, Canada. Nous avons validé le modèle « TRIPLEX-Management » par rapport aux mesures de *eddy covariance*, de stocks de C, et de données de croissance d'arbres. Un scénario d'un climat constant (basé sur des mesures répétées de 1989 à 2008) et quatre scénarios incluant des changements climatiques, générés par le modèle couplé climatique global (CGCM3.1) ou par le modèle de recherche interdisciplinaire sur les changements climatiques (MIROC3.2), ont été utilisés dans des simulations de scénarios. Tous les scénarios incluant des changements climatiques sont basés sur les scénarios d'émission de CO_2 IPCC SRES A2 et B1. Pour chaque type de forêt, les coupes à blanc sont envisagées de se produire entre 2010 et 2055. Des racines de l'erreur quadratique moyenne (REQM) entre les variables simulées et observées, y compris les flux de C, des actions C (par exemple, le C de la biomasse aérienne ou le C organique du sol), et les caractéristiques du peuplement comme la moyenne DHP (diamètre à hauteur de poitrine) et la densité du peuplement variait de 11 % à 22%. L'indice d'accord de Willmott (*d*) entre les variables simulées et observées variaient de 0,95 à 1,00, à l'exception de la productivité nette des écosystèmes (NEP, $d = 0,88$). Le modèle tend à projeter plus de NEP et plus de stocks de C sous un climat chaud mais humide (CGCM3.1 A2 et B1) par rapport à un climat chaud et sec (MIROC3.2 A2 et B1). Le modèle tend à projeter également une légère augmentation du NEP par le GIEC SERS B1 vs A2, pour les deux types de forêts. Au cours des sept à onze ans suivant une coupe à blanc, le modèle projette un NEP négatif (pertes de C) pour les deux types de forêts pour tous scénarios climatiques. La croissance après une coupe à blanc a généralement créé une plus grande accumulation de C lorsque la coupe avait lieu en 2010 qu'en 2055. Globalement, le modèle TRIPLEX-Management est capable de simuler la dynamique du C pour le peuplier faux-tremble et le pin gris, ainsi que leurs réponses à la sécheresse et aux perturbations lors des récoltes. Les changements climatiques à l'extrémité sud de la forêt boréale en Amérique du Nord pourraient améliorer le taux de séquestration de C s'il n'y a pas d'épisodes de sécheresse sévère. Un âge de rotation allongé (> 90 ans), ne serait donc pas nécessaire dans les forêts boréales du sud en vue d'accroître la séquestration du C.

Mots-clés: Coupe à blanc, durée de la rotation, analyse de scénarios, carbone organique du sol

4.2 Abstract

A model that accurately evaluates changes in forest productivity and carbon (C) stocks in response to climate change and forest management will permit us to assess the impact of global changes. The goal of this study is to forecast potential effects of climate change and clearcuts on C dynamics of boreal trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.) forests near the southern edge of the boreal forest in Saskatchewan, Canada. We validated the TRIPLEX-Management model against eddy covariance measurements, C stocks, and growth data. Constant climate (repeated measurements) and four climate change scenarios (IPCC SRES A2 and B1) generated from Coupled Global Climate Model (CGCM3.1) and the Model for Interdisciplinary Research on Climate (MIROC3.2), respectively, were used in scenario simulations. Clearcuts were assumed to occur in 2010 and 2055 for each forest type. Normalized root mean square error (NRMSE) between simulated and observed variables including C fluxes, C stocks (e.g., aboveground biomass C and soil organic C), and stand characteristics such as mean DBH (diameter at breast height) and stand density ranged from 11% to 22%. The Willmott index of agreement (d) between simulated and observed variables ranged from 0.95 to 1.00 with the exception of net ecosystem productivity (NEP, $d = 0.88$). The model tended to project higher NEP and C stocks under warm but wet climate (CGCM3.1 A2 and B1) *vs.* warm and dry climate (MIROC3.2 A2 and B1), and slightly higher NEP under IPCC SERS B1 *vs.* A2, for both forest types. When clearcuts occurred, the model projected negative NEP (C losses) during the seven to 11 years following clearcuts for both forest types under the five climate scenarios. Regrowth of the forest generally led to greater C accumulation when clearcuts occurred in 2010 than in 2055. Overall, the TRIPLEX-Management model is capable of simulating C dynamics for aspen and jack pine forests as well as their responses to drought and harvesting disturbances. Climate change at the southern edge of the boreal forest in North America may enhance the C sequestration rate if there are no severe drought events. A longer rotation age (>90 years), may therefore, not be necessary in southern boreal forests in order to increase C sequestration.

Keywords: Clearcut logging, process-based modeling, rotation length, scenario analysis, soil organic carbon

4.3 Introduction

Widespread concern about global climate change has generated interests in forest carbon (C) balance and the C sink capacity of forests under both current and future climate. Stand development stages largely govern the C balance of a forest (Law *et al.*, 2001; Howard *et al.*, 2004; Kolari *et al.*, 2004; Humphreys *et al.*, 2006; Noormets *et al.*, 2007; Zha *et al.*, 2009), and its C storage ability (Pregitzer and Euskirchen, 2004; Martin *et al.*, 2005; Wang *et al.*, 2011a). Forest management through forest regulation can dramatically affect forest age structure and thereby influence C cycling (Amiro *et al.*, 2010; Liu *et al.*, 2011). Forest management could thus increase the C capture of boreal forests but it could also increase the risk of releasing C stored in boreal forests.

Clearcut logging, the most common harvesting method in the boreal forest, removes almost all commercially sized trees (i.e. those trees greater than 9 cm DBH (diameter at breast height)), largely resulting in considerable C losses not only by direct export of wood biomass C as harvested wood product C, but also by respiration losses if rates of heterotrophic respiration (litterfall and soil organic C decomposition) exceed net primary productivity (NPP) in the years following a clearcut (Grant *et al.*, 2010). Many studies have found that negative net ecosystem productivity (NEP) may last for several years to decades in the early stages of stand development after clearcuts (e.g., Law *et al.*, 2001; Janisch and Harmon, 2002; Kolari *et al.*, 2004; Humphreys *et al.*, 2006; Zha *et al.*, 2009). The implications in term of C losses highlight the importance of including harvesting for a better understanding of regional and global C cycling (Liu *et al.*, 2011).

Droughts, which are expected to become more frequent and intense in this century (IPCC, 2007), can however increase tree mortality (Allen *et al.*, 2010), result in a global reduction of NPP and thereby a reduction in a forest's C sequestration (Zhao and Running, 2010). Previous studies have indicated that droughts threaten not only forest productivity (Ciais *et al.*, 2005; Zhao and Running, 2010) , but also forest C sink ability as a result of massive abnormal tree mortality (Michaelian *et al.*, 2011; Ma *et al.*, 2012). Recent findings have suggested that if climate-induced droughts continue to intensify, the boreal forest in western Canada would become net C sources (Peng *et al.*, 2011; Ma *et al.*, 2012). Thus, there is an urgent need to investigate how boreal forests respond to droughts.

Process-based models have been developed to quantify forest C dynamics at multiple time and space scales in recent decades (see recent reviews by Pretzsch *et al.*, 2008; Medlyn *et al.*, 2011). Several process-based models, such as Biome-BGC (Running and Hunt, 1993), FinnFor (Kellomäki and Väisänen, 1997) and TRIPLEX (Peng *et al.*, 2002b), have been modified and used in managed forests by adding forest management techniques such as thinning and harvesting (e.g., Garcia-Gonzalo *et al.*, 2007; Petritsch *et al.*, 2007; Grant *et al.*, 2010; Wang *et al.*, 2011b). Such process-based models may provide insights into how current management practices can affect C sequestration and stocks, as well as how future climate change may influence forest C cycling across landscapes and forest types.

Trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.) are the most widespread deciduous and pine species, respectively, in North American boreal forests. However, quantifying C dynamics in these forest types remains a challenge due to variations in stand age, climate, soil type, and forest management. It has been estimated that approximately three million hectares of boreal forest is harvested each year (Hagner, 1995). However, it is still not clear how harvest activities affect C dynamics and storage in boreal forests (Seedre *et al.*, 2011).

In this study, we aim to validate a monthly time-step process-based model (TRIPLEX-Management) with forest management functions against multiple sources of measurements, and to test whether the model is able to capture the impacts of a drought between 2001 and 2003 on C fluxes (e.g., decrease of gross primary productivity (GPP)) of aspen and jack pine forests under a boreal continental climate. Jack pine forests which generally are found growing on coarser textured (i.e. sandy) soils have perennially lower water and may be less affected by drought than aspen forests growing on finer textured soils (Bernier *et al.*, 2006). We then forecasted the potential effects of future climate change and clearcut practices on NEP and total ecosystem C stock (TEC). We hypothesized that climatic change around the southern edge of the boreal forest in North America may enhance the C sequestration, whereas clearcuts may decrease TEC in the short-term but could lead to greater C accumulation over the forest life cycle if the proper rotation length is used.

4.4 Material and methods

4.4.1 Site description

Southern Old Aspen sites (SOAS) and Southern Old Jack Pine sites (SOJP) are located near the southern edge of the boreal forest in Saskatchewan, Canada and subject to the same large scale meteorological forcings (Kljun *et al.*, 2006). The SOAS site regenerated from a fire that occurred in 1919. The understory includes hazelnut (*Corylus cornuta* Marsh.) and the overstory is dominated by trembling aspen. The soil type is an orthic gray luvisol, with a sandy clay loam texture with moderate soil drainage (Table 4.S1).

The SOJP site regenerated following a wildfire in 1929 and is dominated by jack pine (Grant *et al.*, 2009). Its understory includes reindeer lichen (*Ckaduba nutus* Sabdst.) and green alder (*Alnus crispa* Ait.). The soil is a glacial till with a sandy texture and good soil drainage (Table 4.S2). The key stand and climate characteristics for the SOAS and SOJP sites in central Canada are given in Table 4.1.

Table 4.1 Key stand, climate, and soil characteristics of Southern Old Aspen (SOAS) and Southern Old Jack Pine (SOJP) sites in Saskatchewan, Canada.

	SOAS	SOJP
Stand regeneration year	Fire 1919	Fire 1929
Location	53.63°N 106.20°W	53.92°N 104.69°W
Mean annual temperature (C)	0.4	0.4
Mean annual precipitation (mm)	467	467
Dominate vegetation	Aspen	Jack pine
Understory vegetation	Hazelnut (*Corylus cornuta* Marsh.)	Reindeer lichen (*Ckaduba nutus* Sabdst.) Green alder (*Alnuscrispa* Ait.)
Stand density (stems ha^{-1})	980[a]	1190[b]
Leaf area index (m^2 m^{-2})	5.6(0.5)[a]	2.4 (0.2)[b]
Mean diameter at breast height (cm)	20.5[a]	12.9[b]
Mean tree height (m)	20.1[a]	12.7[b]
Woody debris carbon (Mg ha^{-1}, 2004)	19.1 (4.9)	6.2 (1.4)
Aboveground biomass carbon (Mg ha^{-1}, 2004)	122.5 (16.5)	52.1 (9.3)
Belowground biomass carbon (Mg ha^{-1}, 2004)	52.3 (6.5)	11.5 (2.2)
Soil type	Orthic gray luvisol	Glzacial till
Soil texture	Sandy clay loam	Sand
Soil drainage	Moderate	Good
Soil organic carbon [c] (Mg ha^{-1})	163.1	30.5
Period of EC measurements [d]	1996-2010	2000-2008
References	Gower et al. (1997); Kljun et al. (2006); Barr. (2008);Grant et al. (2009)	Gower et al. (1997); Howard et al. (2004); Barr. (2008); Grant et al. (2009) : Kljun et al. (2006)

Values in parentheses are standard deviation.

[a] Values for 1986, estimated by the regeneration year and stand age from Gower et al. (1997).

[b] Values for 1995, estimated by the regeneration year and stand age from Gower et al. (1997).

[c] Estimated based on soil properties.

[d] Depending on data availability for participators of Flux-Canada, last visit in 2012-01-15.

Pools of C were measured in 2004 (Barr, 2008), including living aboveground biomass C, living belowground biomass C, and woody debris biomass C (Table 4.1). Soil organic C was estimated based on the detailed soil characteristics at the SOAS and SOJP sites, respectively (Table 4.S1 and 4.S2). Eddy covariance, as described in

Griffis et al. (2003), was used to measure mass and energy exchange at the SOAS and SOJP sites. In order to fill rejected half-hourly eddy covariance measurements, empirical models constrained by eddy covariance measurements such as soil temperature and air temperature were used one year at a time following the Fluxnet-Canada Research Network procedure (Barr *et al.*, 2004). Monthly C fluxes were obtained by way of summing the gap-filled half-hourly eddy covariance measurements. The uncertainties of flux measurements include potential random and systematic errors, which attributes to (1) likely underestimated CO_2 and energy fluxes during nighttimes and (2) incomplete recovery of absorbed radiant energy and CO_2 fluxes (Grant *et al.*, 2005). Griffis et al., (2003) estimated that the annual uncertainty in NEP for SOAS and SOJP sites ranged from 0.64 to 1.42 and 0.61 to 0.91 Mg ha^{-1} of C per year for the year of 2000, respectively.

A severe drought due to the decrease of precipitation occurred in western Canada during 2001 – 2003 (Kljun *et al.*, 2006). Both sites were affected by the severe drought. During the drought, precipitation decreased 35– 50% comparing with the 30-year mean (1971–2000) (Kljun *et al.*, 2006).

4.4.2 The model

The TRIPLEX-Management model originally developed by Peng et al. (2002) was used in this study. The role of climate as a driving force of TRIPLEX-Management is quite simple and principally includes monthly mean temperature, monthly precipitation, and monthly mean relative humidity. In the model, gross primary productivity (GPP) is calculated as a function of leaf area index, a conversion constant, received photosynthetically active radiation, with modifiers constrained by forest age, air temperature, soil water availability, nitrogen (N) availability and percentage of frost days within a month (Landsberg and Waring, 1997). Furthermore, the effect of CO_2 fertilization on forest production was calculated using an empirical logarithmic function (Friedlingstein *et al.*, 1995). Ecosystem respiration (ER) is comprised of autotrophic respiration and heterotrophic respiration. Autotrophic respiration includes growth and maintenance respiration. Maintenance respiration is calculated using a Q_{10} function multiplied by the biomass of each plant component (foliage, roots, and wood) and growth respiration is assumed to be one fourth of NPP. The remaining amount of photosynthesis production (NPP) is allocated to the net growth of stems, branches, foliage, coarse and fine roots.

Volume growth is calculated from the increase in wood C by wood C density, and then allocated to primary growth and secondary growth based on functions of stem wood increment (Bossel, 1996). Tree mortality is estimated annually based on a constant mortality rate and mortality due to canopy competition for light (Bossel, 1996). Stand structure is simulated by incorporating an empirical Weibull diameter distribution model and height-diameter equations (Wang *et al.*, 2011). Thus, total volume and timber yield (DBH > 9cm) can be estimated based on each DBH class.

Monthly input to soil module from litterfall depends on turnover rates of foliage and fine roots and mortality rate. The dynamics of C and C as well as soil water, are simulated based on the corresponding module from the CENTURY4.0 model (Parton *et al.*, 1993). Decomposition rates of soil organic C and litterfall C pools (e.g., passive, slow, and active pools) are calculated as a function of maximum decomposition rates, effects of soil temperature, and effects of soil moisture. Simulating soil water dynamics require using precipitation as an input and evaportranspiration and runoff as outputs.

In addition, forest management such as forest thinning and harvesting has been implemented by Wang et al. (2011). Forest thinning is controlled by the time of thinning, thinning intensity, and thinning types (thinning from below and from above). Two ways of harvesting including stem-only harvesting (100% stem removal, with branches and foliage left on-site) and whole tree harvesting (100% stem removal, with branches and foliage removed from the harvest block) were designed and combined with natural regeneration where initial stand density is largely dependent on-site class. A more detailed description of the mathematical algorithms and sensitivity analyses of the model have been previously reported in Peng et al. (2002) and Wang et al. (2011).

4.4.3 Model validation

4.4.3.1 Parameterization, initialization, and validation

The TRIPLEX model has been parameterized and verified for jack pine and trembling aspen using growth and yield data in Canada by several previous studies (Peng *et al.*, 2002b; Zhou *et al.*, 2004; Zhou *et al.*, 2005; Wang *et al.*, 2011b). The set of species-specific parameters and parameters corresponding to tree species in each component such as GPP and soil water, were mostly left unchanged in this study (Table 4.S3). However, we updated and corrected some species-specific parameters. For example, the parameter of specific leaf area for aspen was modified from 6 to 22.5 $m^2 kg^{-1}$ C (Steele *et al.*, 1997; Barr *et al.*, 2004). Site-specific parameters were input according to soil characteristics.

The model had to be first initialized using historical stand conditions, before testing the model against measurements. Estimated historical stand conditions used in the model include species, year of regeneration, latitude, site class, soil organic C, and stocking level. Stand establishment in the model was simulated based on the recruitment of natural seedlings constrained by site class and estimated stocking level in the year of regeneration. The model was then run from the year of regeneration to 2010 (the end of eddy covariance data availability) under repeated climate data recorded during the eddy covariance measurement period at each site.

The model was validated in parallel against three different data sources that have a same footprint (GPP, ER, and NEP derived from eddy covariance measurements, C stocks in each C pool, as well as growth and yield data). Eddy covariance data provided a great opportunity to monitor NEP. These measurements, combined with measured C stocks, help us to more completely understand the forest C cycle (Law *et al.*, 2001). A large part of NEP is stored in wood C and allocated to primary and secondary growth. Stand characteristics are thus good indicators for testing process-based models. Simulated annual NEP was compared with the eddy covariance measurements to investigate whether the model captures the reduction of annual NEP during the recorded drought events.

4.4.3.2 Model evaluation

Two statistical methods were used to quantify model performance on the simulations. The normalized root mean square error (NRMSE, Eq. (1)) was used to evaluate the difference between predicted (*P*) and observed (*O*) data.

$$NRMSE = (O_{\max} - O_{\min})^{-1}\left[\frac{\sum_{i=1}^{n}(P_i - O_i)^2}{n}\right]^{0.5} \tag{1}$$

where *n* is the number of observations; *i* is the i^{th} observation; and O_{max} and O_{min} are the maximum and minimum observed values, respectively.

The Willmott index of agreement (*d*) is an indicator of modeling efficiency, which takes on values from 0 to 1.0, and is expressed as:

$$d = 1 - \left[\frac{\sum_{i=1}^{n}(P_i - O_i)^2}{\sum_{i=1}^{n}(|P_i| + |O_i|)^2}\right] \tag{2}$$

A value of 1.0 indicates perfect agreement (Willmott, 1982).

4.4.4 Simulation experiments

4.4.4.1 Climate change scenarios

We used five climate scenarios to continually simulate forest C dynamics for the 2011−2100 scenario simulation period, i.e., constant climate, and four climate change scenarios generated by two General Circulation Models (GCM): Coupled Global Climate Model version 3.1 (CGCM3.1) and the Model for Interdisciplinary Research on Climate version 3.2 (MIROC3.2), from the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A2 and B1 emission scenarios. The constant climate scenario was compiled as the repeated values of the currently measured data. IPCC SERS A2 weights economic growth in a heterogeneous world more heavily, which results in the highest temperature increases by 2100 (2.0−5.4 C greater than in 1990) (IPCC, 2001); whereas IPCC SERS B1 has a lower level of fossil fuel consumption in a globalized world, which leads to the lowest predicted temperature increases (1.1−2.9 °C) by 2100 (IPCC, 2001). The atmospheric CO_2 concentration from 1850−2100 was taken as a global mean of the available IPCC SERS A2 and B1 for modeling CO_2 fertilization.

Both of the GCMs under both IPCC SERS A2 and B1 in the study area projected a warmer climate in which both precipitation and temperature generally increased (Figures 4.1 and 4.S1). At the end of the 21st century, the "wet" GCM, CGCM3.1, under IPCC SERS A2 projected a mean annual temperature increase of 3.7 °C and a mean annual precipitation increase of 18% (Figure 4.S1), whereas the "dry" GCM, MIROC3.2, predicted an increase of 4.4 °C and a 9% increase in precipitation (Figure 4.S1). Compared with IPCC SERSS A2, both of the GCMs projected relatively lower increases in temperature and precipitation under IPCC SERS B1 (Figure 4.S1). Therefore, cyclical drought events may last longer and severer in the future in the study area due to the increase of temperature.

4.4.4.2 Harvesting scenarios

Two forest harvesting scenarios (CUT2010 and CUT2055) were designed in this study according to different rotation ages. Stem-only harvesting was carried out in

2010 and 2055, respectively for both SOAS and SOJP sites. The harvested fractions (biomass removed from the system) of foliage, living wood, coarse and fine roots, and standing dead wood were 0.1, 0.8, 0.0, 0.0, and 0.0, respectively, derived from Grant et al. (2010). Therefore, overall 10 scenario simulations were conducted in this study in terms of five climate and two harvesting scenarios at each site.

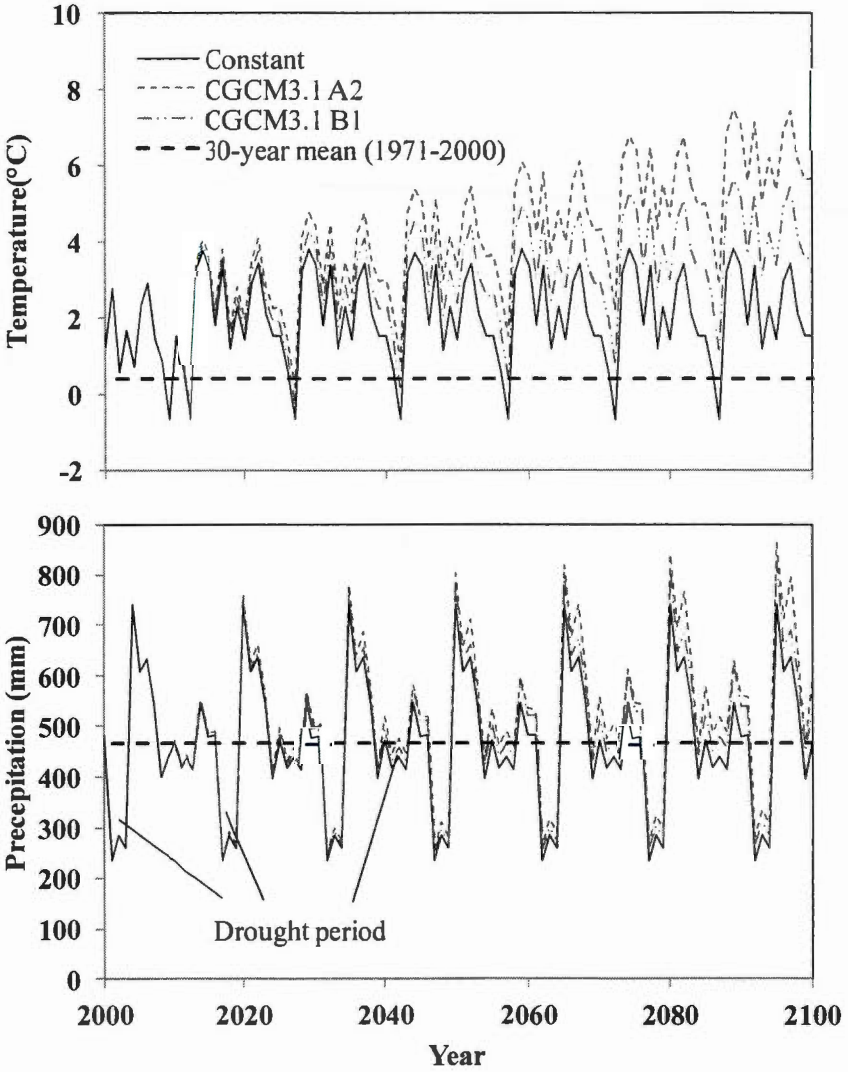

Figure 4.1 Annual variations in annual mean temperature (upper) and precipitation (bottom) for constant climate and potential climate change in Saskatchewan, Canada. The mean annual temperature was 0.4 °C and the mean annual precipitation was 467 mm (the 30-year mean during1971–2000 at Waskesiu Lake weather station, 53.92° N, 106.08° W, Environment Canada).

4.5 Results

4.5.1 Model validation

4.5.1.1 Testing against eddy covariance measurements

Simulated monthly C fluxes (Figures 4.2 and 4.3) for both SOAS and SOJP sites were generally consistent with eddy covariance measurements. Statistical analysis confirmed that the TRIPLEX-Management model predicted the monthly C fluxes reasonably well (Table 4.2). The NRMSE and the Willmott index between simulated and measured/estimated monthly C fluxes (GPP, ER, and NEP) were 11−19% and 0.88−0.97, respectively.

Simulated annual NEP was generally in the reasonable range of measured annual NEP (Figure 4.4). The TRIPLEX-Management model can capture the phenomenon of lower annual NEP (model versus eddy covariance in Mg ha^{-1} year^{-1}: 1.25 *vs.* 0.29 in 2002, 0.94 *vs.* −0.84 in 2003, 0.17 *vs.* −0.54 in 2004) from 2002 to 2004 resulting from the drought from 2001 to 2003 at the SOAS site. But at the SOJP site, the model didn't capture the similar but much weaker impacts of droughts on annual NEP variation and thus overestimated annual NEP during the drought event.

Table 4.2 TRIPLEX-Management model overall performance in carbon fluxes, stand level variables, and carbon pools at the Southern Old Aspen (SOAS) site and the Southern Old Jack Pine (SOJP) site in Saskatchewan, Canada.

	GPP	ER	NEP	Stand density	DBH	Height	LAI	Carbon stock	Overall[b]
NRMSE (%)	12	19	11	19	12	22	15	18	16
d[a]	0.97	0.95	0.88	1.00	1.00	1.00	0.99	0.97	0.97

GPP represents gross primary productivity; ER represents ecosystem respiration; NEP represents net ecosystem productivity; DBH represents diameter at breast height; LAI is leaf area index. NRMSE represents normalized root mean square error.

a. Willmott index.

b. Mean of evaluating statistics (NRMSE and d) for listed variables.

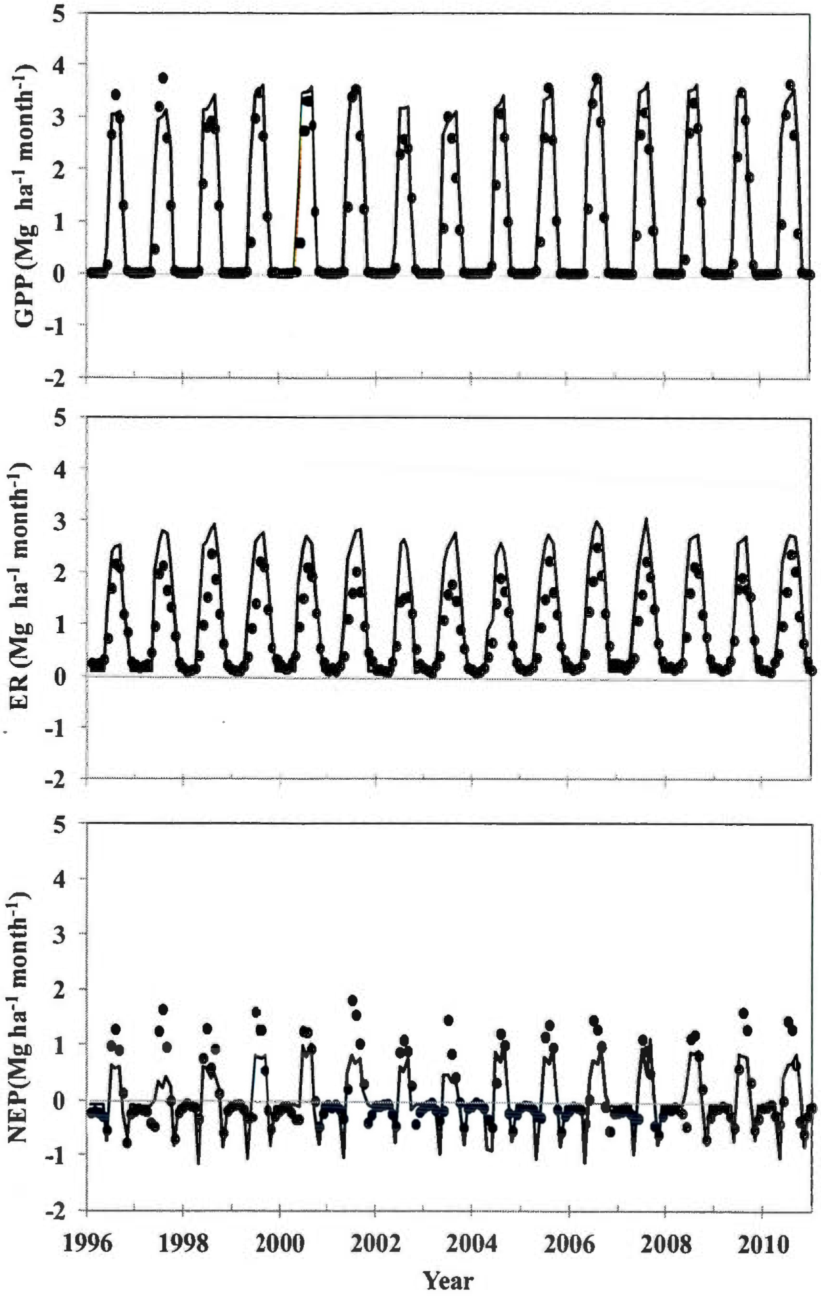

Figure 4.2 Monthly carbon fluxes measured/estimated (symbol) and simulated (lines) at the Southern Old Aspen (SOAS) site from 1996-2010 in Saskatchewan, Canada.

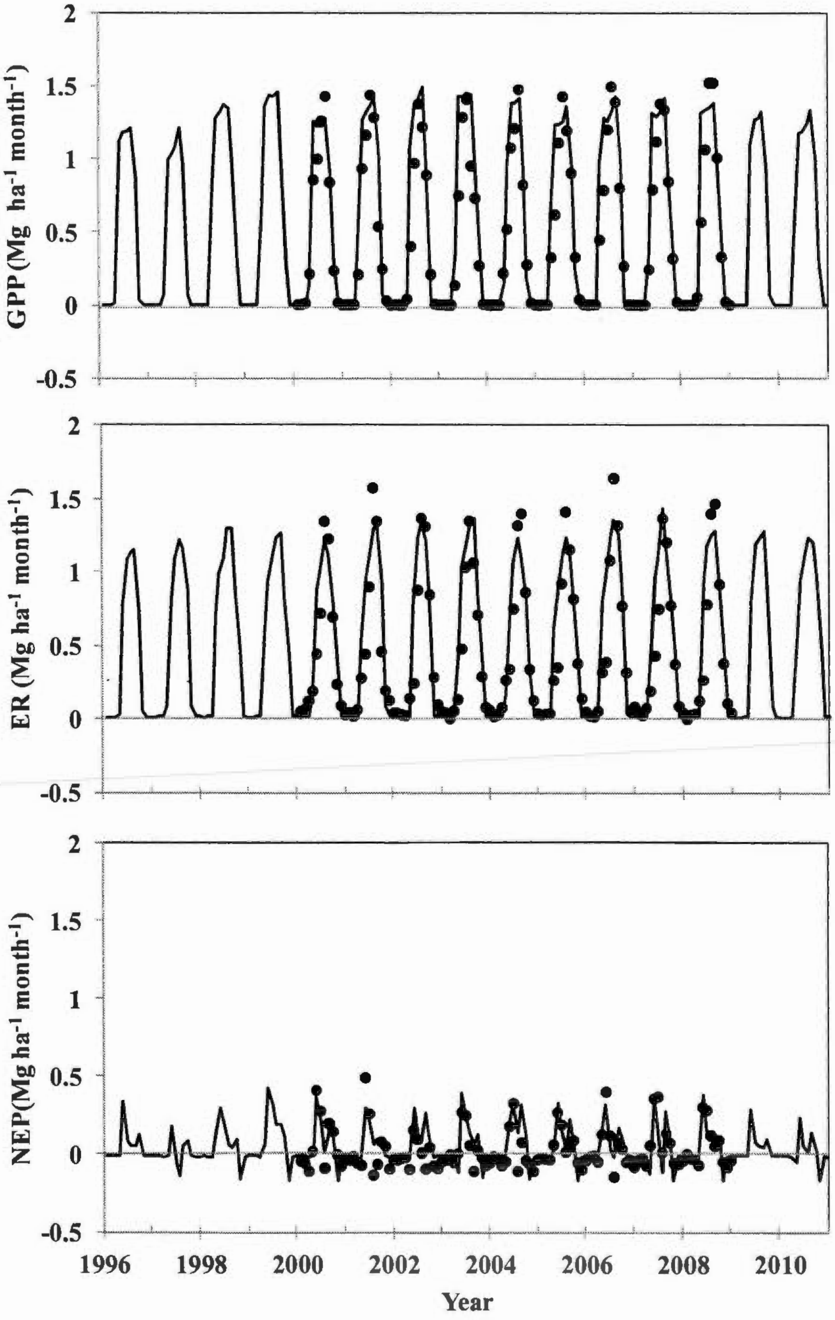

Figure 4.3 Monthly carbon fluxes measured/estimated (symbols) and simulated (lines) at the Southern Old Jack Pine (SOJP) site from 1996-2010 in Saskatchewan, Canada.

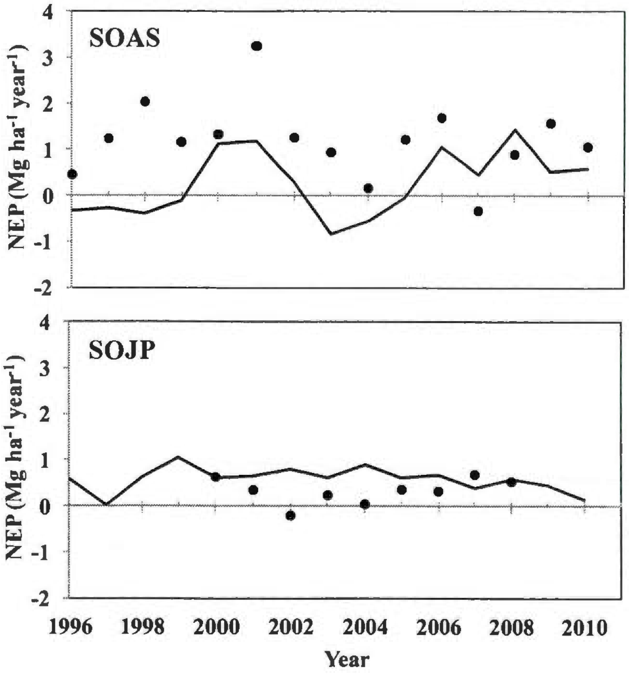

Figure 4.4 Measured (symbols) and simulated (lines) annual NEP variation at Southern Old Aspen (SOAS) and Southern Old Jack Pine (SOJP) sites from 1996 to 2010 in Saskatchewan, Canada.

4.5.1.2 Testing against C stocks

Six C pools (living aboveground biomass C, belowground biomass C, woody debris biomass C, total biomass C, soil organic C, and TEC) were compared with measurements that were conducted in 2004 by Barr (2008) (Figure 4.5). The NRMSE and the Willmott index between simulated and measured C stocks were 18% and 0.97, respectively (Table 4.2).

Simulated living aboveground C biomass (102.4 *vs.* 122.5 ± 16.5 Mg ha^{-1}) and belowground C biomass (29.8 *vs.* 52.3 ± 6.5 Mg ha^{-1}) were underestimated when compared to the measurements taken at the SOAS site. However, the model overestimated woody debris C biomass (56.7 *vs.* 19.1 ± 4.9 Mg ha^{-1}). Total C biomass was thus reasonably predicted as these over and under predictions balance out as some living biomass was predicted to occur as dead biomass. The model probably overestimated tree mortality for the mature aspen forest and allocated too little C to roots for aspen. Soil organic C (158.0 *vs.* 163.1 Mg ha^{-1}) was reasonably simulated at the SOAS site.

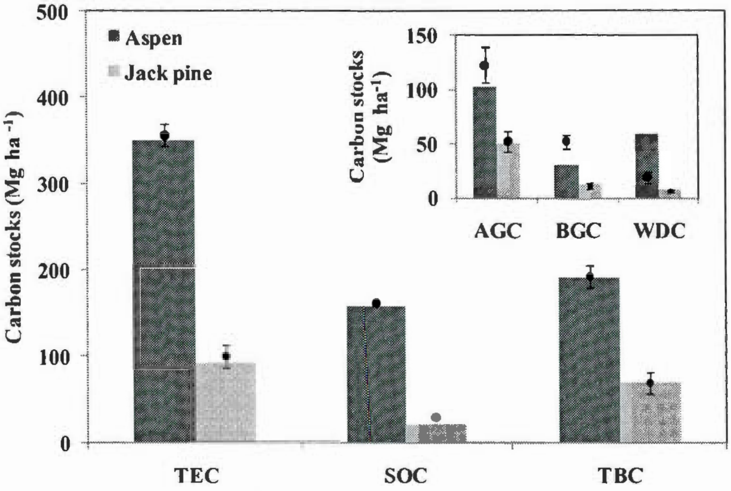

Figure 4.5 Carbon (C) pools measured (symbols) and simulated (column) in 2004 for Southern Old Aspen (SOAS) and Southern Old Jack Pine (SOJP) sites in Saskatchewan, Canada. Total ecosystem C (TEC) is comprised of living aboveground (AGC) and belowground biomass C (BGC), woody debris C (WDC), and soil organic C (SOC). Total biomass C (TBC) is summed by AGC, BGC, and WDC. WDC includes standing dead wood C, wood and branch litterfall on the forest floor. The black points indicate the mean value of measurements. Error bars represent stand deviations.

Simulated living aboveground C biomass (50.3 *vs.* 52.1 ± 9.3 Mg ha^{-1}), belowground C biomass (12.3 *vs.* 11.5 ± 2.2 Mg ha^{-1}), and woody debris C (7.7 *vs.* 6.2 ± 1.4 Mg ha^{-1}) were generally located in realistic ranges of the measurements at the SOJP site (Figure 4.5). But simulated soil organic C (21.2 Mg ha^{-1}) was underestimated compared with the measured values (30.5 Mg ha^{-1}). Overall, the model predicted relatively accurately net primary productivity (NPP), C allocation and tree mortality at the SOJP site.

4.5.1.3 Testing against stand characteristics

The NRMSE and the Willmott index between simulated and measured stand variables (e.g., DBH, height, and stand density) ranged from 12% to 22% and from 0.99 to 1.00, respectively (Table 4.2). Simulated mean DBH, mean height, and stand density generally agreed with measurements by Gower et al. (1997) and Howard et al. (2004) (Table 4.S4). Simulated mean DBH (20.6 *vs.* 20.5 cm), mean height (21.2 *vs.* 20.1 m), stand density (1040 *vs.* 980 stems ha^{-1}) and leaf area index (LAI, 6.3 *vs.* 5.6 ± 0.5) were close to the field measurements at the SOAS site.

Compared to the measurements by Gower et al. (1997) in 1996 and by Howard et al. (2004) in 1999 and 2000 at the SOJP site, the simulated stand density (1136−1206 stems ha^{-1}) was generally within a reasonable range (1022-1342 stems ha^{-1}) of observations (Table 4.S4). Simulated mean DBHs (11.7−12.2 cm) were close to but smaller than the measured values (12.9−13.1 cm). Simulated mean tree height (11.3−11.6m) was close to the lower boundary of the estimated range of 12−15m. Although the model underestimated LAI (1.3 *vs.* 2.4 ± 0.2) in 1995, simulated LAI agreed well with measurements in 1999 (1.3 *vs.* 1.3 ± 0.3) and 2000 (1.2 *vs.* 1.3 ± 0.3).

4.5.2 Effects of climate change on NEP and TEC

At the beginning of the 21st century, the model predicted higher annual NEP under climate change scenarios (IPCC SERS A2 and B1) *vs.* constant climate (Figure 4.6 A, B, E, and F). However, simulated annual NEP under constant climate was intermediate between the values predicted for the two GCMs at the end of the 21st century (Figure 4.6 A, B, E, and F), because a warm and "wet" climate projected by GCM CGCM3.1 was predicted to enhance forest production, whereas a warm but dry climate projected by GCM MIROC3.2 was predicted to reduce the C accumulation ability of the forests. Generally, the TRIPLEX-Management model predicted higher annual NEP under CGCM3.1 *vs.* MIROC3.2, and slightly higher NEP under IPCC SERS B1 *vs.* A2 at both sites at the end of the 21st century (Figure 4.6 A, B, E, and

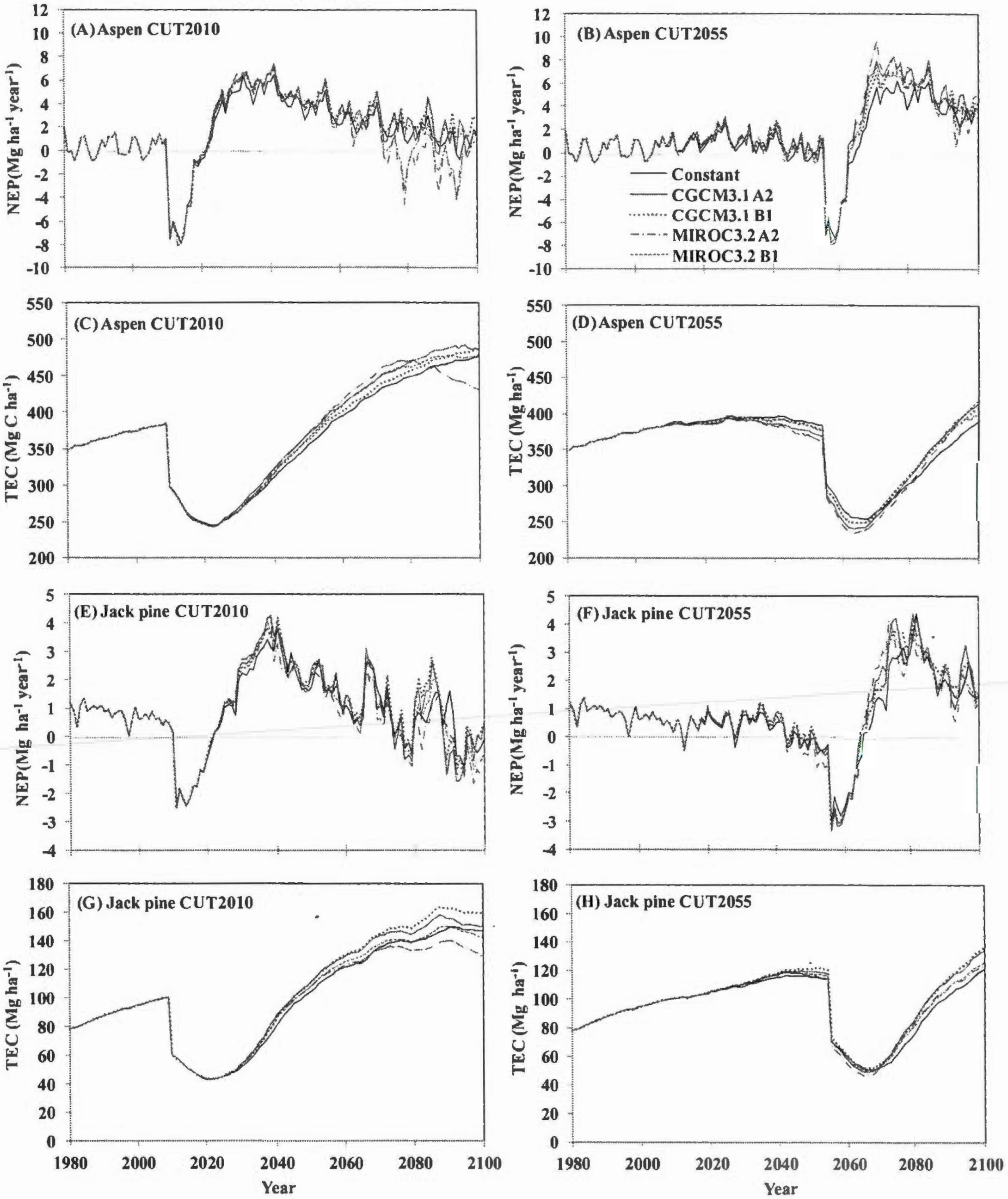

Figure 4.6 Variations in simulated annual net ecosystem productivity (NEP) and total ecosystem carbon (TEC) from 1980 to 2100 under constant climate and four climate change scenarios with clearcutting in 2010 (left) and 2055 (right) at Southern Old Aspen (SOAS, upper) and Southern Old Jack Pine (SOJP, lower) sites in Saskatchewan, Canada.

F). In addition, the model predicted severe decreases in NEP at both sites for both clearcut scenarios during cyclical drought events (decreased annual precipitation, Figure 4.1) under MIROC3.2 SERS A2 and B1 (Figure 4.6 A, B, E, and F).

The model generally predicted greater TEC under GCM CGCM3.1 *vs.* MIROC3.2, and slightly greater TEC under IPCC SERS B1 *vs.* A2 at the SOJP site for both clearcut scenarios (Figure 4.6 C, D, G and H). TEC in 2100 was predicted to change from −9.8% to 7.4% and −12.5% to12.4% at the SOAS and SOJP sites, respectively, under the four climate change scenarios, compared under the constant climate. The model predicted a maximum increase in TEC under CGCM3.1 SERS B1, except for CUT2055 at the SOAS site. Moreover, considerable C losses were predicted at both sites for both clearcut scenarios under MIROC3.2 SERS A2 (Figure 4.6 C, D, G, and H), which forecasted a higher increase in temperature but a smaller increase in precipitation in the study area (Figure 4.S1).

4.5.3 Effects of clearcut on NEP and TEC

Harvested forests are expected to be C sources as C uptake is disrupted with the removal of the canopy and the decomposition of soil organic matter and litter continues. The model predicted negative NEP for the 7−11 years (recovery period, defined as the stage from a net C source to a C sink) following clearcuts at both sites under all climate scenarios for both clearcut scenarios (Figure 4.6 A, B, E, and F). During the recovery period, the mean annual C losses of 4.4 and 4.6 Mg ha^{-1} $year^{-1}$ were estimated for CUT2010 and CUT2055 at the SOAS site, respectively. However, the amounts of total C loss were larger under CUT2010 (48.0 Mg ha^{-1}) than under CUT2055 (41.6 Mg ha^{-1}) for the SOAS site due to different recovery times (11 *vs.* 9 years). Differently, the mean annual C losses of 1.6 and 2.1 Mg ha^{-1} $year^{-1}$ were estimated under CUT2010 and CUT2055 at the SOJP site, respectively; whereas since the recovery time was the same (11 *vs.*11 years), total estimated C loss of 17.9

Mg ha^{-1} under CUT2010 was smaller than the estimated C loss of 21.1 Mg ha^{-1} under CUT2055 at the SOJP site.

Generally, no noticeable decline in TEC was found under CUT2010, because the maximum stand age was 92 (2010) and 90 (2100) at the SOAS and SOJP sites, respectively. However, forest declines in NEP and TEC were predicted due to tree mortality and frequent drought events (Figure 4.1) during the simulation period of 2040–2055 under CUT2055 (Figure 4.6 B and D), when stand age ranged from 122–147 yrs and 112–137 years at the SOAS and SOJP sites, respectively. In addition, TEC in 2100 was greater under CUT2010 *vs.* CUT2055 at both sites (Figure 4.6 C, D, G, and H). Rotation length might, thus, be an important factor to consider for boreal forest C management.

4.5.4 Combined effects of climate change and clearcut on NEP and TEC

No considerable differences of C loss were predicted during recovery periods among the five climate scenarios under CUT 2010 for both tree species. But climate change shortened the recovery period 1–2 years to smoothly alter from a net C source to a net C sink under CUT2055 (Figure 4.6 B and F). Significantly less TEC was projected for both tree species under climate change scenarios compare with those under constant climate (Figure 4.6 D and H), resulting from accelerating woody debris and soil organic C decomposition rates due to rising temperature. Generally, jack pine needed 1 or 2 years more than aspen to attain a positive NEP.

4.6 Discussion

4.6.1 Sensitivity of net ecosystem productivity to droughts

Declines in simulated and observed monthly C fluxes and annual NEP were found during the 2001–2003 drought at the SOAS site (Figures 4.2 and 4.4). Several observations and modeling studies have predicted similar impacts of drought on NEP at the SOAS site (Grant *et al.*, 2006; Kljun *et al.*, 2006). And observations from many other sites have found a similar response of forest C cycling to droughts that addresses reductions in GPP and ER (e.g., Ciais *et al.*, 2005). For example, Zhao and Running (2010) had attributed the reductions of NPP in global terrestrial ecosystems to the droughts occurred in 2000-2099.

No large decline was found in both simulated and observed monthly C fluxes and annual NEP at the SOJP site (Figures 4.3 and 4.4). Kljun et al. (2006) concluded that the reduction in NEP at the SOJP site is much weaker than at the SOAS site because of the low water holding capacity of the soils where jack pine grows in Central Canada. In the model, water limitation in GPP is constrained by the vapor pressure deficit (VPD), soil water moisture and corresponding soil type coefficients and parameters (Peng *et al.*, 2002b). Thus, the moisture modifier does not change much due to the sandy soil texture with poor water holding capacity at the SOJP site. The different response to drought between aspen and jack pine forests is not surprising. Decline of aspen forests, even dieback, following severe droughts on the southern edge of the Canadian boreal forest has been reported over recent decades (e.g., Hogg *et al.*, 2002; Hogg *et al.*, 2008; Michaelian *et al.*, 2011). However, Peng et al., (2011) reported an unusual higher drought-induced tree mortality, which has both direct and indirect effects on NEP, for jack pine than for aspen in recent years (2004–2010) using long-term forest permanent sampling plot data. NEP thus is supposed to be reduced by droughts (Figure 4.6 A, B, E, and F), but varied relying on tree species as well as drought length and intensity.

4.6.2 Climate change affects NEP and TEC

Climate change scenarios (IPCC SERS A2 and B1) enhanced NEP for both tree species during the 2010-2100 period , except during drought events (Figure 4.6 A, B, E, and F), where drops in NEP for both aspen and jack pine sites, especially aspen, were observed in the simulations. Three main factors, including elevated atmospheric

CO_2, rising temperature, and elevated C deposition, are often considered to enhance forest C sequestration if other environmental factors such as water are not limiting (see reviews by Luo *et al.*, 2006, Reay *et al.*, 2008, Boisvenue and Running, 2006, Huang *et al.*, 2007a). In the model, CO_2 fertilization was simulated using an empirical equation, resulting in a potential increase of GPP if there was no C limitation. This approach can simulate the effects of C limitation on the CO_2 enhancement of forest productivity as recently reported by Norby et al. (2010). The simulated GPP has a positive response to rising temperature (Peng *et al.*, 2002), if future temperature is not beyond the optimum growth range.

More C would be extracted by boreal forests under climate change scenarios if our model captures the key processes. Our simulation results also suggest that climate change at the southern edge of the boreal forest might not necessarily accelerate the movement of the prairie-forest ecotone in northern-central North America if no regional forest dieback is induced by severe drought events. Wyckoff and Bowers (2010) have suggested that drought insensitive tree species may delay the northeastern movement of the biome boundary for decades due to increasing CO_2. But the absence of mechanistically modeling forest mortality might limit model credibility (Galbraith *et al.*, 2010). Because multiple natural disturbances, such as frequent droughts, fires, and insect outbreaks, could lead to higher tree mortality and/or inhibit the regeneration of tree species, it is therefore expected that the boreal forest biome could shift to the northeast during global warming (Frelich and Reich, 2010). Such increases in natural disturbances would also influence the C budget and would thus affect the interpretations that ensue from our modeling work in which we consider only the effects of droughts but not fires or insects. However, it would be reasonable to expect that a drier climate would also lead to greater fire-frequency (Flannigan *et al.*, 2009) and greater insect caused mortality (Hogg *et al.*, 2002).

4.6.3 Harvesting effects on NEP and TEC

Our modeling results indicate that negative NEP would occur for 7– 11 years for aspen and 10– 11 years for jack pine, following clearcuts. These results are consistent with recent observations of a jack pine chronosequence study (Howard *et al.*, 2004; Zha *et al.*, 2009). For example, Zha et al. (2009) reported a net C source 2– 3 years after clearcuts, and a weak C sink 10– 11 years after clearcuts, and a moderate C sink 29 – 30 years after clearcuts using eddy covariance measurements. Howard et al. (2004) reported a similar pattern of NEP change after clearcuts using biological data such as biometric estimation, soil and coarse woody debris respiration in the same chronosequence study sites. Amiro et al. (2010) synthesized multi-site eddy covariance data from disturbed sites in North America and concluded that it takes approximately 10 years for a net C source to become a net C sink following stand replacing disturbances. However, Grant et al. (2007) projected a recovery time of 20 years in their modeling study for jack pine. Many other studies confirm that forest sites can switch from being a net C source to a net C sink with stand development after stand replacing disturbance (e.g., Law *et al.*, 2001; Law *et al.*, 2003; Humphreys *et al.*, 2006), although the length of recovery time may vary depending on stand type and site productivity. Recovery time since harvesting can last at least 4 years for a boreal Scots pine (*Pinus sylvestris* L.) forest (Kolari *et al.*, 2004), 6 years for a northern temperate forest (Gough *et al.*, 2007), 10–20 years for conifer forests of the Pacific North-west (Law *et al.*, 2001), and at least15 years for coastal Douglas-fir (*Pseudotsuga menziesii* var. *menziesii* (Mirbel) Franco) forests (Humphreys *et al.*, 2006).

We found that considerable soil C and litterfall C losses (aspen: 41.6–48.0 Mg ha^{-1}, jack pine: 17.9–21.1 Mg ha^{-1}) may contribute to negative NEP in the decade following clearcutting. Harvesting will largely enhance soil C loss (see review by Liu *et al.*, 2011). Pennock and van Kessel (1997) reported that soil C was reduced between 5 and 20 Mg ha^{-1} over 20 years following clearcuts in a mixed wood forest of Saskatchewan, Canada. The process-based model CENTURY4.0 suggests 33.4% soil C loss if stem-only harvesting is used under a 100-year rotation length evaluated for a 500 year simulation period (Peng *et al.*, 2002a). Conversely, a meta-analysis study concluded, on average, no significant effect of harvesting on the whole soil C, but stem-only harvesting may result in a small increase in soil C for coniferous tree species (Johnson and Curtis, 2001). The reasons for this result are not clear. In summary, these earlier studies generally indicated that it is necessary to include stand disturbance history in long-term forest simulations and regional C budgets.

4.6.4 Implications for forest management

Our results suggest that climate change in the study area, where climate is expected to warm in the future (Figure 4.1), may enhance forest C losses after harvesting, but shorten the recovery period from a net C source to a net C sink by 1–2 years for both deciduous and conifer tree species. As such, the original hypothesis was strongly supported by our findings. These findings are consistent with comparative synthesis studies that indicate that a warmer climate may lead to faster recovery after harvesting (Amiro *et al.*, 2010), since high temperature without water limitation may enhance forest regrowth, especially for fast growing tree species.

Our results do not indicate that a longer rotation length would increase C sequestration in Saskatchewan, Canada. Grant et al. (2007) also projected forest decline for mature jack pine forests under climate change in their simulations. However, many other studies have suggested that prolonged rotation lengths would enhance C sequestration (e.g., Liski *et al.*, 2001; Ueyama *et al.*, 2011). For example, longer rotation length (>90 years) in European boreal forests has been suggested to benefit C sequestration (Liski *et al.*, 2001; Kaipainen *et al.*, 2004). Ueyama et al. (2011) also suggested that a 140-year rotation with a harvesting intensity of 70%

might sequester more C in a Japanese cypress (*Chamaecyparis obtuse*) forest. Such conflicting findings are probably because of variations in climate, soil type, and forest type. In western Canada, climate change (e.g., droughts) has consistently contributed to forest decline and tree mortality and is expected to continue to do so (Hogg *et al.*, 2008; Michaelian *et al.*, 2011; Peng *et al.*, 2011; Ma *et al.*, 2012). Therefore, prolonging rotation length might not be a strategic or justifiable choice in such a dry area.

4.7 Conclusions

Forest disturbances like harvesting significantly alter forest growth, C and C dynamics. Future climate change may or may not benefit C sequestration. A process-based model such as TRIPLEX-Management may provide a useful tool for predicting forest ecosystem response to harvesting and climate change, although uncertainties still exist in model structure and parameters. Results presented in this study demonstrate that future climate change with proper forest management at the southern edge of the boreal forest in North America may enhance aspen and jack pine forest growth and C sequestration, if no multiple natural disturbances, such as droughts and insects, disturb these forests. Harvesting may result in significant C losses in the early stage of stand development for both boreal forests. Climate change may enhance C losses after harvesting but may also shorten the recovery time by one or more years. Shortening the rotation length might be a reasonable choice in order to acquire more C without the sacrifice of wood production. Further modeling efforts should investigate the effects of climate change on forest regeneration and tree mortality processes as well as the resilience of different forest ecosystems to droughts.

Table 4.S1 Soil characteristics of the Southern Old Aspen site in Saskatchewan, Canada*.

Luvisol	LF	H	Ae	Bt	Bmk	BC	Ck
Depth to Bottom (m)	0.05	0.09	0.30	0.65	0.85	1.75	3.0
Bulk Density (Mg m^{-3})	0.22	0.38	1.32	1.47	1.59	1.59	1.59
Field Capacity (m^3 m^{-3})	0.45	0.45	0.24	0.23	0.19	0.18	0.21
Wilting Point (m^3 m^{-3})	0.15	0.15	0.10	0.13	0.13	0.13	0.12
K_{sat} (mm h^{-1})	210	210	32	15	15	15	15
Sand (g kg^{-1})	589	589	589	568	485	485	485
Silt (g kg^{-1})	293	293	293	187	280	280	280
Clay (g kg^{-1})	118	118	118	245	235	235	235
Coarse Frag. (m^3 m^{-3})	0	0	0	0	0	0	0
CEC (cmol$^+$ kg^{-1})	120	120	9.2	14	12	11	10
pH	6.5	6.6	6.6	6.5	6.8	8.5	8.5
Organic C (g kg^{-1})	396	331	6.56	3.96	2.46	2.62	0.55
Total N (g Mg^{-1})	21270	20647	544	436	298	224	47
Drainage	moderate						

* Available at Flux Canada Research Network DIS online at http://fluxnet.ccrp.ec.gc.ca.

Table 4.S2 Soil characteristics of the Southern Old Jack Pine site in Saskatchewan, Canada*

Glacial Till	LFH	Ae	AB	Bm	C	Ck	Ck
Depth to Bottom (m)	0.04	0.06	0.10	0.38	0.89	1.17	3.5
Bulk Density (Mg m^{-3})	0.24	1.23	1.45	1.48	1.52	1.60	1.60
Field Capacity (m^3 m^{-3})	0.21	0.062	0.064	0.048	0.038	0.042	0.018
Wilting Point (m^3 m^{-3})	0.07	0.033	0.038	0.027	0.024	0.024	0.011
K_{sat} (mm h^{-1})	420	620	620	830	980	1130	1130
Sand (g kg^{-1})	943	943	934	939	963	975	975
Silt (g kg^{-1})	29	29	39	33	19	10	10
Clay (g kg^{-1})	28	28	27	28	18	15	15
Coarse Frag. (m^3 m^{-3})	0	0	0	0	0	0	0
CEC (cmol$^+$ kg^{-1})	501	46	40	22	21	16	16
pH	4.7	5.3	5.5	5.8	5.8	5.9	6.2
Organic C (g kg^{-1})	250.7	9.95	6.43	1.32	0.42	0.32	0.15
Total N (g Mg^{-1})	4827	430	290	115	42	32	15
Drainage	well drained						

* Available at Flux Canada Research Network DIS online at http://fluxnet.ccrp.ec.gc.ca.

Table 4.S3 Values of key parameters used in simulations of the TRIPLEX-Management model.

Parameter	Description	Species		Reference
		Aspen	Jack pine	
Photosynthetically active radiation				
Absorb	Atmospheric absorption factor	0.15	0.15	Bossel (1996)
Cloud	Time faction of cloud days	0.4	0.4	Bossel (1996)
PAR factor	Sloar radiation fraction	0.47	0.47	Bossel (1996)
Gross primary productivity				
BlCond	Canopy boundary layer conductance (ml m^{-2} s^{-1})	0.2	0.2	Landsberg and Waring (1997)
MaxCond	Max canopy conductance (ml m^{-2} s^{-1})	0.02	0.02	Landsberg and Waring (1997)
StomCond	Stomata conductance (ml m^{-2} s^{-1})	0.006	0.006	Landsberg and Waring (1997)
ExtCoef	Radiation extinction coefficient	0.5	0.5	Landsberg and Waring (1997)
TaMin	Min temperature (°C) for growth	6^{a}	0^{a}	
TaMax	Max temperature (°C) for growth	30	30	Peng et al, (2002)
Topt	Optimum temperature (°C) for growth	18^{a}	15	Kimball et al, (1997)
Nitrogen factor	Nitrogen factor for tree growth	0.2	0.2	Set as 20% for growth
Na	Effect of age to GPP	4	3	Landsberg and Waring (1997)
Sla	Specific leaf area (m^{2} kg^{-1} of carbon)	22.5	6	Kimball et al. (1997)
Net primary productivtiy				
GamaF	Leaves turnover per year	0.0	0.19	Gower et al (1997) [b]
GamaR	Fine roots turnover per year	1.85	1.55	Steele et al. (1997)[c]
Soil C and N				
Lnr	Lignin-nitrogen ratio	0.26	0.26	Parton *et al.*, 1993
Ls	Lignin for leaf, fine root, coarse root, branch, and wood	0.215, 0.215, 0.255, 0.235, 0.255	0.215, 0.215, 0.255, 0.235, 0.255	Parton *et al.*, 1993
Soil water				
A1, A2, A3	Soil water depth of layer 1,2, and 3 (cm)	10, 20, 145	4, 6, 28	data
S1F, S2F, and	Field capacity of layer 1, 2,	0.45, 0.24, 0.19	0.21, 0.06, 0.05	data

S3F	and 3 (m^3 m^{-3})			
S1W, S2W, and S3W	Wilting point of layer 1, 2, and 3 (m^3 m^{-3})	0.15, 0.10, 0.13	0.07, 0.04, 0.03	data
Growth and yield				
MiuNorm	Normal mortality (yearly)	0.015	0.012	Assumption
MiuCrowd	Competition mortality (yearly)	0.02	0.02	Assumption
Species parameter				
CSP	Wood carbon density (Mg m^{-3})	0.19	0.22	Newcomer et al. (2000)
CD	Crown to stem diameter ratio	25	20	Bossel (1996)
AlphaC	Canopy quantum efficiency	0.07	0.05	Landsberg and Waring (1997)
MaxHeight	Max height (m)	25	20	Assumption
AgeMax	Max stand age (year)	200	150	Assumption

[a] Calibrated depend on flux data.

[b] Estimated based on results (0.08-0.36 $year^{-1}$) of Gower et al (1997).

[c] Estimated based on results (1.4-3.3 $year^{-1}$) of Steele et al. (1997).

Table 4.S4 Stand characteristics measured (M) by Gower et al. (1997) and Howard et al. (2004) and simulated (S) at the Southern Old Aspen (SOAS) site and the Southern Old Jack Pine (SOJP) site for different ages in Saskatchewan, Canada.

Age (year)	Site		Stand density (stems ha^{-1})	Mean DBH (cm)	Mean Height (m)	LAI
67 (1986[a])	SOAS	M	980	20.5	20.1[b]	5.6 (0.5)
		S	1040	20.6	21.2	6.3
65 (1995[a])	SOJP	M	1190	12.9	12.7[b]	2.4 (0.2)
		S	1206	11.7	11.3	1.3
71 (1999)	SOJP	M	1196 (146)	13.1[c]	12-15[d]	1.3 (0.3)
		S	1149	12.2	11.5	1.3
72 (2000)	SOJP	M	1160 (138)	13.1[c]	12-15[d]	1.3 (0.3)
		S	1136	12.2	11.6	1.2

Values in parentheses are standard deviation. DBH represents diameter at breast height.

[a] Estimated year based on stand age and regeneration year from Gower et al. (1997).

[b] Estimated mean tree height from DBH-height relationship applied to stand inventory data by Gower et al. (1997).

[c] Measured mean DBH for the 1999 and 2000 growing seasons by Howard et al. (2004).

[d] Estimated tree height range by Howard et al. (2004).

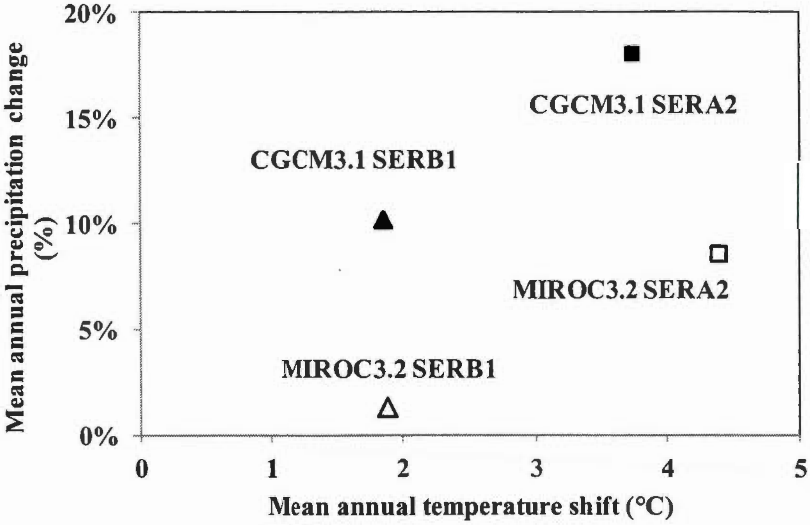

Figure 4.S1 Paired mean annual temperature shift and mean annual precipitation change for the last 20 years (2081-2100) of 21 century under the four climatic change scenarios. CGCM3.1 and MIROC3.2 represent Coupled Global Climate Model developed by Canadian Centre for Climate Modelling and Analysis, and Model for Interdisciplinary Research on Climate (JAPAN), respectively. SERA2 and SERB1 represent Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A2 and B1, respectively.

CHAPTER V

POSITIVE RELATIONSHIP BETWEEN ABOVEGROUND CARBON STOCKS AND STRUCTURAL DIVERSITY IN SPRUCE-DOMINATED FOREST STANDS IN NEW BRUNSWICK, CANADA

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5.1 Résumé

Le maintien de la structure et la fonctionnalité des écosystèmes forestiers est l'objectif principal de la gestion forestière. Dans cette étude, les relations entre la diversité structurelle et les stocks de carbone (C) hors-sol ont été examinés dans les forêts dominées par l'épinette au Nouveau-Brunswick, Canada. Les indices de diversité d'espèces d'arbres, la taille, et la hauteur ainsi qu'une combinaison de ces indices de diversité ont été utilisés pour corréler les stocks de C hors sol. Des régressions linéaires multiples ont ensuite été utilisées pour quantifier les relations entre ces indices et le C aérien. L'analyse de corrélation partielle a également été adoptée pour éliminer les effets des autres variables explicatives. Les résultats montrent que la diversité structurelle du peuplement a un effet positif significatif sur les stocks de C hors sol, même si la relation est faible dans l'ensemble. Les relations positives observées entre les indices de diversité et les stocks de C aériens soutiennent l'hypothèse que l'augmentation de la diversité structurelle améliore la capacité de stockage du C hors-sol. Cela se produit parce que les structures forestières complexes permettent une plus grande infiltration de lumière et promouvaient une utilisation plus efficace des ressources par les arbres, conduisant ainsi à une augmentation de la biomasse et de la production de C. Des mélanges d'arbres tolérants à l'hombre couplés à une gestion non équienne des peuplements vont aider à maintenir une grande diversité structurelle. Ces outils sont recommandés pour préserver les stocks de C dans les forêts dominées par l'épinette.

Mots-clés: gestion des forêts, hypothèse de la complémentarité de niches, indice del Shannon-Wiener, Structure des peuplements forestiers

5.2 Abstract

Maintaining both the structure and functionality of forest ecosystems is a primary goal of forest management. In this study, relationships between structural diversity and aboveground stand carbon (C) stocks were examined in spruce-dominated forests in New Brunswick, Canada. Tree species, size, and height diversity indices as well as a combination of these diversity indices were used to correlate aboveground C stocks. Multiple linear regressions were subsequently employed to quantify the relationships between these indices and aboveground C stocks, and partial correlation analysis was also adopted to remove the effects of other explanatory variables. Results show that stand structural diversity has a significant positive effect on aboveground C stocks even though the relationship is weak overall. Positive relationships observed between the diversity indices and aboveground C stocks support the hypothesis that increased structural diversity enhances aboveground C storage capacity. This occurs because complex forest structures allow for greater light infiltration and promote a more efficient resource use by trees, leading to an increase in biomass and C production. Mixed tolerant species composition and uneven-aged stand management in conjunction with selection or partial cutting to maintain high structural diversity is therefore recommended to preserve biodiversity and C stocks in spruce-dominated forests.

Keywords: forest management, niche complementarity hypothesis, Shannon-Wiener index, stand structure

5.3 Introduction

The role of biodiversity in ecosystem functioning has become a central issue in ecology (Diaz *et al.*, 2009, Loreau *et al.*, 2001). Specifically, in the context of biodiversity conservation and the mitigation of global warming, the relationship between biodiversity and carbon (C) sequestration has become more and more a focal point. Stand structural diversity can be an indicator of overall biodiversity (Staudhammer and LeMay, 2001) and is commonly used when characterising spatial distribution, species diversity, and variation in tree dimensions such as tree size and height or a combination of these factors (McElhinny *et al.*, 2005, Pommerening, 2002b, Staudhammer and LeMay, 2001). It can also be logically linked to forest management practices and objectives (Lei *et al.*, 2009). The idea that biodiversity can be maintained by managing the structural diversity of stands is a common argument among researchers (Buongiorno *et al.*, 1994, Buongiorno *et al.*, 1995, Lindenmayer and Franklin, 1997, FranklinSpiesVan Pelt *et al.*, 2002, Kant, 2002, Varga *et al.*, 2005, Sullivan *et al.*, 2001). In developing appropriate forest management strategies to preserve biodiversity and mitigate the effects of climate change, a more comprehensive understanding is needed concerning the effect of stand structural diversity on C sequestration capacity within forest ecosystems (Bosworth *et al.*, 2008).

Numerous studies have investigated the relationship between species diversity and productivity in forest ecosystems (Bunker *et al.*, 2005, Creed *et al.*, 2009, Caspersen and Pacala, 2001). The literature suggests that the relationship between productivity and species diversity is often positive (Gillman and Wright, 2006, Balvanera *et al.*, 2006, Whittaker and Heegaard, 2003). The effect of plant diversity on C storage has also been explored. For example, Chen (2006) reported a positive relationship between tree species diversity and soil organic C content in the top 30 cm soil layer in an old growth forest in Northeast China. Fornara and Tilman (2008) suggested that there was a positive impact of plant diversity on soil C accumulation in agriculturally degraded soils at Cedar Creek, Minnesota, USA. Saha et al. (2009) observed that soil

C stocks increased with an increase in plant species diversity in tropical homegarden systems. One of hypothesis contributing to explain this relationship is the niche complementarity hypothesis which proposes that species-rich communities are able to more efficiently access and utilize limiting resources (Tilman, 1999). However, Szwagrzyk and Gazda (2007) found that a negative relationship exists between aboveground biomass and tree species diversity in natural forests of Central Europe. In addition, Jonsson and Wardle (2009) also reported in their structural equation modeling study that plant diversity has a weak effect on belowground C storage for C storage drivers in boreal forest ecosystems.

Although studies on species diversity effects on productivity and C stocks are numerous, information concerning forest structural diversity, especially spatial structure, is as yet poorly understood in a comprehensive ecosystem perspective. For example, Lei et al. (2009) reported a positive relationship between structural diversity and forest growth in spruce-dominated forests. In contrast, Edgar and Burk (2001) indicated that productivity was negatively correlated to stand composition and canopy vertical structure in aspen (Populus tremuloides Michx.) forest stands. Moreover, Liang et al. (2005, 2007) found negative and unimodal relationships between productivity and tree size diversity for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco)–western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and mixed coniferous stands, respectively. In addition, Long and Shaw (2010) recently observed that stand growth is not strongly influenced by either compositional or structural diversity in ponderosa pine (*Pinus ponderosa* C. Lawson) stands in the western region of the United States. However, little information exists concerning relationships between structural diversity and C storage at the stand scale. Do high levels of stand structural diversity, therefore, increase C storage, decrease it, or leave it unaffected?

Lei et al. (2009) have previously investigated the relationship between structural diversity and forest growth. Little, however, is known of the relationship between structural diversity and aboveground C stocks in spruce-dominated forest stands in New Brunswick, Canada. Spruce-dominated forests are an important boreal forest ecosystem constituent that possesses simple tree composition but complex forest age and tree size structure. Forest managers tend to be more interested in developing silvicultural solutions to enhance forest growth and C stocks for multiple-use management. According to the niche complementarity hypothesis, a greater overall C pool is assumed in black spruce-dominated forests featuring complex forest structure. Therefore, the objectives of this study were to 1) test the hypothesis that states that increased structural diversity enhances aboveground C stocks and 2) discuss potential managerial implementations to increase stand structural diversity in spruce-dominated forests in order to enhance C stocks.

5.4 Data and methods

5.4.1 Data

Data were compiled from the New Brunswick Permanent Sample Plot Database (PSPDB) (Porter *et al.*, 2001). Spruce-balsam fir (SPBF) plots were selected where the proportion (in volume) of spruce trees was greater than 0.6 and, as a result, designated as spruce-dominated forest stands. In total, we selected 411 plots where trees were measured once. PSPDB sampling is conducted in 400 m^2 circular plots. Since height data was only available for trees greater than 9 cm dbh (diameter at breast height, in centimeters) trees with a dbh less than 9 cm were excluded from our analysis. Stand age reported for the studied PSPs ranged from 32 to 200 years (Porter *et al.*, 2001). Stands were then assigned to forest stand developmental stages defined as young (less than 45 years), immature (46 to 70 years), mature (71 to 110 years), and overmature (greater than 111 years) (Porter *et al.*, 2001). One to seven tree species were found within each plot, and a total of 21 tree species were cataloged after plots were combined. The most frequent tree species observed were black spruce (*Picea mariana* (Mill) BSP), white spruce (*Picea glauca* (Moench) Voss), red spruce

(*Picea rubens* Sarg.), and balsam fir (*Abies balsamea* (L.) Mill) (Table 5.1.). For each plot the following stand variables were calculated (Table 5.2): stand density (N, stems/ha), stand basal area (BA, m^2/ha), the quadratic mean dbh (Dq, cm), and site productivity (Sp, m^3/ha/year), measured as the mean annual increment by stand volume.

Table 5.1 Summary of species composition (percentage of volume).

Tree species	Mean	Std	Min	Max
Black spruce	0.45	0.44	0	1
White spruce	0.08	0.23	0	1
Red spruce	0.32	0.37	0	1
Spruce subtotal	0.85	0.12	0.6	1
Balsam fir	0.05	0.08	0	0.38
Others [a]	0.10	0.11	0	0.40

[a] Tree species besides spruce and balsam fir: white pine (*Pinus strobus* L.), jack pine (*Pinus banksiana* Lamb.), red pine (*Pinus resinosa* Ait.), eastern white cedar (*Thuja occidentalis* L.), eastern hemlock (*Tsuga canadensis* (L.) Cariere) , tamarack (*Larix laricina* (Du Roi) K. Koch), red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britt.), gray birch (*Betula populifolia* Marsh.), beech (*Fagus grandifolia* Ehrh.), white ash (*Fraxinus Americana* L.), white birch (*Betula papyrifera* Marsh.), trembling aspen (*Populus tremuloides* Michx.), largetooth aspen (*Populus grandidentata* Michx.), black ash (*Fraxinus nigra* Marsh.) and balsam poplar (*Populus balsamifera* L.).

5.4.2 Aboveground C stock estimation

For each component (wood, bark, branches, and foliage) of tree biomass the following allometric equation was used:

$$y = \beta_1 D^{\beta_2} \qquad (1)$$

where y is the dry biomass component of living trees; D is the dbh; and β_1 and β_2 are the model parameters to be estimated. This type of model estimates the biomass of the whole tree based on dbh measurements. Model parameters for different species were provided by Lambert et al. (2005). The aboveground biomass of the whole tree was calculated by summing up the aforementioned four tree components. The total biomass of a plot was computed by tallying all trees together. Aboveground C stock was then estimated by way of the product of all tree dry biomass calculated from the biomass equations and a constant factor of 0.5 as suggested by the global C cycle community.

Table 5.2 Stand characteristics during all four developmental stages. Dq is quadratic mean dbh; N is stand density; BA is stand basal area per hectare; V is standing volume per hectare; Sp is site productivity; ACS is aboveground C stock; Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh are the structural diversity indices shown in Table 5.3. The value in parenthesis is the standard deviation.

Characteristic	Young	Immature	Mature	Overmature	Total
Number of stands	24	116	213	58	411
Age (yr)	40 (4)	61 (6)	87 (8)	136 (18)	84 (27)
Height (m)	11.3 (2.1)	12.4 (2.5)	12.9 (2.6)	13.1 (3.0)	12.6 (2.6)
BA (m^2/ha)	26.2 (7.4)	27.5 (8.6)	28.4 (8.8)	31.2 (10.2)	28.4 (8.9)
V (m^3)	134.7 (45.4)	160.1 (57.3)	173.2 (61.0)	198.4 (76.9)	170.8 (63.3)
Dq (cm)	14.2 (2.1)	17.1 (3.3)	18.4 (3.1)	19.8 (4.6)	18.0 (3.6)
Sp (m^3/ha/yr)	3.4 (1.2)	2.7 (1.0)	2.0 (0.7)	1.5 (0.5)	2.2 (1.0)
N (stems/ha)	1682 (534)	1270 (487)	1118 (415)	1041 (337)	1183 (457)
ACS (Mg/ha)	47.4 (13.9)	54.2 (18.1)	58.0 (19.4)	66.5 (24.7)	57.5 (20.1)
Hs	0.508 (0.423)	0.554 (0.426)	0.517 (0.368)	0.496 (0.344)	0.524 (0.384)
Hd	1.267 (0.306)	1.480 (0.278)	1.586 (0.282)	1.717 (0.344)	1.556 (0.309)
Hh	1.292 (0.288)	1.349 (0.207)	1.417 (0.211)	1.496 (2.245)	1.402 (0.226)
Hsd	2.205 (0.491)	2.323 (0.404)	2.356 (0.374)	2.417 (0.395)	2.347 (0.394)
Hsp	1.086 (0.404)	1.165 (0.455)	1.151 (0.408)	1.275 (0.436)	1.169 (0.426)
Hsdh	1.987 (0.542)	2.161 (0.410)	2.192 (0.373)	2.267 (0.373)	2.182 (0.398)
GCd	0.266 (0.058)	0.306 (0.065)	0.335 (0.077)	0.380 (0.094)	0.329 (0.080)
GCh	0.090 (0.023)	0.093 (0.018)	0.100 (0.021)	0.115 (0.029)	0.099 (0.023)

5.4.3 Stand structural diversity indices

The method to determine stand structural diversity indices has been described in detail in an earlier study (Lei *et al.*, 2009). These authors addressed six Shannon-Wiener indices related to tree species (Hs), tree size (Hd), tree height (Hh) and their combined interactions. These include the integrated diversity of species and size

(Hsd), the integrated diversity of species and height or the species profile index (Hsp), and the average structural diversity index (Hsdh) of all three diversity indices of species, dbh, and height, as well as two Gini coefficient indices calculated by means of both tree diameter (Gcd) and height (Gch) values (Table 5.3). The Shannon-Wiener index was calculated using the proportion of tree species basal area, diameter class, and height class (Table 5.3). The use of the Shannon-Wiener index approach (based on species richness and evenness) meant that dbh and height had to be grouped into discrete classes. We used 4cm dbh classes and 2 m hight classes. According to Lei et al. (2009), tree size diversity described using 4 cm dbh classes and tree height diversity using 2 m classes exhibited high correlation coefficients with comparable indices based on other class widths for spruce-dominated forests. The Gini coefficient does not require arbitrarily determined diameter classes and performs better than other stand structural diversity measurements applied to forest management planning and practices (Lexerød and Eid, 2006). It has a minimum value of zero (0) when all trees are of equal size and a theoretical maximum of one (1) when all trees but one have a value of zero. Higher values, therefore, indicate greater structural diversity.

5.4.4 Statistical analysis

The normality of distribution of the structural diversity indices and the aboveground C stock for the entire dataset and subgroup datasets were tested throughout all developmental stages using the Shapiro-Wilk test. When and if distributions were approximately normally distributed, Pearson's coefficient (r) correlations were calculated between the eight structural diversity indices and the aboveground C stock. When and if distributions were not normal, the Spearman's rank coefficients (ρ) correlations were computed instead.

Table 5.3 Stand structural diversity indices used in this study (modified from Lei et al. (2009))

No	Index	Formula	Description
1	Tree species diversity index	$Hs = -\sum_{i=1}^{s} p_i \cdot \log p_i$, where p_i is the proportion of basal area for i th species and s is the number of species.	Shannon-Wiener index for species (Magurran 2004)
2	Tree size diversity index	$Hd = -\sum_{i=1}^{d} p_i \cdot \log p_i$, where p_i is the proportion of basal area for i th diameter class and d is the number of diameter class.	Shannon-Wiener index for tree size (Buongiorno 1994)
3	Tree height diversity index	$Hh = -\sum_{i=1}^{h} p_i \cdot \log p_i$, where p_i is the proportion of basal area for i th height class and h is the number of height class.	Shannon-Wiener index for tree height class (Staudhammer and Lemay 2001)
4	Integrated diversity index of tree species and size	$Hsd = -\sum_{i=1}^{s} \sum_{j=1}^{d} p_{ij} \cdot \log p_{ij}$, where p_{ij} is the proportion of basal area in j th diameter class of the i th species, s is the number of tree species, and d is the number of diameter class.	Integrated Shannon-Wiener index for species and tree size (Buongiorno 1994)
5	Species profile index	$Hsp = -\sum_{i=1}^{s} \sum_{j=1}^{3} p_{ij} \cdot \log p_{ij}$, where p_{ij} is the proportion of basal area of j th height class of the i th species, s is the number of tree species, height class 1: 100 - 80% of maximal tree height (hmax), height class 2: 80% to 50 % of hmax, and height class 3: 50% to 0% of hmax	Integrated Shannon-Wiener index for the proportion of species in different stand layer (Pretzsch 1997)
6	Mean structural diversity index	$Hsdh = (H_s + H_d + H_h)/3$	Mean value of tree species, size, and height indices (Staudhammer and Lemay 2001)
7	Gini coefficient for dbh	$GCd = \frac{\sum_{i=1}^{n} (2j-n-1) ba_j}{\sum_{i=1}^{n} ba_j (n-1)}$, where ba_j is the basal area of the tree with rank j, j is the rank of a tree in ascending order from 1 to n by dbh, n is the number of trees.	Measurements of the deviation from perfect equality (Lexerød and Eid 2006)
8	Gini coefficient for height	$GCh = \frac{\sum_{i=1}^{n} (2j-n-1) ba_j}{\sum_{i=1}^{n} ba_j (n-1)}$, where ba_j is the basal area of the tree with rank j, j is the rank of a tree in ascending order from 1 to n by height, n is the number of trees.	Measurements of the deviation from perfect equality (Lexerød and Eid 2006)

Since stand density, age, and site quality are known to influence stand growth (Larson *et al.*, 2008, Fridley, 2002, Firn *et al.*, 2007, Liang *et al.*, 2007, Pretzsch, 2005) and may also affect relationships between structural diversity and aboveground C stocks, stand age, site productivity, and stand density were chosen as potential additional independent variables in order to quantify the effects of site factors and initial stand conditions to these relationships. Multiple linear regressions (SPSS, Inc., Chicago, IL, United States of America) were used to fit the data and to identify the effects of independent variables selected by way of the stepwise procedure in relation to aboveground C stocks. Multicollinearity diagnosis was carried out using the variance inflation factor (VIF) since multicollinearity may cause inaccurate model parameterization, decreased statistical power, and exclude significant predictor variables (Graham, 2003). Variables with VIF larger than five were excluded from the model.

Eight aboveground C stock models were tested in total (Eq. 2) since they were developed for aboveground C stocks and the eight explanatory diversity variables separately:

$$ACS = b_0 + b_1 diversity + b_2 N + b_3 Age + b_4 Sp \qquad (2)$$

where ACS is the aboveground C stock; diversity is the stand structural diversity index (Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh); N is stand density; Age is stand age; and Sp is site productivity. Model fitting and performance were assessed using the adjusted coefficient of determination (R^2) and significance (F value and p-value) measurements. Partial correlation coefficients for each predictable variable for all models were described. These measure the degree of association between stand structural diversity indices and aboveground C stocks with the effect of removing a set of controlling random variables (e.g., stand density, age, and site productivity for stand structural diversity). Variables with high partial correlation coefficients indicate a strong relationship to aboveground C stocks.

5.5 Results

5.5.1 Stand characteristics

Tree height and dbh ranged from 6.7 m to 24.9 m and from 9.1 cm to 56.9 cm, respectively. The most obvious general stand level trend was that dbh, height, volume, basal area, and the structural diversity indices (Hd, Hh, Hsd, Hsp, Hsdh, GCd, GCh) increased as the age of the stands increased. The only exceptions for this trend were seen in stand density, productivity, and species diversity (Hs) (Table 5.2). Diameter distribution exhibited the typical inverse J curve that exhibited in many old natural forest stands (Figure 5.1). The pattern of expansive larger range of tree dbh in conjunction with stages of stand development was accompanied by decreasing density and productivity (Table 5.2). Although younger stands possessed smaller stand volume overall, it is assumed they undergo higher growth rates and possess greater stem density. Older stands, on the other hand, possessed higher structural complexity both horizontally and vertically (Table 5.2, Figures 5.1 and 5.2). Tree species diversity did not follow this pattern. It increased during the young to immature stages and then decreased in the following stages of stand development.

5.5.2 Aboveground C stocks

Aboveground C stocks in spruce-dominated forests ranged from 13.58 to 110.12 Mg ha^{-1} (with an average of 57.49 Mg ha^{-1}). In addition, aboveground C stocks exhibited a general increasing trend throughout all stand developmental stages (Figure 5.3). Older forests therefore possess both greater quantities of C and a more complex stand structure than younger forests.

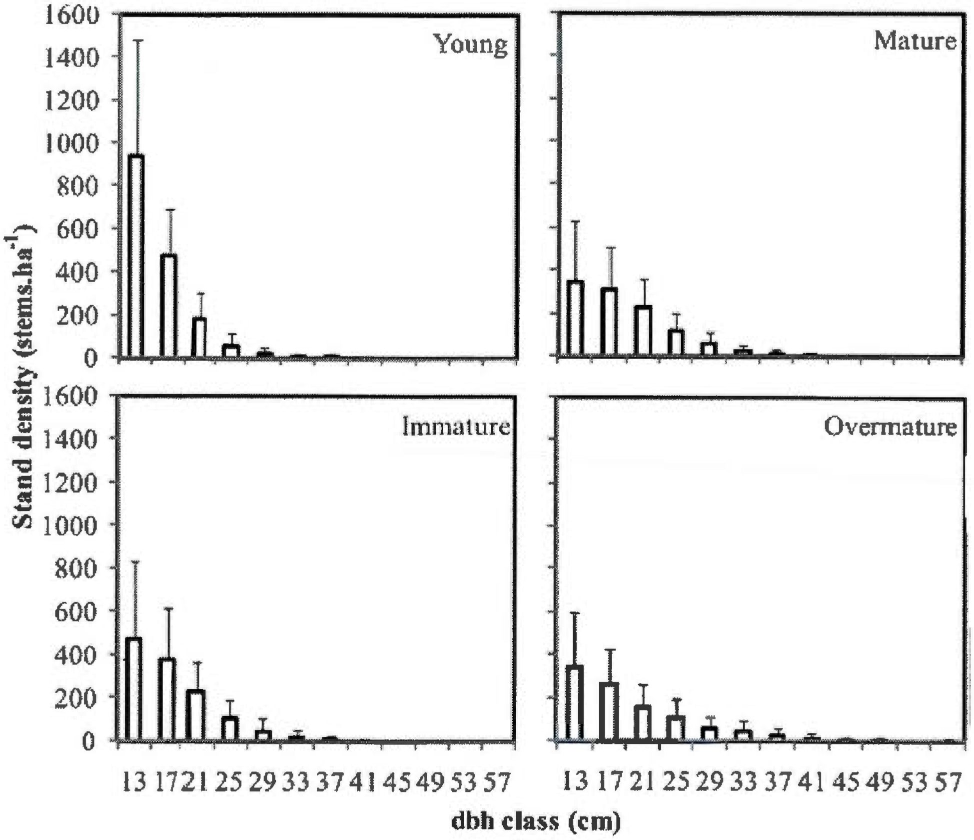

Figure 5.1 Diameter distribution for Spruce-balsam fir plots throughout all four developmental stages. Error bars represent standard deviations.

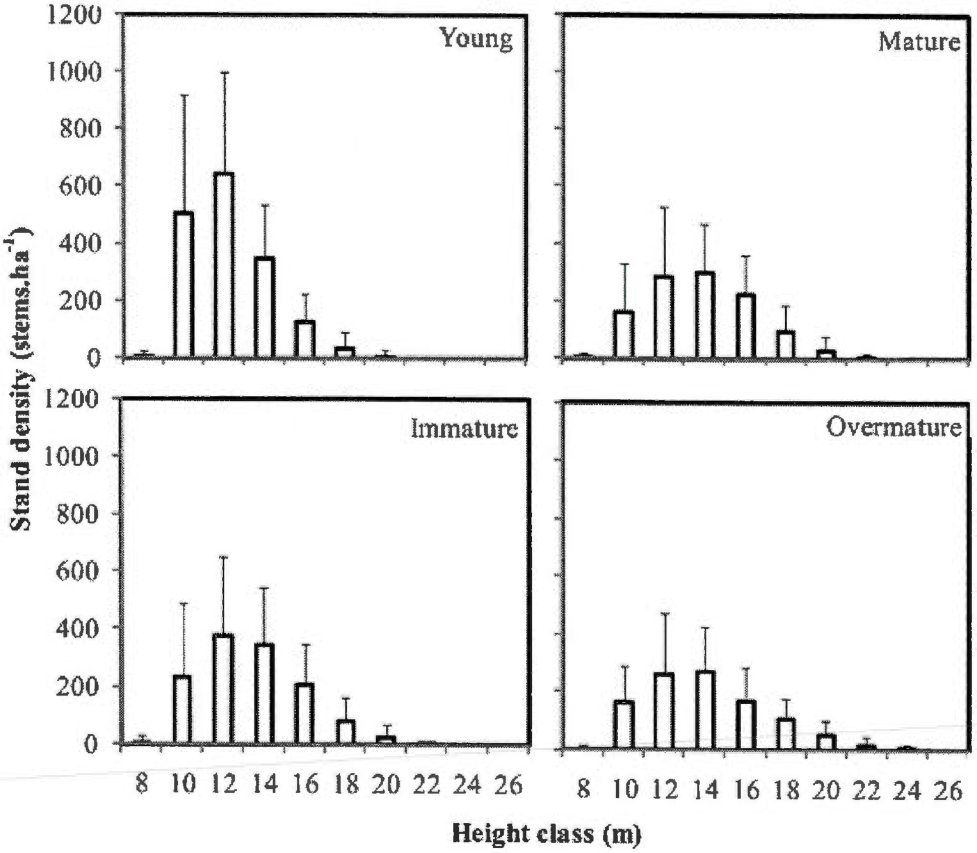

Figure 5.2 Height distributions for Spruce-balsam fir plots throughout all four developmental stages. Error bars represent standard deviations.

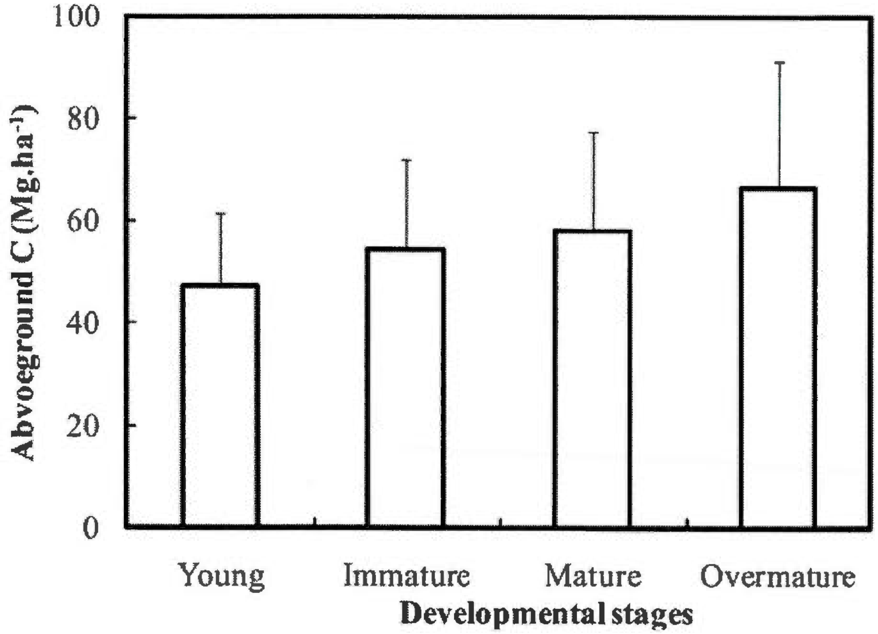

Figure 5.3 Mean aboveground C stocks for Spruce-balsam fir plots during all four developmental stages. Error bars represent standard deviations.

5.5.3 Relationships between aboveground C stocks and structural diversity

Significant positive relationships were found in the dataset between the eight structural diversity indices and aboveground C stocks (Table 5.4, Figure 5.4). Results showed that correlation coefficients changed from 0.314 (Hs) to 0.600 (Hd) throughout all eight diversity indices, all of them being significant at the 0.01 level. Positive relationships between three of the eight correlation coefficients (Hs, Hsd, and Hsdh) generally increased throughout the stand developmental stages (Table 5.4). With the exception of Hs, Hsd, Hsp, and Hsdh that occurred during the early stages, all relationships between the structural diversity indices and aboveground C stocks were significant. However, tree height diversity (Hh and GCh) was related to aboveground C stocks to a lesser extent during the immature stage than it was during the other three stages.

Table 5.4 Relationship between structural diversity indices and aboveground C stocks: Pearson's correlation coefficient (r), Spearman's rank correlation coefficient (ρ); Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh are the structural diversity indices shown in Table 5.3.

Variables	Total data set (n=411)	Young (n=24)	Immature (n=116)	Mature (n=213)	Overmature (n=58)
Hs	$\rho=0.314^{**}$	$\rho=0.189$	$\rho=0.201^{*}$	$\rho=0.397^{**}$	$\rho=0.425^{**}$
Hd	$\rho=0.600^{**}$	$r=0.561^{**}$	$r=0.487^{**}$	$\rho=0.553^{**}$	$\rho=0.724^{**}$
Hh	$\rho=0.380^{**}$	$r=0.508^{*}$	$r=0.218^{*}$	$r=0.379^{**}$	$\rho=0.539^{**}$
Hsd	$\rho=0.552^{**}$	$r=0.307$	$r=0.447^{**}$	$\rho=0.589^{**}$	$\rho=0.632^{**}$
Hsp	$\rho=0.421^{**}$	$\rho=0.265$	$\rho=0.241^{**}$	$\rho=0.447^{**}$	$\rho=0.617^{**}$
Hsdh	$\rho=0.484^{**}$	$r=0.229$	$r=0.350^{**}$	$\rho=0.523^{**}$	$\rho=0.585^{**}$
GCd	$\rho=0.410^{**}$	$r=0.521^{**}$	$r=0.280^{**}$	$r=0.366^{**}$	$\rho=0.598^{**}$
GCh	$\rho=0.319^{**}$	$r=0.445^{*}$	$r=0.177$	$r=0.247^{**}$	$\rho=0.574^{**}$

* P value significant at $\alpha=0.05$; ** P value significant at $\alpha=0.01$.

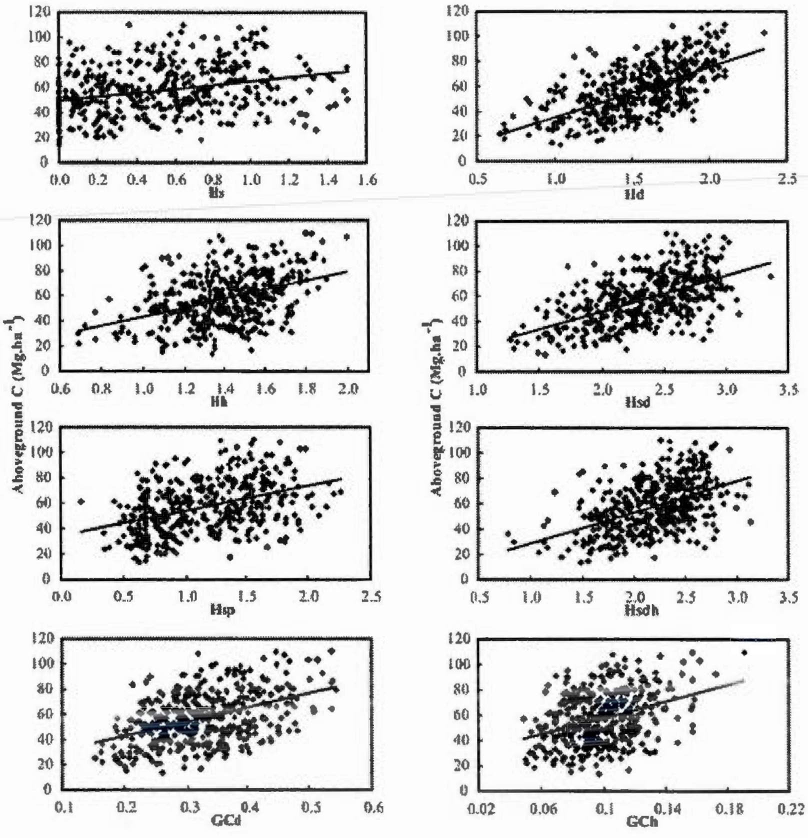

Figure 5.4 Relationships between aboveground C stocks and structural diversity indices (n=411). Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh are the structural diversity indices shown in Table 5.3.

Multicollinearity analysis ascertained the correlations from the explanatory variables used in the multiple regression models such as stand age, productivity, stand density, and the structural diversity indices themselves. These models showed non-significant multicollinearity because the VIF of the stand structural diversity indices, stand density, productivity, and stand age were less than five (Table 5.5). Multiple linear regression analysis integrating stand age, stand density, site productivity, and structural diversity explained more than 80% of the variation in aboveground C stock. All predictable variable parameters for the models were significant with the exception of stand density to height diversity (Hh) (Table 5.5). Among the predictable variables, stand age and productivity always exhibited high values in relation to the partial correlation coefficients (Table 5.5), whereas stand density and the structural diversity indices exhibited low values in relation to the partial correlation coefficients. Results show that stand age and productivity played the most important roles in terms of aboveground C stock. Stand structural diversity indices differed for correlations involving aboveground C stocks. For example, Hd produced the maximum partial correlation coefficient ($r=0.396$, P value<0.001) and Hh produced the minimum partial correlation coefficient ($r=0.131$, P value<0.01) (Table 5.5). All parameters as well as the partial correlation coefficients used for the structural diversity indices of all models were positive and, as a result, aboveground C stocks increased with an increase in the stand structural diversity indices (Table 5.5).

Table 5.5 Summary of multiple linear regression models for aboveground C stocks. Regressions d.f. = 4, 406; b_0 to b_4 refers to interception, diversity, stand density, stand age, and site productivity, respectively; r_1 to r_4 are the partial correlation coefficients of the corresponding explanatory variables; VIF_1 to VIF_4 are the variance inflation factors corresponding to the four explanatory variables; Hs, Hd, Hh, Hsd, Hsp, Hsdh, GCd, and GCh are the structural diversity indices shown in Table 5.3.

Structural	Parameter estimates and partial correlation coefficients														
diversity indices	b_0	b_1	r_1	VIF_1	b_2	r_2	VIF_2	b_3	r_3	VIF_3	b_4	r_4	VIF_4	Adjusted R^2	F value
Hs	-38.4	4.835	0.196***	1.276	0.003	0.125*	1.378	19.953	0.876***	1.704	0.553	0.843***	1.375	0.830	503.1***
Hd	-52.2	17.311	0.396***	2.587	0.007	0.298***	1.911	16.668	0.777***	2.928	0.448	0.733***	2.183	0.851	587.8***
Hh	-39.0	4.512	0.109**	1.227	NS	NS	NS	20.515	0.812***	1.552	0.538	0.888***	1.608	0.826	648.6***
Hsd	-49.5	7.892	0.280***	1.748	0.004	0.177***	1.469	18.467	0.823***	2.389	0.517	0.812***	1.589	0.838	529.5***
Hsp	-40.8	5.767	0.243***	1.452	0.003	0.158***	1.464	19.399	0.861***	1.900	0.535	0.830***	1.462	0.834	516.4***
Hsdh	-44.8	5.380	0.207***	1.521	0.003	0.133**	1.402	19.399	0.849***	2.069	0.531	0.819***	1.539	0.831	505.9***
GCd	-45.9	44.102	0.315***	1.784	0.005	0.215***	1.614	18.930	0.858***	1.928	0.495	0.786***	1.783	0.841	544.1***
GCh	-40.8	68.516	0.153**	1.506	0.002	0.111*	1.411	20.090	0.873***	1.743	0.530	0.802***	1.696	0.828	493.7***

* P value significant at α=0.05;

** P value significant at α=0.01;

*** P value significant at α=0.001;

[a] NS, not significant.

5.6 Discussion

5.6.1 Aboveground C stocks throughout forest developmental stage gradients

It was ascertained that C stocks showed a general increasing trend throughout all forest stand developmental stages (Figure 5.3). Many other studies have found a similar increasing trend for both aboveground and belowground C stocks that addresses age dependence of forest biomass or C stocks (Peichl and Arain, 2006, Taylor *et al.*, 2007). As a result, forest developmental stages play a determining role in the distribution of C pools for different forest ecosystems (Pregitzer and Euskirchen, 2004).

A greater C stock accumulation was found in older stands with high structural diversity compared to young spruce-dominated forest stands because older stands are more likely to incorporate a greater variation in tree size distribution due to the fact that older stands possess a greater number of large trees overall (Fingers 5.1 and 5.2). Moreover, because the coefficients of the original bivariate correlation for each diversity index (Table 5.4) were greater than that of the partial correlation (Table 5.5), it has been identified that the effects of controlled variables (stand density, stand age, and productivity) influence both structural diversity and C stocks and structural diversity itself also partially influences C stocks.

5.6.2 Effects of species diversity on aboveground C stocks

Results indicate that significant and positive relationships exist between tree species diversity and aboveground C stocks in spruce-dominated forest stands (Table 5.5 and Figure 5.4). Several authors have reported positive relationships between species diversity and biomass in forest ecosystems (VilàVayredaComasIbáñez *et al.*, 2007). Ishii et al. (2004) also suggested that structural complexity may in itself increase forest growth by promoting complementary resource utilization among plant species. These findings are consistent with the positive, monotonic relationships between productivity and plant species richness (Balvanera *et al.*, 2006, Gillman and Wright, 2006, Whittaker and Heegaard, 2003). Other studies have produced contrasting results. For example, Firn et al. (2007) reported a significant negative relationship between tree species diversity in the overstory and total basal area of tropical plantations. Negative relationships between tree species diversity and biomass were also reported in temperate forest ecosystems of Central Europe (Jacob *et al.*, 2010, Szwagrzyk and Gazda, 2007). The appearance of contradictory results is not surprising, and reconfirmed the complexity of the ecosystem structure and function. Nevertheless, our findings robustly support the niche complementarity hypothesis which states that above-ground C stocks increased with increasing tree species diversity in spruce-dominated forest stands.

5.6.3 Effects of tree size and height diversity on aboveground C stocks

Tree size diversity (Hd or GCd) exhibits the strongest positive effects on aboveground C stocks and possess the largest partial correlation coefficient among all eight structural diversity indices (Table 5.5). This may be the result of high resource use efficiency due to complex tree size structure, supporting niche differentiation between intraspecific species competition. Tree height diversity (Hh and GCh) showed relatively weak effects on aboveground C stocks. This could be the result of tree height being close to the maximum value in both the mature and overmature stages thereby producing a lack of variation in tree height values. Spatial structure diversity indices indicate that greater variation in tree size and height results in a multilayered foliage structure and enhanced structural complexity and, hence, allows for more efficient light infiltration thereby supporting the hypothesis of better resource utilization by trees. The consequence of this better resource use leads to a greater accumulation of biomass and overall C production. Findings that support intraspecific complementary effects were presented by Lei et al. (2009) who investigated the relationship between structural diversity and forest growth in Canadian spruce-dominated forest stands. In one of the few studies that investigated the effects of tree size and height diversity on C stocks, Merino et al. (2007) reported that unmanaged beech (Fagus sylvatica) stands in central Europe obtained higher values for C accumulation in tree biomass compared to managed forests since unmanaged stands possess a more heterogeneous tree structure that induces soils and trees to act as long-term C sinks.

5.6.4 Effects of combined structural diversity on aboveground C stocks

This study found that the effects of combined structural diversity indices (Hsd, Hsp, and Hsdh) were unexpectedly weaker than the effects of tree size diversity (Hd) on aboveground C stocks (Table 5.5). The combined effects, therefore, produce negative side effects. This unpredicted condition may result from the offset between the effects of tree species diversity and tree size or tree height diversity in combination with stand development. Combined effects (Hsd) were found to contribute the most to net stand growth (Lei *et al.*, 2009). There is an obvious need for this to be further explored; however, the focus of this study was centered on structural diversity measures of living trees deemed as overstock. Thus, it is recommended that other attributes of structural diversity such as shrub species richness, coarse woody debris, and dead wood should be investigated in the future.

5.6.5 Implications for forest management initiatives

Silvicultural practices are commonly applied to control forest establishment, composition and structure, and growth with the purpose of producing timber and other forest products (Smith *et al.*, 1997b). Results show that spruce-dominated forests composed of shade tolerant species (spruce and balsam fir) possess higher C stocks than mono-dominated spruce stands. A recent study conducted by Cavard et al. (2010) within the Canadian boreal forest concluded that mixing effects of shade tolerant species could lead to significantly higher C pools compared to mono-specific forest stands. A plausible explanation for this condition may be that both species retain different ecological niches as a result of complementary effects. Our results suggest that silviculture can be used to increase aboveground C stocks by increasing tree species composition and stand structure since our study confirms that stand structural diversity including tree composition, size, and height as well as combined indices have a significant positive relationship with aboveground C stocks. This finding also supports the initial hypothesis of this study. Therefore, a logical silvicultural decision would be to select tolerant species that occur naturally in a region.

In the intervening time, uneven-aged management practices that apply selective or partial cutting may increase structural diversity and enhance C sequestration. This agrees with the results reported by (Lei *et al.*, 2009) in their study on stand growth. For instance, green tree retention has been encouraged as an alternative management strategy to create structurally complex forest stands (Zenner, 2000, Sullivan *et al.*, 2001). In their process-based model study, Garcia-Gonzalo et al. (2007) concluded that the initial forest structure (in terms of species and age class distribution), if not taken into account, may affect C stocks and timber production. Future forest management practices could be determined by the research presented above.

5.7 Conclusions

This study confirms that stand structural diversity in terms of tree species, size, and height as well as the application of the combined indices exhibited a significant positive relationship with aboveground C stocks, supporting the initial hypothesis of this study. As key constituents of structural diversity, the selected tree species, size, and height components can be logically linked to management practices and objectives. For the purpose of maintaining biodiversity and C stocks in spruce-dominated forests, it is recommended that managers apply uneven-aged silvicultural practices by means of selection or partial cutting and choose a mixed tolerant species composition to maintain both high structural diversity and C stocks.

CHAPTER VI

GENERAL CONCLUSIONS AND FUTURE DIRECTIONS

6.1 Summary of findings

A new forest management sub-model that can explicitly simulate forest management practices (thinning and harvesting) was coupled with a stand level process-based model called TRIPLEX1.0 (Chapters II and III). The newly coupled model, TRIPLEX-Management, was then validated against forest thinning data (Chapter II) and multiple data sources (eddy covariance data, C stocks, growth data, Chapter IV) for two different study areas. I also explored mitigation strategies in terms of forest management using the newly developed model under changing climate conditions (Chapters III and IV). In addition, the relationship between complexity of composition and structure and aboveground C was investigated in eastern spruce-dominated forests (Chapter V).

6.1.1 Ecological modeling

6.1.1.1 The model development and validation

In Chapters II- IV, the TRIPLEX-Management model was developed by designing forest thinning and harvesting (with stand establishment) algorithms. The implementation of forest thinning and harvesting algorithms as reported in this study represents an important step towards improving the applicability of this process-based model for forest resource managers and industrial planning initiatives. The model validation increases the creditability of the model in determining the growth response to forest thinning (Figures 2.2-2.4) and in simulating C dynamics (Figures 4.2-4.5) for jack pine forests under forcings of boreal continental climate, although uncertainties exist in model structure and parameters (see section 6.2). Nevertheless, the TRIPLEX-Management model still provides a realistic and flexible tool for analyzing not only the impacts of forest management strategies on forest growth, timber yield, and C dynamics but also for exploring how to modify forest management strategies in order to increase C sequestration both on-site and off-site for mitigating climate change.

6.1.1.2 Roles of forest management under climate change

Future climate may or may not benefit C sequestration. The modeling results presented in this study demonstrate that possible future climate (modest warming only) in northwestern Ontario and at the southern edge of boreal forests in North America may enhance C sequestration for aspen and jack pine forests (Figures 3.4-3.7 and 4.6), if no multiple natural disturbance, such as droughts and insects, disturb these forests. These findings support our first hypothesis that boreal forests may have a negative feedback on climate warming. However, regular frequent droughts might be an important reason of forest decline (NEP<0) in both old aspen and old jack pine forests, without considering of other natural and anthropogenic disturbances (e.g., insect outbreaks and thinning).

Forest management such as harvesting significantly alters forest growth, as well as C and nitrogen (N) dynamics. Simulation results from this study show that harvesting practices could increase the C capture of boreal forests but such activities could also increase the risk of releasing C stored in forests (Figures 3.4 and 4.6). Clearcut logging may result in significant C losses from the litter C and soil organic C pools in the early stage of stand development for both aspen and jack pine forests. Climate warming may enhance C losses after harvesting, but may shorten the recovery time by one or more years, if the regeneration is not reduced by climate change. These findings support our second hypothesis that forest management could help increase forest C sequestration.

Simulation results under the same rotation length indicate that increasing forest thinning intensity would results in decreasing C stocks in soil organic and litter C pools. Thinning always enhances wood production as shown in Table 3.4 and increasing thinning intensity generally results in increasing enhancement on wood production with an exception when thinning at 15-year of age under A2 scenario. However, the positive effects of thinning on wood production under warmer climate conditions (A2 scenario) are less significant than under cooler climate conditions (B1 scenario).

In summary, findings from this study suggest that shortening rotation length could enhance forest C uptake ability and on-site and off-site C stocks, as well as reduce the potential negative effects of climate change on jack pine forests in northwestern Ontario in this century. At the southern edge of boreal forest in North America, shortening rotation length might be a reasonable choice for sequestering a greater amount of C in forest ecosystem and harvested wood, while reducing the potential climate change induced risk such as fire.

6.1.2 Statistical analysis

In Chapter V, statistical analysis confirmed that stand structural diversity in terms of tree species, size, and height as well as the application of the combined indices exhibited a significant positive relationship with aboveground C stocks, although both structural diversity and aboveground C stocks are positively related throughout forest stand development stages (Table 5.5). The finding supports my third hypothesis that maintaining complexity of species composition and structure could enhance forest C stocks. The niche complementarity hypothesis is strongly supported by my findings.

Overall, maintaining both biodiversity and structural diversity is a sustainable forest management strategy in spruce-dominated forests in New Brunswick, Canada.

Mixtures of shade tolerant species in conjunction with uneven-aged stand management will help maintaining high structural diversity and thus mixtures are recommended as a sustainable forest management practice to preserve C stocks in spruce-dominated forests for increasing C storage.

6.2 Model limitations and future work

In this dissertation, I have focused on examining the role of forest management on mitigation to future climate change by developing a process-based model (TRIPLEX-Management) and a statistical model, respectively. Most process-based modeling studies have been limited in antecedent assumptions and simplified ecological processes. I thus recognize that this study contains uncertainties due to model structure and the parameters of the TRIPLEX-Management model.

6.2.1 Natural disturbances

Natural disturbances such as fires and insects play a critical role in forest ecosystem dynamics and greatly influence the role of Canadian forests to the global C cycle (KurzStinson *et al.*, 2008). Unfortunately, the existing formulation of TRIPLEX-Management has no fire or insect sub-models and is thus unable to explicitly predict the impacts of fire disturbance or insect outbreaks on forest C dynamics. Fire disturbance regimes are recognized as an important factor in forest ecosystem dynamics (e.g., age structure, decomposition rates, and organic layer thickness) under future climate warming (Harden *et al.*, 2000, Bond-Lamberty *et al.*, 2007). Another important natural disturbance for Canadian forests is cyclical insect outbreaks. Interactions between two or more disturbances such as droughts, fires, and/or insects have been little investigated and are poorly understood, but may be important (Seidl *et al.*, 2011). Therefore, incorporating natural disturbances and forest management into process-based models can provide more realistic and judicious simulations, given that sustainable forest management aims to decrease the potential risk of such natural disturbances to forests.

6.2.2 Population dynamics

The simplification or absence of process-based forest population dynamics (i.e., regeneration, recruitment, and mortality) in the model could lead to biased results over the long term. After clearcuts, initial stand density is set as a default value in the model, assuming no strong impacts (density and natural species selection) of climate change on natural forest regeneration. In addition, the lack of a shrub sub-model is another weakness of the model. Shrubs can dominate after clearcutting, resulting in both high photosynthesis and respiration at the early stage of stand establishment. The forest water cycle (e.g., canopy transpiration) could be altered by the lack of a shrub sub-model in open stands due to forest harvesting (Lasch *et al.*, 2005). The absence of recruitment in the model can also lead to difficulty in simulating uneven-aged types of management such as selective cutting. More importantly, the absence of mechanistically modeling tree mortality (e.g., C starvation and hydraulic failure) in most process-based models has limited our understanding of impacts of climate change on forest ecosystem dynamics (Galbraith *et al.*, 2010, McDowell *et al.*, 2011). A multi-cohort approach could provide a solution, but is not a panacea. Overall, limitations of the model could limit our interpretation of simulated effects of adaptive forest management strategies to climate change.

6.2.3 Harvested wood C

The simplified calculation of C in harvested woods limited the overall evaluation of C budget due to the lack of wood product sub-model in the TRIPLEX-Management model. The harvested woods can store huge amounts of C after harvesting for many years depending on wood product life cycle (Law and Harmon 2011; Profft et al. 2009). Long-term C storage in harvested wood products could play an important role in C sequestration in wood products (Chen et al. 2008). It strongly suggests that it is necessary to incorporate a wood product C sub-model based on life-cycle analysis approach into the TRIPLEX-management model in the future. The model could then accurately quantify the net C stock in entire forest and forestry sectors and evaluate the overall net C budget for a given forest ecosystem.

6.3 Concluding remarks

This dissertation provides a novel and useful tool, TRIPLEX-Management, to quantify the effects of forest management practices (thinning and harvesting) and future climate change on forest growth, wood production, and C dynamics of Canadian forests. This work improves our understanding of the role of forest management given an uncertain future climate. Shortening rotation length and maintaining complexity of composition and structure are strongly recommended by the findings. Therefore, this Ph.D. thesis sheds light on the usefulness of sustainable forest management for increasing C sequestration both on-site and off-site and for decreasing the potential risk of climate change on Canadian forests.

REFERENCES

Allen, C.D., Macalady, A.K., Chenchouni, H., Bachelet, D., McDowell, N., Vennetier, M., Kitzberger, T., Rigling, A., Breshears, D.D., Hogg, E.H., Gonzalez, P., Fensham, R., Zhang, Z., Castro, J., Demidova, N., Lim, J.-H., Allard, G., Running, S.W., Semerci, A. & Cobb, N. (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management,* **259,** 660-684.

Álvarez González, J.G., Schröder, J., Rodríguez Soalleiro, R. & Ruíz González, A.D. (2002) Modelling the effect of thinnings on the diameter distribution of even-aged Maritime pine stands. *Forest Ecology and Management,* **165,** 57-65.

Amiro, B.D., Barr, A.G., Barr, J.G., Black, T.A., Bracho, R., Brown, M., Chen, J., Clark, K.L., Davis, K.J., Desai, A.R., Dore, S., Engel, V., Fuentes, J.D., Goldstein, A.H., Goulden, M.L., Kolb, T.E., Lavigne, M.B., Law, B.E., Margolis, H.A., Martin, T., McCaughey, J.H., Misson, L., Montes-Helu, M., Noormets, A., Randerson, J.T., Starr, G. & Xiao, J. (2010) Ecosystem carbon dioxide fluxes after disturbance in forests of North America. *Journal of Geophysical Research,* **115,** G00K02.

Balvanera, P., Pfisterer, A., Buchmann, N., He, J., Nakashizuka, T., Raffaelli, D. & Schmid, B. (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters,* **9,** 1146-1156.

Barr, A.G. (2008) Flux Canada Research Network DIS at http://fluxnet.ccrp.ec.gc.ca.

Barr, A.G., Black, T.A., Hogg, E.H., Kljun, N., Morgenstern, K. & Nesic, Z. (2004) Inter-annual variability in the leaf area index of a boreal aspen-hazelnut forest in relation to net ecosystem production. *Agricultural and Forest Meteorology,* **126,** 237-255.

Battaglia, M., Sands, P., White, D. & Mummery, D. (2004) CABALA: a linked carbon, water and nitrogen model of forest growth for silvicultural decision support. *Forest Ecology and Management,* **193,** 251-282.

Bella, I.E. & DeFranceschi, J. (1974) Commercial thinning improves growth of jack pine. Natural Resources Canada, Canadian Forestry Service - Northern Forestry Centre, Edmonton, AB. Information Report NOR-X-112, 23 p.

Bernier, P.Y., Bartlett, P., Black, T.A., Barr, A., Kljun, N. & McCaughey, J.H. (2006) Drought constraints on transpiration and canopy conductance in mature aspen and jack pine stands. *Agricultural and Forest Meteorology,* **140,** 64-78.

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

Bond-Lamberty, B., Peckham, S.D., Ahl, D.E. & Gower, S.T. (2007) Fire as the dominant driver of central Canadian boreal forest carbon balance. *Nature,* **450,** 89-92.

Bossel, H. (1996) TREEDYN3 forest simulation model. *Ecological Modelling,* **90,** 187-227.

Bosworth, D., Birdsey, R., Joyce, L. & Millar, C. (2008) Climate change and the nation's forests: challenges and opportunities. *Journal of Forestry,* **106,** 214-221.

Brown, S., Sathaye, J., Cannell, M., Kauppi, P., Burschel, P., Grainger, A., Heuveldop, J., Leesman, R., Moura Costa, R., Pinard, M., Nilsson, S., Schopfhauser, W., Sedjo, R., Singh, N., Trexler, M., van Minnen, J. & Weyers, S. (1996) Management of forests for mitigation of greenhouse gas emissions. *Climate Change 1995. Impacts, Adaptation and Mitigation of Climate Change: Scientific–Technical Analyses.* (eds R. Watson, M. Zinyowera & R. Moss), pp. 773-797. Cambridge University Press, Cambridge.

Bunker, D., DeClerck, F., Bradford, J., Colwell, R., Perfecto, I., Phillips, O., Sankaran, M. & Naeem, S. (2005) Species loss and aboveground carbon storage in a tropical forest. *Science,* **310,** 1029-1031.

Buongiorno, J., Dahir, S., Lu, H.C. & Lin, C.R. (1994) Tree size diversity and economic returns in uneven-aged forest stands. *Forest Science,* **40,** 83-103.

Buongiorno, J., Peyron, J.L., Houllier, F. & Bruciamacchie, M. (1995) Growth and management of mixed-species, uneven-aged forests in the French Jura: implications for economic returns and tree diversity. *Forest Science,* **41,** 397-429.

Campbell, J., Alberti, G., Martin, J. & Law, B.E. (2009) Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. *Forest Ecology and Management,* **257,** 453-463.

Cao, Q.V. (2004) Predicting parameters of a weibull function for modeling diameter distribution. *Forest Science,* **50,** 682-685.

Caspersen, J.P. & Pacala, S.W. (2001) Successional diversity and forest ecosystem function. *Ecological Research,* **16,** 895-903.

Cavard, X., Bergeron, Y., Chen, H.Y.H. & Pare, D. (2010) Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests. *Canadian Journal of Forest Research,* **40,** 37-47.

Chen, J., Colombo, S.J., Ter-Mikaelian, M.T. & Heath, L.S. (2008) Future carbon storage in harvested wood products from Ontario's Crown forests. *Canadian Journal of Forest Research,* **38,** 1947-1958.

Chen, X. (2006) Tree diversity, carbon storage, and soil nutrient in an old-growth forest at Changbai Mountain, Northeast China. *Communications in Soil Science and Plant Analysis,* **37,** 363-375.

Chertov, O., Bhatti, J.S., Komarov, A., Mikhailov, A. & Bykhovets, S. (2009) Influence of climate change, fire and harvest on the carbon dynamics of black spruce in Central Canada. *Forest Ecology and Management,* **257,** 941-950.

Ciais, P., Reichstein, M., Viovy, N., Granier, A., Ogee, J., Allard, V., Aubinet, M., Buchmann, N., Bernhofer, C., Carrara, A., Chevallier, F., De Noblet, N., Friend, A.D., Friedlingstein, P., Grunwald, T., Heinesch, B., Keronen, P., Knohl, A., Krinner, G., Loustau, D., Manca, G., Matteucci, G., Miglietta, F., Ourcival, J.M., Papale, D., Pilegaard, K., Rambal, S., Seufert, G., Soussana, J.F., Sanz, M.J., Schulze, E.D., Vesala, T. & Valentini, R. (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature,* **437,** 529-533.

Cienciala, E. & Tatarinov, F.A. (2006) Application of BIOME-BGC model to managed forests: 2. Comparison with long-term observations of stand production for major tree species. *Forest Ecology and Management,* **237,** 252-266.

Coops, N., Waring, R., Brown, S. & Running, S. (2001) Comparisons of predictions of net primary production and seasonal patterns in water use derived with two forest growth models in Southwestern Oregon. *Ecological Modelling,* **142,** 61-81.

Creed, R.P., Cherry, R.P., Pflaum, J.R. & Wood, C.J. (2009) Dominant species can produce a negative relationship between species diversity and ecosystem function. *Oikos,* **118,** 723-732.

D'Amato, A.W., Bradford, J.B., Fraver, S. & Palik, B.J. (2011) Forest management for mitigation and adaptation to climate change: Insights from long-term silviculture experiments. *Forest Ecology and Management,* **262,** 803-816.

Davidson, E.A. & Janssens, I.A. (2006) Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. *Nature,* **440,** 165-173.

Diaz, S., Hector, A. & Wardle, D.A. (2009) Biodiversity in forest carbon sequestration initiatives: not just a side benefit. *Current Opinion in Environmental Sustainability,* **1,** 55-60.

Edgar, C.B. & Burk, T.E. (2001) Productivity of aspen forests in northeastern Minnesota, USA, as related to stand composition and canopy structure. *Canadian Journal of Forest Research,* **31,** 1019-1029.

Evans, A.M. & Perschel, R. (2009) A review of forestry mitigation and adaptation strategies in the Northeast U.S. *Climatic Change,* **96,** 167-183.

Firn, J., Erskine, P.D. & Lamb, D. (2007) Woody species diversity influences productivity and soil nutrient availability in tropical plantations. *Oecologia,* **154,** 521-533.

Flannigan, M., Stocks, B., Turetsky, M. & Wotton, M. (2009) Impacts of climate change on fire activity and fire management in the circumboreal forest. *Global Change Biology,* **15,** 549-560.

Fornara, D. & Tilman, D. (2008) Plant functional composition influences rates of soicl carbon and nitrogen accumulation. *Journal of Ecology,* **96,** 314-322.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Berg, D.R., Lindenmayer, D.B., Harmon; M.E., Keeton, W.S., Shaw, D.C., Bible, K. & Chen, J. (2002) Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. *Forest Ecology and Management,* **155,** 399-423.

Frelich, L.E. & Reich, P.B. (2010) Will environmental changes reinforce the impact of global warming on the prairie–forest border of central North America? *Frontiers in Ecology and the Environment,* **8,** 371-378.

Fridley, J.D. (2002) Resource availability dominates and alters the relationship between species diversity and ecosystem productivity in experimental plant communities. *Oecologia,* **132,** 271-277.

Friedlingstein, P., Fung, I., Holland, E., John, J., Brasseur, G., Erickson, D. & Schimel, D. (1995) On the contribution of CO_2 fertilization to the missing biospheric sink. *Global Biogeochemical Cycles,* **9,** 541-556.

Galbraith, D., Levy, P.E., Sitch, S., Huntingford, C., Cox, P., Williams, M. & Meir, P. (2010) Multiple mechanisms of Amazonian forest biomass losses in three dynamic global vegetation models under climate change. *New Phytologist,* **187,** 647-665.

Garcia-Gonzalo, J., Peltola, H., Briceño-elizondo, E. & Kellomäki, S. (2007a) Changed thinning regimes may increase carbon stock under climate change: A case study from a Finnish boreal forest. *Climatic Change,* **81,** 431-454.

Garcia-Gonzalo, J., Peltola, H., Briceño-Elizondo, E. & Kellomäki, S. (2007b) Effects of climate change and management on timber yield in boreal forests, with economic implications: A case study. *Ecological Modelling,* **209,** 220-234.

Garcia-Gonzalo, J., Peltola, H., Zubizarreta-Gerendiain, A. & Kellomäki, S. (2007) Impacts of forest landscape structure and management on timber production and carbon stocks in the boreal forest ecosystem under changing climate. *Forest Ecology and Management,* **241,** 243-257.

Gillman, L.N. & Wright, S.D. (2006) The influence of productivity on the species richness of plants: a critical assessment. *Ecology,* **87,** 1234-1243.

Goble, B.C. & Bowling, C. (1993) Five-Year Growth Response of Thinned Jack Pine Near Atikokan, Ontario. Ontario Government, Ministry of Natural Resources.

Gough, C.M., Vogel, C.S., Harrold, K.H., George, K. & Curtis, P.S. (2007) The legacy of harvest and fire on ecosystem carbon storage in a north temperate forest. *Global Change Biology,* **13,** 1935-1949.

Gower, S.T., Vogel, J.G., Norman, J.M., Kucharik, C.J., Steele, S.J. & Stow, T.K. (1997) Carbon distribution and aboveground net primary production in aspen, jack pine, and black spruce stands in Saskatchewan and Manitoba, Canada. *Journal of Geophysical Research,* **102,** 29029-29042.

Graham, M.H. (2003) Confronting multicollinearity in ecological multiple regression. *Ecology,* **84,** 2809-2815.

Grant, R.F., Barr, A.G., Black, T.A., Gaumont-Guay, D., Iwashita, H., Kidson, J., McCaughey, H., Morgenstern, K., Murayama, S., Nesic, Z., Saigusa, N., Shashkov, A. & Zha, T. (2007) Net ecosystem productivity of boreal jack pine stands regenerating from clearcutting under current and future climates. *Global Change Biology,* **13,** 1423-1440.

Grant, R.F., Barr, A.G., Black, T.A., Margolis, H.A., McCaughey, J.H. & Trofymow, J.A. (2010) Net ecosystem productivity of temperate and boreal forests after clearcutting—a Fluxnet-Canada measurement and modelling synthesis. *Tellus B,* **62,** 475-496.

Grant, R.F., Black, T.A., Gaumont-Guay, D., Klujn, N., Barr, A.G., Morgenstern, K. & Nesic, Z. (2006) Net ecosystem productivity of boreal aspen forests under drought and climate change: Mathematical modelling with Ecosys. *Agricultural and Forest Meteorology,* **140,** 152-170.

Griffis, T.J., Black, T.A., Morgenstern, K., Barr, A.G., Nesic, Z., Drewitt, G.B., Gaumont-Guay, D. & McCaughey, J.H. (2003) Ecophysiological controls on the carbon balances of three southern boreal forests. *Agricultural and Forest Meteorology,* **117,** 53-71.

Groot, A., Brown, K., Morrison, I. & Barker, J. (1984) A 10-year tree and stand response of jack pine to urea fertilization and low thinning. *Canadian Journal of Forest Research,* **14,** 44-50.

Hagner, S. (1995) Silviculture in boreal forests. *Unasylva,* **181.**

Harden, J.W., Trumbore, S.E., Stocks, B.J., Hirsch, A., Gower, S.T., O'Neill, K.P. & Kasischke, E.S. (2000) The role of fire in the boreal carbon budget. *Global Change Biology,* **6,** 174-184.

Hartmann, H. (2010) Will a 385 million year-struggle for light become a struggle for water and for carbon? – How trees may cope with more frequent climate change-type drought events. *Global Change Biology,* **17,** 642-655.

Hogg, E.H., Brandt, J.P. & Kochtubajda, B. (2002) Growth and dieback of aspen forests in northwestern Alberta, Canada, in relation to climate and insects. *Canadian Journal of Forest Research,* **32,** 823-832.

Hogg, E.H., Brandt, J.P. & Michaelian, M. (2008) Impacts of a regional drought on the productivity, dieback, and biomass of western Canadian aspen forests. *Canadian Journal of Forest Research,* **38,** 1373-1384.

Howard, E., Gower, S., Foley, J. & Kucharik, C. (2004) Effects of logging on carbon dynamics of a jack pine forest in Saskatchewan, Canada. *Global Change Biology,* **10,** 1267-1284.

Huang, J.-G., Bergeron, Y., Denneler, B., Berninger, F. & Tardif, J. (2007) Response of forest trees to increased atmospheric CO_2. *Critical Reviews in Plant Sciences,* **26,** 265-283.

Hudiburg, T.W., Law, B.E., Wirth, C. & Luyssaert, S. (2011) Regional carbon dioxide implications of forest bioenergy production. *Nature Climate Change,* **1,** 419-423.

Humphreys, E.R., Black, T.A., Morgenstern, K., Cai, T., Drewitt, G.B., Nesic, Z. & Trofymow, J.A. (2006) Carbon dioxide fluxes in coastal Douglas-fir stands at different stages of development after clearcut harvesting. *Agricultural and Forest Meteorology,* **140,** 6-22.

Hyvonen, R., Agren, G.I., Linder, S., Persson, T., Cotrufo, M.F., Ekblad, A., Freeman, M., Grelle, A., Janssens, I.A. & Jarvis, P.G. (2007) The likely impact of elevated [CO_2], nitrogen deposition, increased temperature and management on carbon sequestration in temperate and boreal forest ecosystems: a literature review. *New Phytologist,* **173,** 463-480.

IPCC (2001) *Climate Change 2001: The Scientific Basis.* Cambridge University Press Cambridge.

IPCC (2007) *Climate change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change.* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,.

Ishii, H., Tanabe, S. & Hiura, T. (2004) Exploring the relationships among canopy structure, stand productivity, and biodiversity of temperate forest ecosystems. *Forest Science,* **50,** 342-355.

Jacob, M., Leuschner, C. & Thomas, F.M. (2010) Productivity of temperate broad-leaved forest stands differing in tree species diversity. *Annals of Forest Science,* **67,** 503.

Jandl, R., Lindner, M., Vesterdal, L., Bauwens, B., Baritz, R., Hagedorn, F., Johnson, D.W., Minkkinen, K. & Byrne, K.A. (2007) How strongly can forest management influence soil carbon sequestration? *Geoderma,* **137,** 253-268.

Janisch, J.E. & Harmon, M.E. (2002) Successional changes in live and dead wood carbon stores: implications for net ecosystem productivity. *Tree Physiology,* **22,** 77-89.

Johnsen, K., Samuelson, L., Teskey, R., McNulty, S. & Fox, T. (2001) Process Models as Tools in Forestry Research and Management. *Forest Science,* **47,** 2-8.

Johnson, D.W. & Curtis, P.S. (2001) Effects of forest management on soil C and N storage: meta analysis. *Forest Ecology and Management,* **140,** 227-238.

Johnston, M.H., Campagna, M., Gray, P., Kope, H., Loo, J., Ogedn, A., O'Neill, G.A., Price, D. & Williamson, T. (2009) Vulnerability of Canada's tree species to climate change and management options for adaptation: An overview for policy makers and practitioners. Canadian Council of Forest Ministers, Ottawa, Ontario, Canada.

Jonsson, M. & Wardle, D.A. (2009) Structural equation modelling reveals plant-community drivers of carbon storage in boreal forest ecosystems. *Biology letters,* **6,** 116-119.

Kaipainen, T., Liski, J., Pussinen, A. & Karjalainen, T. (2004) Managing carbon sinks by changing rotation length in European forests. *Environmental Science & Policy,* **7,** 205-219.

Kant, S. (2002) The marginal cost of structural diversity of mixed uneven-aged hard maple forests. *Canadian Journal of Forest Research,* **32,** 616-628.

Kellomäki, S., Peltola, H., Nuutinen, T., Korhonen, K.T. & Strandman, H. (2008) Sensitivity of managed boreal forests in Finland to climate change, with implications for adaptive management. *Philosophical Transactions of the Royal Society B: Biological Sciences,* **363,** 2339-2349.

Kellomäki, S. & Väisänen, H. (1997) Modelling the dynamics of the forest ecosystem for climate change studies in the boreal conditions. *Ecological Modelling,* **97,** 121-140.

Kimball, J., Thornton, P., White, M. & Running, S. (1997) Simulating forest productivity and surface-atmosphere carbon exchange in the BOREAS study region. *Tree Physiology,* **17,** 589-600.

Kljun, N., Black, T., Griffis, T., Barr, A., Gaumont-Guay, D., Morgenstern, K., McCaughey, J. & Nesic, Z. (2006) Response of net ecosystem productivity of three boreal forest stands to drought. *Ecosystems,* **9,** 1128-1144.

Kolari, P., Pumpanen, J., Rannik, Ü., Ilvesniemi, H., Hari, P. & Berninger, F. (2004) Carbon balance of different aged Scots pine forests in Southern Finland. *Global Change Biology,* **10,** 1106-1119.

Komarov, A., Chertov, O., Zudin, S., Nadporozhskaya, M., Mikhailov, A., Bykhovets, S., Zudina, E. & Zoubkova, E. (2003) EFIMOD 2--a model of growth and cycling of elements in boreal forest ecosystems. *Ecological Modelling,* **170,** 373-392.

Korol, R.L., Milner, K.S. & Running, S.W. (1996) Testing a mechanistic model for predicting stand and tree growth. *Forest Science,* **42,** 139-153.

Kurz, W.A., Stinson, G., Rampley, G.J., Dymond, C.C. & Neilson, E.T. (2008) Risk of natural disturbances makes future contribution of Canada's forests to the global carbon cycle highly uncertain. *Proceedings of the National Academy of Sciences,* **105,** 1551-1555.

Lal, R. (2005) Forest soils and carbon sequestration. *Forest Ecology and Management,* **220,** 242-258.

Lambert, M., Ung, C. & Raulier, F. (2005) Canadian national tree aboveground biomass equations. *Canadian Journal of Forest Research,* **35,** 1996-2018.

Landsberg, J. (2003) Modelling forest ecosystems: state of the art, challenges, and future directions. *Canadian Journal of Forest Research,* **33,** 385-397.

Landsberg, J.J., Johnsen, K.H., Albaugh, T.J., Allen, H.L. & McKeand, S.E. (2001) Applying 3-PG, a simple process-based model designed to produce practical results, to data from loblolly pine experiments. *Forest Science,* **47,** 43-51.

Landsberg, J.J. & Waring, R.H. (1997) A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management,* **95,** 209-228.

Larson, A.J., Lutz, J.A., Gersonde, R.F., Franklin, J.F. & Hietpas, F.F. (2008) Potential site productivity influences the rate of forest structural development. *Ecological Applications,* **18,** 899-910.

Lasch, P., Badeck, F.-W., Suckow, F., Lindner, M. & Mohr, P. (2005) Model-based analysis of management alternatives at stand and regional level in Brandenburg (Germany). *Forest Ecology and Management,* **207,** 59-74.

Law, B.E. & Harmon, M.E. (2011) Forest sector carbon management, measurement and verification, and discussion of policy related to climate change. *Carbon Management,* **2,** 73-84.

Law, B.E., Sun, O.J., Campbell, J., Van Tuyl, S. & Thornton, P.E. (2003) Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change Biology,* **9,** 510-524.

Law, B.E., Thornton, P.E., Irvine, J., Anthoni, P.M. & Van Tuyl, S. (2001) Carbon storage and fluxes in ponderosa pine forests at different developmental stages. *Global Change Biology,* **7,** 755-777.

Lei, X., Lu, Y., Peng, C., Zhang, X., Chang, J. & Hong, L. (2007) Growth and structure development of semi-natural larch-spruce-fir (*Larix olgensis-Picea jezoensis-Abies nephrolepis*) forests in northeast China: 12-year results after thinning. *Forest Ecology and Management,* **240,** 165-177.

Lei, X., Wang, W. & Peng, C. (2009) Relationships between stand growth and structural diversity in spruce-dominated forests in New Brunswick, Canada. *Canadian Journal of Forest Research,* **39,** 1835-1847.

Lexerød, N.L. & Eid, T. (2006) An evaluation of different diameter diversity indices based on criteria related to forest management planning. *Forest Ecology and Management,* **222,** 17-28.

Li, Z., Kurz, W., Apps, M. & Beukema, S. (2003) Belowground biomass dynamics in the Carbon Budget Model of the Canadian Forest Sector: recent improvements and implications for the estimation of NPP and NEP. *Canadian Journal of Forest Research,* **33,** 126-136.

Liang, J., Buongiorno, J. & Monserud, R.A. (2005) Growth and yield of all-aged Douglas-fir-western hemlock forest stands: a matrix model with stand diversity effects. *Canadian Journal of Forest Research,* **35,** 2368-2381.

Liang, J., Buongiorno, J., Monserud, R.A., Kruger, E.L. & Zhou, M. (2007) Effects of diversity of tree species and size on forest basal area growth, recruitment, and mortality. *Forest Ecology and Management,* **243,** 116-127.

Lindenmayer, D. & Franklin, J. (1997) Managing stand structure as part of ecologically sustainable forest management in Australian mountain ash forests. *Conservation Biology,* **11,** 1053-1068.

Liski, J., Pussinen, A., Pingoud, K., Mäkipää, R. & Karjalainen, T. (2001) Which rotation length is favourable to carbon sequestration? *Canadian Journal of Forest Research,* **31,** 2004-2013.

Liu, C., Beaulieu, J., Pregent, G. & Zhang, S.Y. (2009) Applications and comparison of six methods for predicting parameters of the Weibull function in unthinned Picea glauca plantations. *Scandinavian Journal of Forest Research,* **24,** 67-75.

Liu, J., Peng, C., Dang, Q., Apps, M. & Jiang, H. (2002) A component object model strategy for reusing ecosystem models. *Computers and Electronics in Agriculture,* **35,** 17-33.

Liu, L. & Greaver, T. (2009) A review of nitrogen enrichment effects on three biogenic GHGs: the CO 2 sink may be largely offset by stimulated N 2 O and CH 4 emission. *Ecology Letters,* **12,** 1103-1117.

Liu, S., Bond-Lamberty, B., Hicke, J.A., Vargas, R., Zhao, S., Chen, J., Edburg, S.L., Hu, Y., Liu, J., McGuire, A.D., Xiao, J., Keane, R., Yuan, W., Tang, J., Luo, Y., Potter, C. & Oeding, J. (2011) Simulating the impacts of disturbances on forest carbon cycling in North America: Processes, data, models, and challenges. *Journal of Geophysical Research,* **116,** G00K08.

Long, J.N. & Shaw, J.D. (2010) The influence of compositional and structural diversity on forest productivity. *Forestry,* **83,** 121-128.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001) Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science,* **294,** 804-808.

Luo, Y., Hui, D. & Zhang, D. (2006) Elevated CO_2 stimulates net accumulations of carbon and nitrogen in land ecosystems: a meta-analysis. *Ecology,* **87,** 53-63.

Ma, Z., Peng, C., Zhu, Q., Chen, H., Yu, G., Li, W., Zhou, X., Wang, W. & Zhang, W. (2012) Regional drought-induced reduction in the biomass carbon sink of Canada's boreal forests. *Proceedings of the National Academy of Sciences of the United States of America,* **109,** 2423-2427.

Magurran, A.E. (2004) *Measuring biological diversity.* Blackwell Publishing, Oxford, United Kingdom.

Mäkelä, A., Landsberg, J., Ek, A.R., Burk, T.E., Ter-Mikaelian, M., Ågren, G.I., Oliver, C.D. & Puttonen, P. (2000) Process-based models for forest ecosystem management: current state of the art and challenges for practical implementation. *Tree Physiology,* **20,** 289-298.

Mäkinen, H. & Isomaki, A. (2004) Thinning intensity and long-term changes in increment and stem form of Norway spruce trees. *Forest Ecology and Management,* **201,** 295-309.

Mäkinen, H. & Isomäki, A. (2004a) Thinning intensity and growth of Norway spruce stands in Finland. *Forestry,* **77,** 349-364.

Mäkinen, H. & Isomäki, A. (2004b) Thinning intensity and growth of Scots pine stands in Finland. *Forest Ecology and Management,* **201,** 311-325.

Malmsheimer, R.W., Heffernan, P., Brink, S., Crandall, D., Deneke, F., Galik, C., Gee, E., Helms, J.A., McClure, N., Mortimerl, M., Ruddell, S., Smith, M. & Stewart, J. (2008) Forest management solutions for mitigating climate change in the United States. *Journal of Forestry,* **106,** 115-173.

Martin, J.L., Gower, S.T., Plaut, J. & Holmes, B. (2005) Carbon pools in a boreal mixedwood logging chronosequence. *Global Change Biology,* **11,** 1883-1894.

Matala, J., Hynynen, J., Miina, J., Ojansuu, R., Peltola, H., Sievänen, R., Väisänen, H. & Kellomäki, S. (2003) Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests. *Ecological Modelling,* **161,** 95-116.

McDowell, N.G., Beerling, D.J., Breshears, D.D., Fisher, R.A., Raffa, K.F. & Stitt, M. (2011) The interdependence of mechanisms underlying climate-driven vegetation mortality. *Trends in Ecology & Evolution,* **26,** 523-532.

McElhinny, C., Gibbons, P., Brack, C. & Bauhus, J. (2005) Forest and woodland stand structural complexity: Its definition and measurement. *Forest Ecology and Management,* **218,** 1-24.

Medlyn, B.E., Duursma, R.A. & Zeppel, M.J.B. (2011) Forest productivity under climate change: a checklist for evaluating model studies. *Wiley Interdisciplinary Reviews: Climate Change,* **2,** 332-355.

Merino, A., Real, C., Álvarez-González, J.G. & Rodríguez-Guitián, M.A. (2007) Forest structure and C stocks in natural Fagus sylvatica forest in southern Europe: The effects of past management. *Forest Ecology and Management,* **250,** 206-214.

Michaelian, M., Hogg, E.H., Hall, R.J. & Arsenault, E. (2011) Massive mortality of aspen following severe drought along the southern edge of the Canadian boreal forest. *Global Change Biology,* **17,** 2084-2094.

Miehle, P., Battaglia, M., Sands, P.J., Forrester, D.I., Feikema, P.M., Livesley, S.J., Morris, J.D. & Arndt, S.K. (2009) A comparison of four process-based models and a statistical regression model to predict growth of *Eucalyptus globulus* plantations. *Ecological Modelling,* **220,** 734-746.

Millar, C., Stephenson, N. & Stephens, S. (2007) Climate change and forests of the future: managing in the face of uncertainty. *Ecological Applications,* **17,** 2145-2151.

Morris, D., Bowling, C. & Hills, S. (1994) Growth and form responses to pre-commercial thinning regimes in aerially seeded jack pine stands: 5th year results. *Forestry Chronicle,* **70,** 780-787.

Nabuurs, G.J., Thürig, E., Heidema, N., Armolaitis, K., Biber, P., Cienciala, E., Kaufmann, E., Mäkipää, R., Nilsen, P., Petritsch, R., Pristova, T., Rock, J., Schelhaas, M.J., Sievanen, R., Somogyi, Z. & Vallet, P. (2008) Hotspots of the European forests carbon cycle. *Forest Ecology and Management,* **256,** 194-200.

Newcomer, J., Landis, D., Conrad, S., Curd, S., Huemmrich, K., Knapp, D., Morrell, A., Nickeson, J., Papagno, A. & Rinker, D. (2000) *Collected Data of the Boreal Ecosystem-Atmosphere Study.* CD-ROM, NASA, Goddard Space Flight Center, Greenbelt, MD

Newton, P. & Amponsah, I. (2005) Evaluation of Weibull-based parameter prediction equation systems for black spruce and jack pine stand types within the context of developing structural stand density management diagrams. *Canadian Journal of Forest Research,* **35,** 2996-3010.

Noormets, A., Chen, J. & Crow, T. (2007) Age-dependent changes in ecosystem carbon fluxes in managed forests in Northern Wisconsin, USA. *Ecosystems,* **10,** 187-203.

Norby, R.J., Warren, J.M., Iversen, C.M., Medlyn, B.E. & McMurtrie, R.E. (2010) CO_2 enhancement of forest productivity constrained by limited nitrogen availability. *Proceedings of the National Academy of Sciences of the United States of America,* **107,** 19368-19373.

Nord-Larsen, T. & Cao, Q.V. (2006) A diameter distribution model for even-aged beech in Denmark. *Forest Ecology and Management,* **231,** 218-225.

Nunery, J.S. & Keeton, W.S. (2010) Forest carbon storage in the northeastern United States: Net effects of harvesting frequency, post-harvest retention, and wood products. *Forest Ecology and Management,* **259,** 1363-1375.

Nuutinen, T., Matala, J., Hirvelä, H., Härkönen, K., Peltola, H., Väisänen, H. & Kellomäki, S. (2006) Regionally optimized forest management under changing climate. *Climatic Change,* **79,** 315-333.

OMNR (1997) Silvicultural guide to managing for black spruce, jack pine and aspen on boreal forest ecosites in Ontario. Version 1.1 (ed Ontario Ministry of Natural Resource), pp. 822. Queen's Printer for Ontario, Toronto.

Parton, W., Scurlock, J., Ojima, D., Gilmanov, T., Scholes, R., Schimel, D., Kirchner, T., Menaut, J., Seastedt, T. & Moya, E. (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles,* **7,** 785-809.

Peichl, M. & Arain, M.A. (2006) Above- and belowground ecosystem biomass and carbon pools in an age-sequence of temperate pine plantation forests. *Agricultural and Forest Meteorology,* **140,** 51-63.

Peng, C. (2000) Understanding the role of forest simulation models in sustainable forest management. *Environmental Impact Assessment Review,* **20,** 481-501.

Peng, C., Apps, M. & Price, D.T. (1998) Simulation carbon dynamics along the Boreal Forest Transect Case Study (BFTCS) in central Canada. *Global Biogeochemical Cycles,* **12,** 381-402.

Peng, C., Jiang, H., Apps, M.J. & Zhang, Y. (2002) Effects of harvesting regimes on carbon and nitrogen dynamics of boreal forests in central Canada: a process model simulation. *Ecological Modelling,* **155,** 177-189.

Peng, C., Liu, J., Dang, Q., Apps, M.J. & Jiang, H. (2002) TRIPLEX: a generic hybrid model for predicting forest growth and carbon and nitrogen dynamics. *Ecological Modelling,* **153,** 109-130.

Peng, C., Ma, Z., Lei, X., Zhu, Q., Chen, H., Wang, W., Liu, S., Li, W., Fang, X. & Zhou, X. (2011) A drought-induced pervasive increase in tree mortality across Canada's boreal forests. *Nature Climate Change,* **1,** 467-471.

Peng, C., Zhou, X., Zhao, S., Wang, X., Zhu, B., Piao, S. & Fang, J. (2009) Quantifying the response of forest carbon balance to future climate change in Northeastern China: Model validation and prediction. *Global and Planetary Change,* **66,** 179-194.

Pennock, D.J. & van Kessel, C. (1997) Clear-cut forest harvest impacts on soil quality indicators in the mixedwood forest of Saskatchewan, Canada. *Geoderma,* **75,** 13-32.

Petritsch, R., Hasenauer, H. & Pietsch, S.A. (2007) Incorporating forest growth response to thinning within biome-BGC. *Forest Ecology and Management,* **242,** 324-336.

Plonski, W.L. (1974) Normal yield tables (metric) for major forest species of Ontario. pp. 44. Ontario Ministry of Natural Resources, Toronto.

Pommerening, A. (2002) Approaches to quantifying forest structures. *Forestry,* **75,** 305-324.

Porter, K.B., MacLean, D.A., Beaton, K.P. & Upshall, J. (2001) *New Brunswick permanent sample plot database (PSPDB v1.0): User's guide and analysis.* Canadian Forest Service, Atlantic Forest Centre, Natural Resources Canada.

Pregitzer, K.S. & Euskirchen, E.S. (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology,* **10,** 2052-2077.

Pretzsch, H. (1997) Analysis and modeling of spatial stand structures. Methodological considerations based on mixed beech-larch stands in Lower Saxony. *Forest Ecology and Management,* **97,** 237-253.

Pretzsch, H. (2005) Diversity and productivity in forests: evidence from long-term experimental plots. *Forest Diversity and Function: Temperate and Boreal Systems* (eds M. Scherer-Lorenzen, C. Körner & E.-D. Schulze), pp. 41-64. Springer, Berlin.

Pretzsch, H., Grote, R., Reineking, B., Rotzer, T. & Seifert, S. (2008) Models for forest ecosystem management: A European perspective. *Annals of Botany* **101,** 1065.

R Development Core Team (2009) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, ISBN 3-900051-07-0, URL http://www.R-project.org.

Reay, D.S., Dentener, F., Smith, P., Grace, J. & Feely, R.A. (2008) Global nitrogen deposition and carbon sinks. *Nature Geoscience,* **1,** 430-437.

Running, S. & Gower, S. (1991) FOREST-BGC, a general model of forest ecosystem processes for regional applications. II. Dynamic carbon allocation and nitrogen budgets. *Tree physiology,* **9,** 147-160.

Running, S.W. & Hunt, E.R.J. (1993) Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global-scale models. *Scaling Physiological Processes: Leaf to Globe* (eds J. R. Ehleringer & C. B. Field), pp. 141-158. Academic Press Inc, San Diego.

Ryan, M., Lavigne, M. & Gower, S. (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research,* **102,** 28871-28884.

Sands, P.J., Battaglia, M. & Mummery, D. (2000) Application of processbased models to forest management: experience with PROMOD, a simple plantation productivity model. *Tree Physiology,* **20,** 383-392.

Sara, S., Nair, P., Nair, V. & Kumar, B. (2009) Soil carbon stock in relation to plant diversity of homegardens in Kerala, India. *Agroforestry Systems,* **76,** 53-65.

Seedre, M., Shrestha, B.M., Chen, H.Y.H., Colombo, S. & Jõgiste, K. (2011) Carbon dynamics of North American boreal forest after stand replacing wildfire and clearcut logging. *Journal of Forest Research,* **16,** 168-183.

Seidl, R., Fernandes, P.M., Fonseca, T.F., Gillet, F., Jönsson, A.M., Merganicová, K., Netherer, S., Arpaci, A., Bontemps, J.-D., Bugmann, H., González-Olabarria, J.R., Lasch, P., Meredieu, C., Moreira, F., Schelhaas, M.-J. & Mohren, F. (2011) Modelling natural disturbances in forest ecosystems: a review. *Ecological Modelling,* **222,** 903-924.

Seidl, R., Rammer, W., Jäger, D., Currie, W.S. & Lexer, M.J. (2007) Assessing trade-offs between carbon sequestration and timber production within a framework of multi-purpose forestry in Austria. *Forest Ecology and Management,* **248,** 64-79.

Siltanen, R.M., Apps, M.J., Zoltai, S.C., Mair, R.M. & Strong, W.L. (1997) *A soil profile and organic carbon data base for Canadian forest and tundra mineral* *soils.* Natural Resources Canada, Canadian Forest Service, Northern Forestry Centre, Edmonton, Alberta, Canada.

Simard, S.W., Blenner-Hassett, T. & Cameron, I.R. (2004) Pre-commercial thinning effects on growth, yield and mortality in even-aged paper birch stands in British Columbia. *Forest Ecology and Management,* **190,** 163-178.

Smith, D.M., Larson, B.C., Kelty, M.J. & Ashton, P.M.S. (1997a) *The Practice of Silviculture: Applied Forest Ecology.* Wiley, New York.

Smith, D.M., Larson, B.C., Kelty, M.J. & Ashton, P.M.S. (1997b) Silviculture and Its Place in Forestry. *The Practice of Silviculture: Applied Forest Ecology*, pp. 3-19. Wiley, NY, USA.

Spittlehouse, D.L. & Stewart, R.B. (2003) Adaptation to climate change in forest management. *BC Journal of Ecosystems and Management,* **4,** 7-17.

Staudhammer, C.L. & LeMay, V.M. (2001) Introduction and evaluation of possible indices of stand structural diversity. *Canadian Journal of Forest Research,* **31,** 1105-1115.

Steele, S., Gower, S., Vogel, J. & Norman, J. (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. *Tree Physiology,* **17,** 577-588.

Sullivan, T.P., Sullivan, D.S. & Lindgren, P.M.F. (2001) Influence of variable retention harvests on forest ecosystems. I. Diversity of stand structure. *Journal of Ecology,* **38,** 1221-1233.

Szwagrzyk, J. & Gazda, A. (2007) Above-ground standing biomass and tree species diversity in natural stands of Central Europe. *Journal of Vegetation Science,* **18,** 555-562.

Tatarinov, F.A. & Cienciala, E. (2006) Application of BIOME-BGC model to managed forests: 1. Sensitivity analysis. *Forest Ecology and Management,* **237,** 267-279.

Taylor, A.R., Wang, J.R. & Chen, H.Y.H. (2007) Carbon storage in a chronosequence of red spruce (*Picea rubens*) forests in central Nova Scotia, Canada. *Canadian Journal of Forest Research,* **37,** 2260-2269.

Thornley, J.H. & Cannell, M.G. (2000) Managing forests for wood yield and carbon storage: a theoretical study. *Tree Physiology,* **20,** 477-484.

Tilman, D. (1999) The ecological consequences of changes in biodiversity: a search for general principles. *Ecology,* **80,** 1455-1474.

Tong, Q.J. & Zhang, S.Y. (2005) Impact of initial spacing and precommercial thinning on tree growth and stem quality in Jack pine. *Forestry Chronicle,* **81,** 418-428.

Tong, Q.J., Zhang, S.Y. & Thompson, M. (2005) Evaluation of growth response, stand value and financial return for pre-commercially thinned jack pine stands in Northwestern Ontario. *Forest Ecology and Management,* **209,** 225-235.

Ueyama, M., Kai, A., Ichii, K., Hamotani, K., Kosugi, Y. & Monji, N. (2011) The sensitivity of carbon sequestration to harvesting and climate conditions in a temperate cypress forest: Observations and modeling. *Ecological Modelling,* **222,** 3216-3225.

UNFCCC (1997) Kyoto Protocol to the United Nations Framework Convention on Climate Change. Bonn, Germany, Document FCCC/CP/1997/7/Add.1. http://www.unfccc.int.

Varga, P., Chen, H.Y.H. & Klinka, K. (2005) Tree-size diversity between single-and mixed-species stands in three forest types in western Canada. *Canadian Journal of Forest Research,* **35,** 593-601.

Vesala, T., Suni, T., Rannik, Ü., Keronen, P., Markkanen, T., Sevanto, S., Grönholm, T., Smolander, S., Kulmala, M., Ilvesniemi, H., R. Ojansuu, A. Uotila, J. Levula, Mäkelä, A., Pumpanen, J., Kolari, P., Kulmala, L., Altimir, N., Berninger, F., Nikinmaa, E. & Hari, P. (2005) Effect of thinning on surface fluxes in a boreal forest. *Global Biogeochemical Cycles,* **19,** doi:10.1029/2004GB002316.

Vilà, M., Vayreda, J., Comas, L., Ibáñez, J.J., Mata, T. & Obón, B. (2007) Species richness and wood production: a positive association in Mediterranean forests. *Ecology Letters,* **10,** 241-250.

Wallman, P., Svensson, M.G.E., Sverdrup, H. & Belyazid, S. (2005) ForSAFE--an integrated process-oriented forest model for long-term sustainability assessments. *Forest Ecology and Management,* **207,** 19-36.

Wang, W., Lei, X., Ma, Z., Kneeshaw, D.D. & Peng, C. (2011) Positive relationship between aboveground carbon stocks and structural diversity in spruce-dominated forest stands in New Brunswick, Canada. *Forest Science,* **57,** 506-515.

Wang, W., Peng, C., Kneeshaw, D.D., Larocque, G.R. & Luo, Z. (2012) Drought-induced tree mortality: ecological consequences, causes, and modeling. *Environmental Reviews,* **20,** 109-121.

Wang, W., Peng, C., Kneeshaw, D.D., Larocque, G.R., Song, X. & Zhou, X. (2012) Quantifying the effects of climate change and harvesting on carbon dynamics of boreal aspen and jack pine forests using the TRIPLEX-Management model. *Forest Ecology and Management,* **281,** 152-162.

Wang, W., Peng, C., Zhang, S.Y., Zhou, X., Larocque, G.R., Kneeshaw, D.D. & Lei, X. (2011) Development of TRIPLEX-Management model for simulating the response of forest growth to pre-commercial thinning. *Ecological Modelling,* **222,** 2249-2261.

Whittaker, R.J. & Heegaard, E. (2003) What is the observed relationship between species richness and productivity? Comment. *Ecology,* **84,** 3384-3390.

Willmott, C.J. (1982) Some comments on the evaluation of model performance. *Bulletin of the American Meteorological Society,* **63,** 1309-1313.

Wyckoff, P.H. & Bowers, R. (2010) Response of the prairie-forest border to climate change: Impacts of increasing drought may be mitigated by increasing CO_2. *Journal of Ecology,* **98,** 197-208.

Yanai, R.D., Currie, W.S. & Goodale, C.L. (2003) Soil carbon dynamics after forest harvest: An ecosystem paradigm reconsidered. *Ecosystems,* **6,** 197-212.

Zarnoch, S.J., Roamm, C.W., Rudolph, V.J. & Day, M.W. (1982) The Effects of red pine thinning regimes on diameter distribution fitted to the Weibull function. Michigan State University, Agricultural Experiment Station, East Lansing.

Zenner, E. (2000) Do residual trees increase structural complexity in pacific northwest coniferous foress? *Ecological Applications,* **10,** 800-810.

Zha, T., Barr, A.G., Black, T.A., McCaughey, J.H., Bhatti, J., Hawthorne, I., Krishnan, P., Kidston, J., Saigusa, N., Shashkov, A. & Nesic, Z. (2009) Carbon sequestration in boreal jack pine stands following harvesting. *Global Change Biology,* **15,** 1475-1487.

Zhang, J., Chu, Z., Ge, Y., Zhou, X., Jiang, H., Chang, J., Peng, C., Zheng, J., Jiang, B., Zhu, J. & Yu, S. (2008) TRIPLEX model testing and application for predicting forest growth and biomass production in the subtropical forest zone of China's Zhejiang Province. *Ecological Modelling,* **219,** 264-275.

Zhang, L., Peng, C., Huang, S. & Zhou, X. (2002) Development and evaluation of ecoregion-based jack pine height-diameter models for Ontario. *Forestry Chronicle,* **78,** 530-538.

Zhang, S.Y., Chauret, G., Swift, D.E. & Duchesne, I. (2006) Effects of precommercial thinning on tree growth and lumber quality in a jack pine stand in New Brunswick, Canada. *Canadian Journal of Forest Research,* **36,** 945-953.

Zhao, M. & Running, S.W. (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science,* **329,** 940-943.

Zhou, X., Peng, C. & Dang, Q. (2004) Assessing the generality and accuracy of the TRIPLEX model using in situ data of boreal forests in central Canada. *Environmental Modelling & Software,* **19,** 35-46.

Zhou, X., Peng, C., Dang, Q., Chen, J. & Parton, S. (2005) Predicting forest growth and yield in northeastern Ontario using the process-based model of TRIPLEX1.0 *Canadian Journal of Forest Research,* **35,** 2268-2280.

Zhou, X., Peng, C., Dang, Q., Sun, J., Wu, H. & Hua, D. (2008) Simulating carbon exchange in Canadian Boreal forests: I. Model structure, validation, and sensitivity analysis. *Ecological Modelling,* **219,** 287-299.