STAND STRUCTURAL CHANGES FOLLOWING COMMERCIAL THINNING OF WHITE SPRUCE

by

Kwadwo Omari

BSc. Natural Resources Management, K.N.U.S.T., Kumasi, Ghana, 2007
MSc. Forest Ecology and Management, University of Freiburg, Germany, 2010
MSc. Agriculture and Forestry, University of Eastern Finland, Joensuu, Finland, 2010

A Dissertation Submitted in Partial Fulfillment of
the Requirements for the Degree of

Doctor of Philosophy

in the Graduate Academic Unit of Forestry and Environmental Management

Supervisor: David A. MacLean, PhD, Forestry and Environmental Management

Examining Board: Stephen Heard, PhD, Department of Biology
Marek Krasowski, PhD, Forestry and Environmental Management
Fan-Rui Meng, PhD, Forestry and Environmental Management

External Examiner: David Larsen, PhD, University of Missouri

This dissertation is accepted by the Dean of Graduate Studies

THE UNIVERSITY OF NEW BRUNSWICK

July, 2016

ABSTRACT

This thesis investigates effects of commercial thinning of 22-30 years old white spruce (*Picea glauca* (Moench) Voss) on tree growth and standing and downed deadwood dynamics, and elucidates mechanisms of growth response to thinning. Four treatments were applied: (i) an unthinned control and three 40% basal area removal commercial thinning treatments; with (ii) slash and tops remaining on the site; (iii) most branches and tops extracted from the site; and (iv) clumps of unthinned trees left, with one-half of the trees in each clump girdled to create snags. Growing space was expressed as area potentially available (APA), and was related to tree growth, leaf area, and growth efficiency (stem growth per leaf area). Light-saturated photosynthetic rate, photosynthetic quantum efficiency (mole of CO_2 fixed per mole of incident light) and foliar nitrogen concentration were measured 1 and 3 years after thinning. Three years after thinning, basal area increment and crown diameter were significantly higher for thinned than unthinned trees. Thinning increased new deadwood amounts but did not significantly affect total deadwood volume. Relative annual volume increment increased linearly with increasing APA 2 and 3 years after thinning, but growth efficiency was not related to APA. Leaf area was positively related to APA 3 years after thinning, and volume increment was related to leaf area. Thinned trees had higher light-saturated net photosynthetic rates in their lower crowns compared to unthinned trees, and after thinning, light-saturated net photosynthetic rates of new foliage in lower crowns equalled that in upper crowns. Foliar nitrogen concentration and photosynthetic quantum efficiency did not differ significantly between the upper and lower crowns of thinned

and unthinned trees. Results showed that increasing APA through thinning increased tree growth by increasing crown leaf area and photosynthetic rates of the lower crown foliage. Thinning produced fine debris but had little effect on overall deadwood amount. Leaving unharvested islands and clumps during harvest would be a more effective way of providing quality deadwood.

DEDICATION

To my parents, Kofi and Afua Omari, and wife, Adelaide

ACKNOWLEDGEMENTS

My foremost thanks and appreciation go to my supervisor, Dr. David A. MacLean, for his mentorship, support, and encouragement. I would also like to thank my advisory committee (Dr. John Kershaw and Dr. Michael Lavigne) and Mr. Greg Adams for their advice and helpful editorial comments. Thanks to my fellow lab members for their friendship, insightful discussions, and computing assistance.

I gratefully acknowledge Gretta Goodine and James Farrell of Canadian Forest Service-Atlantic Forestry Centre and Dean McCarthy of the UNB Wood Science and Technology Center, the Forest Research and Advisory Committee of J.D. Irving, Limited (JDI) and staff at JDI for their input, support and assistance with this project. I thank my family and friends for their prayers, support, and encouragement. I am particularly grateful to my wife and mother for their encouragement and understanding.

This project was funded by J.D. Irving, Limited and by a Natural Sciences and Engineering Research Council of Canada (NSERC) Collaborative Research and Development grant to a team led by David A. MacLean. I was funded by a NSERC Industrial Post-graduate Scholarship supported by JDI.

TABLE OF CONTENTS

List of Tables

List of Figures

CHAPTER 1: GENERAL INTRODUCTION

1.1 Introduction

Plantations are an important part of intensive forest management. By increasing the forest resource base and having a relatively shorter rotation period, plantations ensure a regular supply of forest products. Thus, they help prevent over-exploitation of natural and/or old growth forests. Intensification of forest management for at least part of Canada's forest will continue over the next decades through plantation forestry (MacLean et al., 2015).

White spruce (*Picea glauca* (Moench) Voss) is the most commonly planted species in Canada (Kuhnke, 1989). The species is highly valued as a source of pulpwood and construction-grade timber (Lapointe et al., 2006), and is one of the most economically and ecologically important tree species native to Canada (Hodgetts et al., 2001). Over 114 000 ha of white spruce were planted in Canada in 2012 (Canadian Council of Forest Ministers, 2014).

Thinning is commonly used to increase merchantable productivity of plantations, and has effects on both timber production and non-timber values. By reducing the number of trees within a stand, thinning improves the supply of growth resources to residual trees, thereby enhancing tree growth (Aussenac, 2000; Zeide, 2001). Commercial thinning is applied in immature stands at ages where the size of thinned trees permits conversion to usable wood products and the remaining trees are vigorous enough to utilize the increased growing space (Nyland, 2002). This increases the commercial productivity of stands. These commercial thinning practices are however relatively new to Canada (Pelletier and Pitt, 2008).

The benefits of thinning are well documented, e.g. 10% and 24% increase in quadratic mean diameter and mean merchantable volume per stem, respectively, over unthinned stands over a 16-year period in white and red spruce (*Picea rubens* Sarg.) plantations have been observed (Pelletier and Pitt, 2008). However thinning, as traditionally implemented, tends to homogenize stand structure and composition, and can negatively impact deadwood maintenance (Franklin et al., 2007). Plantation forests are therefore commonly perceived as ecological deserts that do not provide habitats for valued organisms (Brockerhoff et al., 2008). Understanding the effect of alternative thinning treatments on deadwood dynamics is essential to develop and adopt silvicultural practices that are compatible with biodiversity values, especially in stands primarily managed for wood production.

Thinning increases tree growth by increasing the amount of growing space available to the remaining trees. Several measures of growing space have been suggested in the literature, e.g., crown projection area (Assmann, 1970), leaf area (O'Hara, 1998), and area potentially available (APA) (Brown, 1965; Assmann, 1970). All of these methods have strengths and weaknesses. Crown projection area excludes the vertical dimension of a tree's aerial growing space, and allocation of growing space by leaf area is difficult operationally. The APA defined as the area of an irregular polygon constructed around a subject tree (Moore et al., 1973) may serve as a surrogate for the degree of root spread, available belowground resource pool, and/or the degree of crown crowding (Mainwaring and Maguire, 2004). Although the APA describes the horizontal growing space, it can be of practical use to forest managers, especially if expressed in terms of the number of trees removed around a subject tree and the resulting growth

increment. Increasing APA through thinning affects tree growth through its influence on the amount of foliage and possibly the efficiency with which resources are used. Understanding the relationship among tree growth, foliage amount, resource use efficiency, and change in APA by thinning can help forest managers design silvicultural treatments that can potentially optimize both foliage distribution among trees and resource use efficiency, and thereby increase tree growth.

Thinning causes changes in stand microclimate, which lead to changes in tree physiological behaviour, crown size and growth (Aussenac, 2000). Although the benefits of thinning have long been recognized, the specific physiological processes underlying the increased growth response are not well known (Ginn et al., 1991; Peterson et al., 1997). Increasing growing space through thinning enlarges tree crowns (e.g. Ginn et al., 1991; Juodvalkis et al., 2005), and can also increase nutrient supply per tree due to a reduction in the number of competing individuals (Carlyle, 1995). Higher nutrient supply to trees could increase foliar nitrogen concentration, which can influence photosynthetic rates by altering levels of photosynthetic enzymes (Reich et al., 1994; Kozlowski and Pallardy, 1997). Increase in light intensity to lower crowns following thinning could lead to preferential allocation of nitrogen to foliage in areas of high irradiance (Field, 1983; Givnish, 1988), and can also increase the photosynthetic quantum efficiency (efficiency with which light is converted to fixed carbon (Lambers et al., 2008)) of the whole crown (Han, 2012). Thus, it could be presumed that increased growth response of white spruce to thinning results from increase in crown size as well as increases in foliar nitrogen concentration, photosynthetic rates, and photosynthetic quantum efficiency of the lower crown foliage due to their exposure to higher light

levels following thinning. The validity of these hypotheses need to be tested. Knowledge of the mechanisms of growth response to stand treatment is important because it may account for much of the variation found among different treatments or between studies on different sites, and may allow a more precise prediction of the growth response (Binkley and Reid, 1984). Understanding effects of silvicultural treatments on the physiology and morphology of tree crowns can help to develop mechanistic models of the functioning of forest stands (Medhurst and Beadle, 2005) and improve existing empirical growth and yield models (Weiskittel et al., 2011).

1.2 Overall goal and specific objectives

This study forms part of a larger Natural Sciences and Engineering Research Council of Canada (NSERC) Collaborative Research and Development (CRD) funded project, using six white spruce plantations in northern New Brunswick to evaluate effects of commercial thinning treatments on birds, small mammals, saproxylic insects, bryophytes, ground vegetation, and tree growth response. The overall CRD project determined the influence of key habitat structures, early in the rotation of planted stands, on animal and plant taxa and thereby on key ecosystem processes, and how these can be incorporated into management strategy. This specific study will determine the effects of commercial thinning on tree growth response and deadwood dynamics, and elucidate mechanisms of tree growth response to thinning. Specific objectives are to:

1. Determine the effect of commercial thinning on stand structural attributes: diameter at breast height (DBH), DBH increment, basal area, basal area

increment, crown diameter, crown length, and live crown ratio. (These results were combined with results of thinning effects on birds, small mammals, saproxylic insects, bryophytes and ground vegetation, from other collaborators on the NSERC Collaborative Research and Development project and were published in MacLean et al. (2015; Appendix 1);

2. Evaluate thinning effects on downed coarse woody debris (CWD) and standing dead trees (snags) by (i) quantifying the pre-thinning amount of CWD and snag deadwood and decay status, (ii) determining effects of commercial thinning on amount and type of deadwood, and (iii) determining effects of biomass removal and enhanced structure treatments on deadwood dynamics (Chapter 2);
3. Test the hypotheses that individual tree volume increment and growth efficiency increase with APA in young spruce stands, and determine the relative importance of growth efficiency and leaf area to stem volume increment in young spruce trees in the three years immediately following thinning (Chapter 3);
4. Determine the effect of thinning on photosynthetic quantum efficiency of upper and lower crowns of spruce trees and test if thinning increases photosynthetic rates and foliar nitrogen concentration of the upper and lower crown foliage in the three years immediately following thinning (Chapter 4).

1.3 Study area

The study was conducted in the Black Brook District, an intensively managed 220 000 ha forest owned by J.D. Irving, Limited (JDI) in northern New Brunswick,

Canada (47° 9′ 51″ to 67° 55′ 27″). The Black Brook District is located in the Southern Uplands Ecoregion, which is underlain by meta-sedimentary and calcareous sedimentary bedrock, and drained to the South and West by tributaries of the Saint John River (New Brunswick Department of Natural Resources and Energy (NBDNRE), 1998). Elevation ranges from 180 to 600 m, increasing from South to North.

The Black Brook District includes 85 000 ha planted with primarily species of spruce (*Picea spp.*). Clearcuts are generally replanted within one year of harvest, and a variable retention approach is used, where islands of mature trees and clumps of advanced regeneration are left on site to provide structural diversity. All six plantations used in this study originated from clearcuts followed by mechanical site preparation used to create favourable seedling microsites and aerial herbicide application, whenever required to control competing vegetation. Three plantations (Brown Brook, Airstrip and Yellow Brook) were established using bare-root 2+2 spruce seedlings (4 years old, so planted tree age would be 4 years older than the plantation establishment year), and the other three plantations (Roussel Brook, Canton and Paget) used container stock seedlings (1 year old when planted). Five of the plantations were planted from 1985-1988, the year following harvest, with the Airstrip plantation planted in 1979-1980 and the Airstrip biomass removal block planted in 1987. One-half of the plantations were cleaned between ages 10 and 15 years, to release the best crop trees and maintain optimum density: Roussel Brook and Brown Brook cleaned in 1998, Canton unthinned, biomass removal, and enhanced structure blocks and the Airstrip biomass removal block cleaned in 2001. JDI policy was to clean all plantations that required it (i.e., had significant hardwood competition), so the post-cleaning condition of all plantations

should have been similar.

1.3.1 Experimental design

The study design consisted of six large (>20 ha) white spruce plantations aged 22-30 years old, which underwent commercial thinning in the fall of 2010 or winter of 2011**.** The plantations were selected on the basis of similar stand characteristics, each plantation was divided into four blocks and randomly assigned four treatments: 1) an unthinned control, and three 40% basal area removal thinning treatments, with 2) slash and tops remaining on site (status quo), 3) branches and tops extracted from the site (biomass removal), and 4) 11-12 clumps of unthinned trees (10 trees per clump) left per treatment block (minimum block size of ~5 ha), and one-half of the trees in each clump girdled with a draw knife to create snags (enhanced structure). Five 0.04 ha circular permanent sample plots (PSPs) were randomly located in each treatment block. Approximately 12% of each thinned treatment block area was harvested as trails. Harvest trail width and spacing were ~3.5 m and 23 m, respectively.

1.4 Application

A critical issue for the future of plantation forests is how to combine biodiversity conservation and wood production (Spellerberg and Sawyer, 1996). This study determined effects of alternative commercial thinning treatments, which created varying amounts of deadwood, on tree growth (Chapters 3 and 4, and Appendix 1) as well as on downed CWD and standing dead trees (Chapter 2). The study provides a comprehensive

understanding of deadwood dynamics following commercial thinning and gives guidelines on how deadwood maintenance can be incorporated into intensively managed forests to enhance biodiversity values.

The total growth of a stand is driven heavily by the combination of greater light use and higher light use efficiency of the larger trees (Binkley et al., 2013). The spatial relationships between trees, particularly how much space dominant trees need, remain a major question that needs to be addressed (Binkley et al., 2013). Chapter 3 of this thesis examined the relationship between tree growth, leaf area, and growth efficiency (growth per unit leaf area) and an increase in available growing space for dominant and codominant trees. Knowledge of these relationships could help forest managers develop thinning strategies that could maximize tree growth and efficiency of the largest trees within a stand to meet management objectives.

Knowledge of the effect of silviculture on tree physiology can help in the development of process-based models that predict growth response to stand treatment (Medhurst and Beadle, 2005). Such models include light use efficiency models (epsilon growth models), which predict growth as a function of absorbed light and a radiation use efficiency coefficient, and are simplified enough to be of value and/or interest to practical forest managers (Landsberg and Waring, 1997). A constant radiation use efficiency coefficient (e.g. Landsberg and Waring, 1997) or species specific coefficients (e.g. Girardin et al., 2008) are used in such models. However, the effects of silvicultural treatments on tree physiological behaviour are not represented in these models. This study elucidates mechanisms of tree growth response to thinning by examining thinning effects on leaf area, growth efficiency, photosynthetic rates, photosynthetic quantum

efficiency, and foliar nitrogen concentration (Chapters 3 and 4). Knowledge of the difference in photosynthetic rates and resource use efficiency between thinned and unthinned trees, temporal trend of resource use efficiency after thinning, and relationships between tree or stand growth and growth efficiency versus photosynthetic rates can guide forest scientists to accurately represent tree physiological processes following thinning in epsilon growth models. This will aid the improvement of these models to predict tree growth response to thinning.

1.5 Thesis structure

This thesis is presented in an "article" format. The body of the thesis consists of three distinct chapters (Chapters 2, 3, and 4), which are described below. The last chapter of the thesis (Chapter 5) presents a general discussion of the conclusions from these chapters. Appendix 1 describes thinning effects on stand structure from this study with the effects on birds, small mammals, saproxylic insects, bryophytes and ground vegetation from the work of other collaborators on the NSERC Collaborative Research and Development project. Appendix 1 was published in The Forestry Chronicle (*MacLean, D.A., Dracup, E., Gandiaga, F., Haughian, S.R., MacKay, A., Nadeau, P., Omari, K., Adams, G., Frego, K.A., Keppie, D., Moreau, G., and Villard, M-A. 2015. Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. For. Chron., 91:161-175*).

Chapter 2 quantifies the amount of prethinning CWD and snag deadwood and decay status, and determines the effects of alternative commercial thinning treatments on deadwood dynamics. This chapter has been published in the Canadian Journal of Forest Research (*Omari, K., and MacLean D.A. 2015. Do biomass removal and structure-enhancing treatments influence deadwood characteristics following commercial thinning in spruce plantations in New Brunswick, Canada? Can J. For. Res., 45:1407-1418*).

Chapter 3 examines the influence of stand structure surrounding individual dominant and codominant trees on leaf area, tree growth, and growth efficiency. The study tested the hypothesis that individual tree volume increment and growth efficiency increase with increasing growing space, and determined the relative importance of growth efficiency and leaf area to stem volume increment following thinning. This chapter has been published in Forest Ecology and Management (*Omari, K., MacLean, D.A., Lavigne, M.B., Kershaw, J.A. Jr., and Adams, G.W. 2016. Effect of local stand structure on leaf area, growth, and growth efficiency following thinning of white spruce. For. Ecol. Manage., 368:55-62*).

Chapter 4 elucidates the mechanisms underlying the observed increase in growth following thinning. To achieve this goal, the response of upper and lower crown light-saturated photosynthetic rates, photosynthetic quantum efficiency, and foliar nitrogen concentration to thinning are examined. The relationships between stand growth versus leaf area index or photosynthetic rates, as well as between growth efficiency versus

photosynthetic rates are also examined for thinned and unthinned plots. This chapter is planned for submission as: *Omari, K., MacLean, D.A., Lavigne, M.B., Kershaw, J.A. Jr., and Adams, G.W. 2016. Effect of commercial thinning of white spruce on photosynthesis, photosynthetic efficiency and foliar nitrogen. Planned for submission in Forest Ecology and Management*.

I was the primary author for all the manuscripts in the body of the thesis (Chapters 2, 3, and 4). Dr. David A. MacLean is included as a co-author on Chapters 2, 3 and 4. Dr. John A. Kershaw Jr., Dr. Michael B. Lavigne, and Mr. Greg W. Adams are included as co-authors on Chapters 3 and 4.

1.6 References

Assmann, E. 1970. The principles of forest yield study. Pergamon Press Ltd., Oxford. 506 p.

Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Ann. For. Sci., 57:87-301.

Binkley, D., and Reid, P. 1984. Long-term responses of growth and leaf area to thinning and fertilization in a Douglas-fir plantation. Can. J. For. Res., 14:656-660.

Binkley, D., Laclau, J-P., and Sterba, H. 2013. Why one tree grows faster than another: Patterns of light use and light use efficiency at the scale of individual trees and stands. For. Ecol. Manage. 288:1-4.

http://dx.doi.org/10.1016/j.foreco.2012.08.009.

Brockerhoff, E.G., Jactel, H., Parrotta, J.A., Quine, C.P., Sayer, J. 2008. Plantation forests and biodiversity: oxymoron or opportunity? Biodivers. Conserv., 17:925-951.

Brown, G.S. 1965. Point density in stems per acre. For. Res. Inst., N.Z. For. Serv. No. 38.

Canadian Council of Forest Ministers 2014. National Forestry Database Program. Can. For. Serv., Ottawa, Ontario, Canada. Available from http://nfdp.ccfm.org/silviculture/quick_facts_e.php.

Carlyle, J.C. 1995. Nutrient management in a *Pinus radiata* plantation after thinning: the effect of thinning and residues on nutrient distribution, mineral nitrogen fluxes, and extractable phosphorus. Can. J. For. Res., 25:1278-1291.

Field, C., 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. Oecologia, 56:341–347.

Franklin, J.F., Mitchell, R.J., and Palik, B.J. 2007. Natural disturbance and stand development principles for ecological forestry. USDA For. Serv. Gen. Tech. Rep. NRS-19.

Ginn, S.E., Seiler, J.R., Cazell, B.H., and Kreh, R.E. 1991. Physiological and growth responses of eight-year-old loblolly pine stands to thinning. For. Sci., 37:1030-1040.

Girardin, M.P., Raulier, F., Bernier, P.Y., and Tardif, J.C. 2008. Response of tree growth to a changing climate in boreal central Canada: A comparison of empirical, process-based, and hybrid modeling approaches. Ecol. Model., 213:209-228.

Givnish, T.J. 1988. Adaption to sun and shade: a whole-plant perspective. Aust. J. Plant Physiol., 15:63–92.

Han, Q. 2012. Leaf photosynthetic responses to thinning. *In* Applied Photosynthesis (Ed. M.M. Najafpour). InTech, Rijeka, pp. 215-228.

Hodgetts, R.B., Aleksiuk, M.A., Brown, A., Clarke, C., Macdonald, E., Nadeem, S., and Khasa, D. 2001. Development of microsatellite markers for white spruce (Picea glauca) and related species. Theor. Appl. Genet., 102:1252-1258.

Juodvalkis, A., Kairiukstis, L., and Vasiliauskas, R. 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. Eur. J. For. Res., 124: 187-192.

Kozlowski, T.T., and Pallardy, S.G. 1997. Physiology of Woody Plants. Academic Press, Inc., San Diego, CA.

Kuhnke, D.H. 1989. Silviculture statistics for Canada: an 11-year summary. Forestry Canada, Information Report NOR-X-301.

Lambers, H., Chapin III, F.S., and Pons, T.L. 2008. Plant Physiological Ecology. 2nd Ed. Springer, New York.

Landsberg, J.J., and Waring, R.H. 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and portioning. For. Ecol. Manage., 95:209-228.

Lapointe, B., Bradeley, R., Parsons, W., and Brais, S. 2006. Nutrient and light availability to white spruce seedlings in partial and clearcut harvested aspen stands. Silva Fennica, 40:459-471.

MacLean, D.A., Dracup, E., Gandiaga, F., Haughian, S.R., MacKay, A., Nadeau, P.,

Omari, K., Adams, G., Frego, K.A., Keppie, D., Moreau, G., and Villard, M-A. 2015. Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. For. Chron., 91:161-175.

Mainwaring, D.B., and Maguire, D.A. 2004. The effect of local stand structure on growth and growth efficiency in heterogeneous stands of ponderosa pine and lodgepole pine in central Oregon. Can. J. For. Res., 34:2217-2229.

Medhurst, J.L., and Beadle, C.L. 2005. Photosynthetic capacity and foliar nitrogen distribution in *Eucalyptus nitens* is altered by high-intensity thinning. Tree Physiol., 25:981-991.

Moore, J.A., Budelsky, C.A., and Schlesinger, R. C. 1973. A new index representing individual tree competitive status. Can. J. For. Res., 3:459-500.

NBDNRE. 1998. Ecological land classification for New Brunswick: ecoregion, ecodistrict, and ecosite levels. New Brunswick Department of Natural Resources and Energy, Fredericton, NB, Canada.

Nyland, R.D. 2002. Silviculture: concepts and applications. 2nd ed. McGraw-Hill, New York.

O'Hara, K.L. 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can. J. For. Res., 18:859-866.

Pelletier, G., and Pitt, D.G. 2008. Silvicultural responses of two spruce plantations to midrotation commercial thinnings in New Brunswick. Can. J. For. Res., 38:851-867.

Peterson, J.A., Seiler, J.R., Nowak, J., Ginn, S.E., and Kreh, R.E. 1997. Growth and

physiological responses of young loblolly pine stands to thinning. For. Sci., 43: 529-534.

Reich, P.B., Walters, M.B., Ellsworth, D.S., and Uhl, C. 1994. Photosynthesis-nitrogen relations in Amazonian tree species. I. Patterns among species and communities. Oecologia, 97:62-72.

Spellerberg, I.F., and Sawyer, J.W.D. 1996. Standards for biodiversity: a proposal based on biodiversity standards for forest plantations. Biodivers. Conserv., 5:447–459.

Weiskittel, A.R., Hann, D.W., Kershaw, J.A., and Vanclay, J.K. 2011. Forest growth and yield modelling. John Wiley and Sons, Ltd., UK.

Zeide, B. 2001. Thinning and growth. J. For., 99:20-25.

CHAPTER 2: DO BIOMASS REMOVAL AND STRUCTURE-ENHANCING TREATMENTS INFLUENCE DEADWOOD CHARACTERISTICS FOLLOWING COMMERCIAL THINNING IN SPRUCE PLANTATIONS IN NEW BRUNSWICK, CANADA?

Paper published as:

Omari, K., and MacLean D.A., 2015. Do biomass removal and structure-enhancing treatments influence deadwood characteristics following commercial thinning in spruce plantations in New Brunswick, Canada? Can. J. For. Res., 45:1407-1418.

2.1 Abstract

Effects of commercial thinning on downed coarse woody debris (CWD) and standing dead trees (snags) were examined in six intensively managed 22- to 30-year-old white spruce (*Picea glauca* (Moench) Voss) plantations in northern New Brunswick, Canada. Four alternative treatments were applied: (i) an unthinned control and three commercial thinning 40% basal area removals, with (ii) slash and tops remaining on the site (status quo), (iii) most of the branches and tops extracted from the site (biomass removal), and (iv) clumps of unthinned trees left, with one-half of the trees in each clump girdled to create snags (enhanced structure). Three years after thinning, CWD volume increased by 14%–27% in the status quo and enhanced structure treatments, by 6% in the biomass removal treatment, and by 0.1% in the unthinned treatment. Mean snag volume changed little, i.e., less than 1m^3 ha^{-1} among treatments, and stumps of thinned trees were 4.6-4.9 m^3 ha^{-1}. The girdled trees added 0.7 m^3 ha^{-1} of snags, and 1.3 m^3 ha^{-1} is expected to be added from girdling the remaining live trees in the unthinned clumps in 2016. The girdled trees and future to-be-girdled trees added up to 50% of the new deadwood in the enhanced structure treatments, but thinning treatments did not significantly affect total deadwood. The results indicate that commercial thinning produced fine debris but had little effect on overall deadwood amount. Girdling trees during commercial thinning, at the intensity used in this study, is unlikely to produce sufficient snags. Leaving islands and clumps during harvest before plantation establishment would be a more effective way of adding structure.

2.2 Introduction

Downed deadwood, referred to here as coarse woody debris (CWD), and snags (standing dead trees) play important roles in the functioning of forest ecosystems. Deadwood contributes to physical and chemical processes such as nutrient cycling and carbon storage and provides habitat for nesting birds, saproxylic insects, and many wildlife species (Harmon et al., 1986; Drapeau et al., 2002). A large amount of deadwood is associated with natural old growth forests (Siitonen et al., 2000), but planted stands are often criticized as 'sanitized', with less structural diversity, fewer species, and an absence of downed and standing deadwood (Franklin, 1990; Kerr, 1999). Intensive forest management practices such as thinning, which is frequently used in plantations, are also viewed as having detrimental effects on deadwood maintenance (McCarthy and Bailey, 1994; Siitonen, 2001) and, consequently, on biodiversity.

There is, however, little information about the quantitative and qualitative patterns of deadwood in plantations (Food and Agriculture Organization (FAO), 2007). Most of the research on CWD has also focused on volume or biomass estimates in old growth forests and comparisons of CWD among stands of different ages (Fraver et al., 2002). Deadwood volume is typically higher in old growth stands (e.g. 224 m^3 ha^{-1} for a Sierran old-growth, mixed-conifer forest; Innes et al., 2006) compared with younger stands (e.g. 32 m^3 ha^{-1} in a 36-year second growth forest; Sturtevant et al., 1997) and varies regionally (Table 2.1). The natural mortality process in the stem exclusion stage of stand development can be mimicked by low thinning, which captures imminent mortality by removing smaller, suppressed, and less vigorous stems that will eventually die out of the live canopy (Harvey and Brais, 2007). The major difference between the

natural process and its silvicultural analogue is that when live trees are removed through thinning, the density of both live and dead stems is reduced, and the recruitment of deadwood is also reduced (Harvey and Brais, 2007). Therefore, volume of deadwood in managed forests is typically lower than in unmanaged or natural forests, e.g. 4.5 m^3 ha^{-1} of CWD in managed forest in Fennoscandia compared to 20.0 m^3 ha^{-1} in natural forest in the same region (Rouvinen et al. 2002; Table 2.1).

The benefits of thinning operations on growth and yield are well documented, e.g. 20%-100% higher 10-year post-treatment radial growth increment in black spruce (*Picea mariana* (Mill.) BSP) stands compared with the pre-treatment 10-year mean growth (Vincent et al., 2009). Thinning of immature stands at ages in which the size of thinned trees permits conversion to useable wood products (commercial thinning) focuses diameter and volume growth on a reduced number of stems and makes merchantable volume available during the rotation (Nyland, 2002; Pelletier and Pitt, 2008). Debris or residues resulting from logging operations (slash) also comprise a renewable energy source (Rudolphi and Gustafsson, 2005), and the increasing demand for bioenergy production has resulted in renewed interest in management using slash from logging operations (Gunnarsson et al., 2004). Ecological consequences and effects of slash removal on biodiversity are poorly understood (Gunnarsson et al., 2004; Rudolphi and Gustafsson, 2005). There are no consistent, unequivocal, and universal effects of forest biomass harvesting on soil productivity (Thiffault et al., 2011). However climate, mineral soil texture and organic carbon content, capacity of the soil to provide base cations and phosphorus, and tree species autecology appear to be critical determinants of site sensitivity to biomass harvesting (Thiffault et al., 2011).

Leaving standing dead trees at harvest (McCarthy and Bailey, 1994) and creating some dead trees (Jonsell et al., 1998; Kerr, 1999) have been suggested as ways to increase deadwood, and consequently increase the amount of habitat for some saproxylic species in managed forests. Opportunities for snag creation exist through silvicultural operations such as cleaning and thinning and more innovative ideas such as girdling (Kerr, 1999). Combined thinning and girdling can serve to experimentally create contrasting amounts of deadwood in intensively managed forests to evaluate habitat creation for saproxylic species.

McCarthy and Bailey (1994) presumed that although CWD dynamics (reversion to small-diameter low decay state CWD) would be affected by commercial thinning, overall volume or biomass patterns would not be affected; however, the validity of this needs to be tested. Knowledge of how different thinning treatments affect deadwood dynamics is the basis for the development and adoption of silvicultural practices that enhance biodiversity values, especially in stands primarily managed for wood production. Controlled experiments that quantify changes in CWD in both managed and unmanaged forests are needed (Fraver et al., 2002).

We examined deadwood dynamics in a total of 120 thinned and unthinned sample plots in six intensively managed white spruce (*Picea glauca* (Moench) Voss) plantations in northern New Brunswick, Canada. Changes in CWD and snag volume were assessed in response to commercial thinning treatments that created varying amounts of deadwood: an unthinned control and three 40% basal area removal thinning treatments, with slash and tops remaining on site (status quo treatment), branches and tops removed from the site (biomass removal treatment), and clumps of unthinned trees

left and one-half girdled to create snags (enhanced structure treatment). Collaborators are examining the treatment effects on birds, small mammals, plants, and beetles. Our objectives were to: (i) quantify the prethinning amount of CWD and snag deadwood and decay status, (ii) determine effects of commercial thinning on amount and type of deadwood, and (iii) determine effects of biomass removal and enhanced structure treatments on deadwood dynamics. Our prediction was that treatments would create a gradient in CWD and snag deadwood, with enhanced structure > status quo > biomass removal > unthinned control, which would influence effects on other taxa (some overall taxa response results are described in MacLean et al. (2015) and Nadeau et al. (2015).

2.3 Methods

2.3.1 Study area

The study was conducted in the Black Brook District, an intensively managed 220 000 ha forest owned by J.D. Irving, Limited (JDI) in northern New Brunswick, Canada (47° 9′ 51″ to 67° 55′ 27″) (Fig. 2.1). The area falls within Ecoregion 3 (Zelazny et al., 2003), and includes over 50 000 ha planted with primarily species of spruce (*Picea spp.*), as well as high-value shade tolerant hardwood stands that are managed for sawlogs and veneer logs by single-tree selection and patch cut systems. Conifer species in planted stands are managed as even-aged, including up to three commercial thinnings over a rotation period (Higdon et al., 2005). Clearcuts are generally replanted within one year of harvest, and a variable retention approach is used, where islands of mature trees and clumps of advanced regeneration are left on site to provide structural diversity.

All six study plantations originated from clearcuts followed by mechanical site preparation used to create favourable seedling microsites and aerial herbicide application, whenever required to control competing vegetation. Five of the plantations were planted from 1985 to 1988, the year following the harvest, with the Airstrip plantation planted in 1979-1980 and the Airstrip biomass removal block planted in 1987. Three plantations (Brown Brook, Airstrip, and Yellow Brook) were established using bare-root 2+2 spruce seedlings (4 years old, so planted tree age would be 4 years older than the plantation establishment year), and the other three plantations used container stock seedlings (1 year old when planted). We have used plantation establishment year to indicate plantation age. One-half of the plantations were cleaned between ages 10 and 15 years to release the best crop trees and maintain optimum density: Roussel Brook and Brown Brook cleaned in 1998, Canton unthinned, biomass removal, and enhanced structure blocks and the Airstrip biomass removal block, cleaned in 2001. JDI policy was to clean all plantations that required it (i.e., had significant hardwood competition), so the postcleaning condition of all plantation blocks should have been similar. Further details on forest conditions and management in the Black Brook District can be found in Higdon et al. (2005), Montigny and MacLean (2006), and Hennigar et al. (2007).

2.3.2 Experimental design

The study design consisted of six white spruce plantations that were >20 ha and aged 22-30 years that underwent commercial thinning treatments for this study in the fall of 2010 or winter of 2011**.** The plantations were selected on the basis of similar stand characteristics, each plantation was divided into four blocks, and randomly assigned four

treatments: (i) an unthinned control and three 40% basal area removal thinning treatments, with (ii) slash and tops remaining on site (status quo), (iii) branches and tops extracted from the site (biomass removal), and (iv) 11-12 clumps of unthinned trees (10 trees per clump) left per treatment block (minimum block size of ~5 ha), with one-half of the trees in each clump girdled with a draw knife to create snags (enhanced structure). Five 0.04 ha circular permanent sample plots (PSPs) were randomly located in each treatment block and measured before and after thinning and 3 years after thinning. Approximately 12% of each thinned treatment block area was harvested as trails, which did not avoid the PSPs. Harvest trail width and spacing were ~3.5 m and 23 m, respectively.

2.3.3 Data collection

We established 25 m transects from the center of each PSP in all four cardinal compass directions to sample CWD before thinning (2010) as well as 2 and 3 years after thinning. CWD pieces that intersected the transects were measured for diameter at point of intersection (≥ 8 cm), small-end diameter (≥ 5 cm), large-end diameter, distance of log from plot center, and length up to 5 cm minimum diameter. Species, if identified, and decay class were also recorded for CWD pieces. Logs that crossed more than one transect were sampled only once. Stumps and roots of uprooted trees were excluded from measurement because they are largely below ground and unavailable for many deadwood requiring species; however, we determined density and volume of stumps from before and after thinning plot data. Decay class system definitions of Taylor and MacLean (2007) for CWD and snags were used to assign decay classes to all deadwood.

Although not included in their classification system, very decayed subterranean CWD that could be seen as bulges on the forest floor were assigned class 5 of Taylor and MacLean (2007) decay class for downed deadwood. All snags with a diameter at breast height (DBH, 1.3 m) ≥ 5cm that occurred within PSPs and all girdled trees in unthinned clumps in the enhanced structure treatment blocks were measured for DBH and height, and their decay class and species were recorded.

In each plantation, DBH (≥ 5 cm) and density of live trees were measured before thinning in 2010. After thinning, some minor modifications were made to the original sampling plan, with 8 of the 120 PSPs re-established after the thinning because of treatment logistics (e.g., untreated portion due to site accessibility). In these post-thinning established PSPs, we calculated the prethinning DBH of cut trees based on local DBH versus stump diameter relationships developed for that plantation, and calculated prethinning DBH of live trees based on the mean periodic annual increment from year of plot establishment to 2013. The DBH and density of live stems were remeasured for all 120 PSPs in 2013.

Prethinning and newly added post-thinning CWD in the plots established after thinning were determined based on decay status. Prethinning CWD was typically class 4 or 5 (for decay class definition, see Taylor and MacLean (2007)), whereas 3 years after thinning, newly added post-thinning CWD was typically class 2 or 3. Prethinning and newly added post-thinning snags were also determined based on decay status, and whether or not the tree was alive at plot establishment.

2.3.4 Data analyses

Pre-and post-thinning DBH, basal area, and density of live stems were calculated for each plot and averaged by plantation and treatment. Volume of individual CWD pieces was calculated using Smalian's formula (Husch et al., 1972):

$$V_m = \frac{(\pi/8)(D^2+d^2)l}{10\,000} \quad (1)$$

where V_m is volume in cubic meters, D and d are the log large- and small-end diameters (cm), respectively, and l is the log length in (m). Per hectare volume and density of CWD were calculated using equations from Van Deusen and Gove (2011) for estimating per unit area attribute of CWD sampled along spoked transects (transects that radiate from the centre of a circular plot):

$$y_j = A \times \sum_{i=1}^{n_j} \frac{y_{ij}}{p(C,S)} \quad (2)$$

where y_j is the per hectare attribute of CWD in plot j, n_j is the number of selected logs on the plot, y_{ij} is the individual log volume or density, $p(C,S)$ is the joint probability of a log being in the circular plot and crossing a spoked transect, and A =10 000, to scale $P(C,S)$ to a per hectare selection probability. Species-based equations in Raile (1982) for estimating stump volume were used to calculate volume of cut stumps per plot from stump height and DBH of cut trees.

Volume of snags was calculated using Honer et al. (1983) metric volume equations for central and eastern Canada. Height of snags present before thinning but absent after thinning was estimated using local, species-based quadratic height-DBH equations for live trees measured in our study area. For each plantation, separate equations were developed for unthinned and thinned treatments, and combined if the

equations did not differ significantly. Otherwise, the equation for the unthinned treatment was used because snag height prior to thinning was being estimated. Equations were also combined across plantations if they did not differ significantly. We used the periodic annual increment for DBH and height specific to the enhanced structure treatment block in each plantation to estimate height and DBH for the remaining live trees in the unthinned clumps 6 years after thinning. Expected volumes of the planned future to-be-girdled trees 6 years after thinning were then estimated for the enhanced structure treatment of each plantation.

In the enhanced structure treatment blocks, none of the unthinned clumps were located within PSPs but, rather, were distributed across the treatment block. Consequently, PSPs from the enhanced structure and status quo plots had the same treatment, and we reported CWD and snag volume and density for the status quo and enhanced structure treatments combined, in comparison with values for the biomass removal and unthinned treatments. In comparing overall total deadwood volume among treatments, we included volume of girdled trees and estimated future snag volume, from planned future to-be-girdled trees in unthinned clumps, in the enhanced structure treatment.

Differences in live tree attributes (DBH, density, and basal area), deadwood volume, and deadwood density between treatments and plantations were tested using nested analysis of variance (ANOVA) with treatment as a fixed factor, plantation as a random factor, and plot as a random factor nested within plantation. Except for prethinning basal area and post-thinning DBH data, which required no transformation, Box-Cox transformations were applied to all live tree attributes data as well as post-

thinning CWD volume, and CWD plus snag volume present before thinning and retained after thinning, in order for residuals to meet ANOVA assumptions of normality and homoscedasticity. Data for prethinning and newly added post-thinning CWD volume, new CWD plus snag volume, total deadwood volume, pre-and post-thinning CWD densities, and all snag data (excluding girdled trees), had residuals that were not normally distributed and (or) had unequal variance even after Box-Cox transformations were applied. Therefore, we analyzed their rank transformations (Conover and Iman, 1981; Fraver et al., 2002). All ANOVA tests were performed using Minitab® statistical software, version 17 (Minitab Inc., 2010). In all statistical comparisons, means were considered to be significantly different at $p < 0.05$. Post-hoc analysis (pairwise comparisons) was performed on the corresponding raw or transformed (Box-Cox transformed or rank transformed) data, when there was a significant difference in treatment using Tukey's test. For post-thinning CWD and total deadwood volumes, we compared each thinned treatment with the unthinned using Dunnett's test, and used the resulting *t* values together with sample sizes to calculate effect sizes (Hedges' *g;* see Hedges and Olkin, 1985). Effect size calculations were performed using *R* statistical software (R Core Team, 2015). All range and mean values of deadwood and live tree attributes reported were calculated from the untransformed data.

2.4 Results

We present results before thinning (live tree and deadwood data), 2 years after thinning (CWD decay classes), and 3 years after thinning (live tree and deadwood data).

2.4.1 Stand characteristics

Pre-and post-thinning DBH, density, and basal area of live trees are summarized in Table 2.2. Prior to thinning, mean DBH was significantly different between plantations ($p < 0.001$) but not between treatment blocks ($p = 0.52$). DBH ranged from 5 to 31 cm for individual trees, and averaged 13.4-13.8 cm for the four treatments blocks. Three years after thinning, mean DBH ranged from 16.6 to 16.7 cm in the three thinned, i.e., status quo, biomass removal, and enhanced structure. The unthinned treatment had a significantly lower mean DBH (15.3 cm) compared with the other treatments. Post-thinning DBH was also significantly different between the plantations ($p < 0.0001$).

Mean tree density, although significantly different between plantations ($p < 0.0001$), did not differ significantly between treatment blocks before thinning ($p = 0.94$). Three years after thinning, stand density ranged from 1102 to 1142 stems ha^{-1} in the status quo, biomass removal, and enhanced structure treatments versus 2127 stems ha^{-1} in the unthinned treatment. Stand density 3 years after thinning was not significantly different among the three thinned treatments, but the unthinned treatment had significantly higher mean density. Mean basal area ranged from 32.3 to 33.1 m^2 ha^{-1} in all four treatments prior to thinning. Three years after thinning, mean basal area was significantly higher in the unthinned treatment (40 m^2 ha^{-1}) compared with the status quo, biomass removal, and enhanced structure treatments (25-26 m^2 ha^{-1}).

2.4.2 Prethinning CWD and snags

Mean volume of CWD and snags present before thinning in each of the six

plantations are shown in Fig. 2.2. Prethinning CWD volume averaged 24.5 m^3 ha^{-1} and ranged from 9-38 m^3 ha^{-1} among plantations, but individual PSP CWD was more variable, ranging from 0 to174 m^3 ha^{-1} (Fig. 2.2a). Mean CWD volume prior to thinning differed significantly among plantations (p = 0.001) (Fig. 2.2a). In all plantations, CWD volume was primarily (54%-79%) logs with decay class 4, which averaged 16.2 m^3 ha^{-1} for the six plantations. Mean CWD volume of decay classes 3 and 5 were similar, 4.6 and 3.5 m^3 ha^{-1}, respectively, and decay class 2 was 0.2 m^3 ha^{-1} (Fig. 2.2c). Mean CWD density prior to thinning also varied significantly among plantations (p = 0.005), ranging from 0 to 3206 logs ha^{-1} in individual PSPs and averaging 284-788 logs ha^{-1} per plantation.

Snag volume (Fig. 2.2b) before thinning ranged from 0 to 5.8 m^3 ha^{-1} for individual PSPs and averaged 0.4 m^3 ha^{-1} across the six plantations. The volume of snags prior to thinning differed among plantations (p < 0.001) and was 1.0 m^3 ha^{-1} for the Paget and Airstrip plantations versus only 0.1-0.3 m^3 ha^{-1} for the Roussel Brook, Brown Brook, and Yellow Brook plantations. No snags were present in the Canton plantation prior to thinning. Snag density also differed among plantations (p < 0.001), averaging 0-71 stems ha^{-1} and ranging from 0 to 275 stems ha^{-1} in the PSPs.

2.4.3 Effect of commercial thinning on CWD and snags

Three years after thinning, CWD increased by 14%-27% in the status quo and enhanced structure treatments, by 6% in the biomass removal, and by 0.1% in the unthinned treatment. The status quo and enhanced structure treatments had an average of 3.9-5.7 m^3 ha^{-1} of new CWD, significantly more than the 1.6 m^3 ha^{-1} of new CWD added

in the biomass removal treatment (Fig. 2.3a). The unthinned treatment added only 0.03 $m^3 ha^{-1}$ of CWD from 2011 to 2013 (Fig. 2.3a). Mean CWD in 2013 was 23.3 $m^3 ha^{-1}$ in the unthinned treatment, 26.5 $m^3 ha^{-1}$ in the biomass removal treatment, and 26.6-33.1 $m^3 ha^{-1}$ in status quo and enhanced structure treatments (Table 2.2). Post-thinning CWD (total CWD present in year 2013) differed among plantations ($p = 0.001$) but not among treatments ($p = 0.44$). The effect of commercial thinning on post-thinning CWD volume was small: biomass removal versus unthinned (effect size, 95% confidence interval (CI)); (0.10, -0.41-0.61), status quo versus unthinned (0.25, -0.26-0.76), and enhanced structure versus unthinned (0.39, -0.12-0.91). The density of newly added post-thinning CWD differed between treatments ($p < 0.001$), and was highest in the status quo and enhanced structure (583-1053 logs ha^{-1}) treatments, followed by the biomass removal (290 logs ha^{-1}) and unthinned (1 log ha^{-1}) treatments (Fig. 2.4a). Two years after thinning, the decay status of CWD (Fig. 2.3c) was generally similar to the prethinning decay status. In each treatment, most CWD (53%-70%) was in decay class 4. Logs in decay class 2 were primarily from logging residues and were most abundant (39%-50%) in the status quo and enhanced structure treatments, with 12% in the biomass removal treatment. CWD pieces in decay class 1 were only found in the status quo and enhanced structure treatments and contributed 0.1%-0.2% to the total volume in these treatment blocks. CWD added by the thinning treatment showed early to intermediate signs of decay 3 years after thinning. The density of cut stumps ranged from 375 to 1475 stumps ha^{-1} in the biomass removal plots and from 400 to 2150 stumps ha^{-1} in the status quo and enhanced structure plots. Volume of cut stumps was similar among treatments, averaging 4.7 $m^3 ha^{-1}$ in the biomass removal treatment and 4.6-4.9 $m^3 ha^{-1}$ in the status

quo and enhanced structure treatments.

Mean snag volume changed little, decreasing by 0.1-0.4 m^3 ha^{-1} in the status quo and enhanced structure treatments, and increasing by 0.1-0.5 m^3 ha^{-1} in the biomass removal treatment and unthinned treatment. Volume and density of snags present before thinning but absent after thinning (AAT in Figs. 2.3b and 2.4b) did not differ between treatments (p = 0.14 for volume and p = 0.20 for density). However, volume and density of snags present before thinning and retained after thinning (BT in Figs. 2.3b and 2.4b) differed between unthinned and status quo treatments, but were similar among all thinned treatments. Snags added by the thinning treatment (AT in Figs. 2.3b and 2.4b) ranged in size from 5 to 15 cm. The unthinned treatment added a greater volume and density of snags from 2011-2013 than the thinned treatments, and there were no significant differences among thinned treatments. Trees girdled in 2011 in the enhanced structure treatments added a volume of 0.8-1.1 m^3 ha^{-1} in four plantations (Roussel Brook, Brown Brook, Yellow Brook, and Paget) but given larger treatment block areas (ca. 10 ha) and a similar number of unthinned clumps, was only 0.4-0.5 m^3 ha^{-1} in the Airstrip and Canton plantations. Snag volumes of 0.6-0.8 m^3 ha^{-1} from the Airstrip and Canton plantations and 1.3-2.0 m^3 ha^{-1} from the rest of the plantations are estimated to be added from girdling the remaining live trees in the unthinned clumps 6 years post-thinning in 2016. Mean size of these planned future to-be-girdled trees is expected to increase from ca. 14 cm to 18 cm.

2.4.4 Total deadwood volume

Total deadwood volume includes downed CWD and snags present before

thinning and retained after thinning, newly added post-thinning CWD and snags, volume of girdled trees, and estimated volume 6 years after thinning from the remaining live trees in unthinned clumps that are planned to be girdled in 2016. Volume of total deadwood averaged 24 m^3 ha^{-1} in the unthinned treatment, 27 m^3 ha^{-1} in the biomass removal treatment, 27 m^3 ha^{-1} in the status quo treatment, and 34 m^3 ha^{-1} in the enhanced structure treatment. Including the volume of commercial thinning treatment cut stumps would add an additional 4.6-4.9 m^3 ha^{-1} (15%-17%). Volume of CWD and snags present before thinning and retained after thinning differed among the plantations ($p = 0.001$) but not among treatments ($p = 0.66$) (Fig. 2.5a). New CWD and snags added by the thinning (Fig. 2.5b) were similar among plantations ($p = 0.11$). The unthinned and biomass removal treatments had similar volumes of new deadwood, which was less than the amount in the status quo and enhanced structure treatments ($p < 0.001$). In the enhanced structure treatments of four plantations, the volume of 2011 girdled trees plus planned 2016 girdled trees added 31%-50% of new deadwood, and in the Airstrip and Canton plantations, it contributed 21%-23% of new deadwood (Fig. 2.5b).

Total deadwood volume (Figs. 2.5a and b combined) differed between plantations ($p = 0.002$) but not among the four treatments ($p = 0.70$). Effect sizes for each of the thinned versus unthinned treatments total deadwood volumes were also small: 0.01, CI = -0.51-0.52; 0.09, CI= -0.42-0.6; 0.27, CI = -0.25-0.78 for each of the biomass removal, status quo, and enhanced structure treatments versus unthinned treatment, respectively. This was because of the overriding effect of older, prethinning, and in many cases, preharvest CWD on total deadwood volume.

The Airstrip plantation was denser (2285-3615 stems ha^{-1} versus 1595-2730

stems ha^{-1}) than the other five plantations, with smaller trees (mean prethinning DBH of 11-13 cm versus 12-16 cm) than the other plantations (Table 2.2). Species composition also differed, with 22%-49% planted black spruce and 35%-75% planted white spruce in the Airstrip plantation versus 65%-96% planted white spruce in the other five plantations prior to thinning. Therefore, we tested whether excluding the Airstrip plantation from analyses would change results for treatment differences for prethinning and newly added post-thinning CWD and snag volumes. Excluding the Airstrip plantation did not change the results (significant differences between treatments), so we retained the Airstrip plantation in all analyses.

2.5 Discussion

2.5.1 Amount and decay status of deadwood prethinning

Prethinning CWD volume in this study was similar to amounts found in mixed broadleaf and pure broadleaf forests in Switzerland (Böhl and Brändli, 2007) and old-growth boreal forests in northern Sweden (Gibb et al., 2005), as well as in natural, selectively logged, and managed stands in old Scots pine (*Pinus sylvestris* L.) dominated forests in the middle boreal vegetation zone (Rouvinen et al., 2002). However, the prethinning CWD volume recorded in this study was substantially (78%) lower than preharvest CWD reported by Fraver et al. (2002) in the Acadian forest region of central Maine, USA. Although Fraver et al. (2002) and the current study are in the same forest region, a spruce budworm (*Choristoneura fumiferana* (Clemens)) outbreak contributed to the high volume of deadwood in their study. A multicohort structure of many species

in stands studied by Fraver et al. (2002) also contributed to higher CWD volume, as tree species and stand age markedly influence the total amount of deadwood (Sturtevant et al., 1997; Sippola et al., 1998).

Species-specific drying and case hardening between the bark and inner wood (Seedre et al., 2013) influence deadwood decomposition rates, and different decay rates between species affect persistence time of predisturbance and disturbance-generated debris (Muller and Liu, 1991). Consequently, the availability of CWD over time in single-species and mixed-species forests can vary considerably. Mean density of CWD present before thinning was only a little higher (570 logs ha^{-1}) than new additions recorded after the thinning treatment (482 logs ha^{-1}), but the prethinning logs, many of which originated with the previous stand harvest, were much larger than those added during thinning.

Prethinning snags were small (5-15 cm DBH) because the plantations were young (22-30 years old) and had a low mean volume (0.4 m^3 ha^{-1}) and density (31 stems ha^{-1}). Low snag density (<200 stems ha^{-1}) and rare snags within the youngest stands occurred in a chronosequence of 19 second-growth stands that were 33-80 years old and 7 old-growth stands that were 87-110 years old (Sturtevant et al., 1997). In pole (15-28 year old) stands, a high density of low basal area snags dominate, probably nonfunctional as habitat for most wildlife (McCarthy and Bailey, 1994). Larger snags (DBH ≥30 cm) are suitable to provide cavity sites and to increase woodpecker food supplies (DeGraaf, 1978b).

Most prethinning CWD (65%) were in decay class 4, or logs that have fallen to the ground and have oval cross sections and light-red spongy wood (Taylor and

MacLean, 2007). In the current study, classification of logs as decay class 4 was not based on oval cross sections of logs; decay class 4 logs were softer than the less decayed and more intact decay class 3, but not extremely decayed. The time required for decay varies considerably with climate (Söderström, 1988), and the transition rate between decay classes may also be influenced by species, stem size, age of tree at death, or the decomposer community (Ranius et al., 2003; Angers et al., 2012). For example, a mean residence time of 34 years was reported for spruce trees (CWD and snags) in mid-northern Sweden (Ranius et al., 2003), and 22 years was reported for 99% of CWD to degrade in the warmer, more humid conditions of south-western France (Brin et al., 2008). In the maritime climate of Newfoundland, Canada, Sturtevant et al. (1997) observed both downed and standing residual birch (*Betula spp.*) remaining as long as 60 years after disturbance. Russell et al. (2014) estimated residence times of 84 years and 83 years for birch and eastern white cedar (*Thuja occidentalis* L.), respectively. In our study, large logs (intersect diameter > 30 cm), were mostly decay class 4 and included eastern white cedar and birch. Large-diameter, well-decayed CWD are good substrates for cryptogram and seedling establishment and provide high water retention (Fraver et al., 2002).

2.5.2 Effect of alternative commercial thinning treatments on deadwood dynamics

The presumption by McCarthy and Bailey (1994) that commercial thinning would significantly influence specifics of CWD dynamics but probably not have an overall effect on volume patterns was confirmed in this study. Commercial thinning produced small-diameter CWD and increased CWD volume by 14%-27%. The newly

added post-thinning CWD volume was significantly greater in the status quo and enhanced structure treatments than in the biomass removal and unthinned treatments. However, the volume of post-thinning CWD was not significantly different between treatments, and the standardized mean difference between the post-thinning CWD of each of the thinned versus unthinned treatments was small (0.1-0.39). Volume of total deadwood (Figs. 2.5a and 2.5b combined) was also not significantly different 3 years after thinning between treatments; effect sizes ranged from 0.01-0.27 for each of the thinned versus unthinned treatments. This indicates that commercial thinning had little short-term effect on total amount of deadwood.

Under most current harvest and silvicultural practices, biological legacies such as snags and CWD are drastically reduced (Franklin, 1990). Consequently, young forests that develop following traditional clear-cut practices are typically simpler in composition and structure than those that develop following natural disturbances (Franklin, 1990). Silvicultural practices that are analogues of natural disturbances are one means of retaining CWD and snags in managed forests (Seymour and Hunter, 1999). Such practices include leaving biological legacies from the previous stand, particularly CWD or trees to become snags and future CWD, before plantation establishment (Franklin, 1990; Seymour and Hunter, 1999).

The average harvest interval (Russell et al., 2012) and age since previous harvest influence the amount of deadwood in managed forests, as forests with short management histories carry structural legacies from previous stages of the forest (Rouvinen et al., 2002). Legacy deadwood was a major portion of total CWD in our study. However, depending on harvesting method, large logs in advanced decay stages that are retained

may be crushed by logging equipment, making them less useful ecologically than intact logs (McCarthy and Bailey, 1994). This is less so in commercial thinning harvesting that uses small- to medium-sized harvesters.

Newly added post-thinning CWD resulting from the thinning treatment was within early to intermediate stages of decay 3 years after thinning. Unlike large CWD from mature trees that may persist for several decades, slash decomposes rapidly in the first decade after harvest because it is mostly small in diameter (Maser et al., 1988). Such logging slash may, however, provide habitat for saproxylic insects (Gunnarsson et al., 2004; Nadeau et al., 2015), and stumps after thinning favor some beetle species (Sippola et al., 1998).

Thinning captures mortality, controls spacing, and decreases competition, all of which reduce snag production (Duvall and Grigal, 1999). Commercial thinning reduced snag volume in the status quo and enhanced structure treatments and produced a negligible increase in the biomass removal treatment. Duvall and Grigal (1999) reported snag biomass of 150 kg ha^{-1} in young (0-30 years) red pine (*Pinus resinosa* Aiton) managed forests in the Great Lakes States, USA, which was less than 1% of that in young unmanaged forests (58 200 kg ha^{-1}). They noted that timber management affects the distribution and amount of snags more heavily than that of downed logs, especially in young forests. Brin et al. (2008) also found few snags in thinned maritime pine (*Pinus pinaster* Aiton) plantations, with snag volumes < 1 m^3 ha^{-1}, < 1.5 m^3 ha^{-1}, and < 3 m^3 ha^{-1} following first, second, and third thinnings, respectively. Snag volume, however, increased in our unthinned treatment by 0.5 m^3 ha^{-1} (156%) from 2011-2013. The large snag volume in unthinned treatments resulted mostly from the Airstrip plantation (Fig.

2.5b), which had unthinned plots that were densest and produced snags from density-dependent self-thinning. Large numbers of small snags typify stands in the stem exclusion stage of development (Lang, 1985).

In our study, mean volume of newly-added CWD in the biomass removal treatment averaged 1.6 m^3 ha^{-1} compared with 3.9-5.7 m^3 ha^{-1} in the status quo and enhanced structure treatments, whereas addition of new CWD in the unthinned treatment over the same 3-year period was only 0.03 m^3 ha^{-1}. Although there was no significant difference in post-thinning CWD volume between treatments, aggressive slash removal may lead to a decline in the functional role of deadwood in thinned stands. In a study of small mammal responses to thinning on the same study sites, red-backed voles (*Clethrionomys gapperi* (Vigors, 1830)) were significantly more abundant ($p = 0.02$) in thinning treatments with debris retained (status quo and enhanced structure) than in either unthinned or biomass removal treatments (MacLean et al., 2015).

Slash resulting from logging operations is a unique habitat with no clear equivalent in natural conifer dominated forests (Rudolphi and Gustafsson, 2005). Even major windthrow differs as it includes large tree boles, whereas logging or thinning slash is mostly fine material. Piles of slash may provide important refuges for ground-active beetles and small mammals, whereas extensive extraction of slash results in poor species richness of Coleoptera at a local scale (Gunnarsson et al., 2004). Slash also decomposes quickly and contributes substantially to nutrient cycling. These functions to some degree may compensate for the loss of integrity of structural legacies, which results mainly from crushing during logging. Coupled with the general degradation of ecological function of well decayed large logs after thinning, adverse effects of logging residue

removal, ranging from loss of special habitats to nutrient loss, should encourage caution about the practice of widespread biomass removal during commercial thinning. It is important to note that in the current study area, biomass removal during commercial thinning is not practiced, and this was an experimental treatment only for this study to determine responses of selected taxa. However, based on microhabitat associations of mainly saproxylic beetles and landscape history, a general conclusion for Sweden is that coniferous wood can be harvested as forest fuel to a rather large extent but deciduous tree species should be retained to a larger degree (Jonsell, 2007; Jonsell et al., 2007).

Using a theoretical model and logistic regression analysis of empirical data, Bütler et al. (2004) recommended that a snag volume of 18 m^3 ha^{-1} or 14 (DBH≥21cm) snags per hectare in an area of 100 ha would allow for the local persistence of three-toed woodpeckers (*Picoides tridactylus* (Linnaeus, 1758)) in forest patches. As part of the criteria for certification, the Forest Stewardship Council standard in Sweden requires forest managers to create at least three high stumps or girdled trees per hectare in areas harvested through regeneration felling or large-stem thinning, in addition to conserving all snags that have been dead over one year, if they do not constitute a safety risk or breeding substrate for insect pests (Forest Stewardship Council, 2010). All snags dead less than one year are also conserved if they meet special requirements, e.g., if they originate from trees with high biodiversity values (Forest Stewardship Council, 2010). In our study, mean volume of trees girdled 1 year after thinning (0.7 m^3 ha^{-1}) was approximately equal to mean snag volume in the unthinned treatments and slightly higher than the mean of 0.2-0.5 m^3 ha^{-1} of snags in the status quo, biomass removal, and enhanced structure (without girdling) treatments 3 years after thinning. This is not

surprising given the young age and low mortality rates in the plantations. Total snag volume from girdling (current and planned future to-be-girdled trees) increased new deadwood by up to 50 % in the enhanced structure treatment. However, this did not result in differing overall deadwood volume between treatments. Girdling more or larger trees would produce more volume, but this will not produce large-sized snags in young stands. Leaving trees, either current snags or live trees to produce future snags, during the harvest preceding plantation establishment would be a preferable means to ensure retention of sufficient large diameter snags. This will provide habitat for cavity- nesting wildlife species and also provide a near future supply of large CWD on the forest floor (McCarthy and Bailey, 1994).

2.6 Conclusions

Prior to commercial thinning in white spruce plantations, CWD volume averaged 24.5 m^3 ha^{-1} and ranged from 9-38 m^3 ha^{-1}. Three years after thinning, volume of new CWD added was two to four times less in the biomass removal treatment than in the enhanced structure and status quo treatments. Little new CWD (0.03 m^3 ha^{-1}) was added over 3 years in the unthinned treatment. Snag volume averaged 0.4 m^3 ha^{-1} prior to thinning, and 3 years after thinning, it declined by 0.1-0.4 m^3 ha^{-1} in the status quo and enhanced structure treatments, increased minimally (0.07 m^3 ha^{-1}) in the biomass removal treatment, and increased by 0.5 m^3 ha^{-1} in unthinned plots. Girdling trees to produce standing dead trees in the enhanced structure treatment added 0.7 m^3 ha^{-1} of snags, with approximately twice that volume expected from girdling the remaining live trees in the unthinned clumps 6 years after thinning. Stumps of cut trees contributed 4.6-

4.9 m^3 ha^{-1}.

Three take-home messages from this study are that: (i) structure-enhancing commercial thinning treatment increased new deadwood amounts, but did not contribute a great deal to increasing total deadwood quantities in intensively managed white spruce plantations, primarily because trees are relatively small; (ii) most deadwood in these stands originated prior to the commercial thinning treatments and, in fact, from the previous stand; and (iii) the best strategy for providing (quality) deadwood and actually generating deadwood dynamics is to intentionally leave patches of trees at the time of harvesting. Girdling trees during commercial thinning, at intensities comparable with the one used in this study, will likely not yield sufficient snags for functional habitat for all deadwood-requiring wildlife. We therefore recommend that islands and clumps should be left during the harvest before plantation establishment as a more effective approach to increase deadwood amount in intensively managed forests.

2.7 Acknowledgements

This study was funded by J.D. Irving, Limited and by a Natural Sciences and Engineering Research Council of Canada (NSERC) Collaborative Research and Development grant to a team led by D.A. MacLean. Kwadwo Omari was funded by a NSERC Industrial Postgraduate Scholarship. We thank Greg Adams, Jason Killam, and other staff at J.D. Irving, Limited for considerable input and assistance with the project.

2.8 References

Angers, V-A., Bergeron, Y., and Drapeau, P. 2012. Morphological attributes and snag classification of four North American boreal tree species: relationships with time since death and wood density. For. Ecol. Manage., 263(1):138-147. DOI: 10.1016/j.foreco.2011.09.004.

Böhl, F., and Brändli, U.-B. 2007. Deadwood volume assessment in the third Swiss National Forest Inventory: methods and first results. Eur. J. For. Res., 126(3):449-457. DOI 10.1007/s10342-007-0169-3.

Brin, A., Meredieu, C., Piou, D., Brustel, H., and Jactel, H. 2008. Changes in quantitative patterns of dead wood in maritime pine plantations over time. For. Ecol. Manage., 256 (5):913-921. DOI: 10.1016/j.foreco.2008.05.042.

Bütler, R., Angelstam, P., and Schlaepfer, R. 2004. Quantitative snag targets for the three-toed woddpecker *Picoides tridactylus*. Ecol. Bull., 51:219-232.

Conover, W.J., and Iman, R.L. 1981. Rank transformations as a bridge between parametric and nonparametric statistics. Am. Stat., 35:124-129.

DeGraaf, R.M. 1978b. New life from dead trees. Natl. Wildl., 16(4):29-31.

Drapeau, P., Nappi A., Giroux, J.-F., Leduc, A., and Savard, J.-P. 2002. Distribution patterns of birds associated with snags in natural and managed eastern boreal forests. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181.

Duvall, M.D., and Grigal, D.F. 1999. Effects of timber harvesting on coarse woody debris in red pine forests across the Great Lakes states, U.S.A. Can. J. For. Res., 29 (12):1926-1934.

Food and Agriculture Organization. 2007. The state of the world's forests. FAO, Rome,

Italy. Available from ftp.fao.org/docrep/fao/009 [accessed 7 July 2014].

Forest Stewardship Council. 2010. Swedish FSC Standard for Forest Certification including SLIMF indicators. V2-1 050510. Available from http://ic.fsc.org/download.fsc-std-swe-02-2010-sweden-natural-plantation-and-slimf.274.htm [accessed 7 July 2014].

Franklin, J.F. 1990. Biological legacies: A critical management concept from Mount St. Helens. Transactions of the North American Wildlife and Natural Resources Conference, 55:216-219.

Fraver, S., Wagner, R.G., and Day, M. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. Can. J. For. Res., 32(12):2094-2105. DOI: 10.1139/X02-131.

Fridman, J., and Walheim, M. 2000. Amount, structure and dynamics of dead wood on managed forestland in Sweden. For. Ecol. Manage., 131(1-3):23-36. DOI: 10.1016/S0378-1127(99)00208-X.

Gibb, H., Ball, J.P., Johansson, T., Atlegrim, O., Hjälten, J., and Danell, K. 2005. Effects of management on coarse woody debris volume and composition in boreal forests in northern Sweden. Scand. J.For. Res., 20:213-222. DOI: 10.1080/02827580510008392.

Graves, A.T., Fajvan, M.A., and Miller, G.W. 2000. The effects of thinning intensity on snag and cavity tree abundance in an Appalachian hardwood stand. Can. J. For. Res., 30(8):1214-1220. DOI: 10.1139/x00-051.

Gunnarsson, B., Nittérus, K., and Wirdenäs, P. 2004. Effects of logging residue removal on ground-active beetles in temperate forests. For. Ecol. Manage., 201(2-3):229-

239. DOI: 10.1016/j.foreco.2004.06.028.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K., Jr., and Cummins, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecol. Res., 15:133–302.

Harvey, B.D., and Brais, S. 2007. Partial cutting as an analogue to stem exclusion and dieback in trembling aspen (*Populus tremuloides*) dominated boreal mixedwoods: implications for deadwood dynamics. Can. J.For. Res., 37(9):1525-1533.

Hedges, L.V. and Olkin, I.1985. Statistical Methods for Meta-Analysis. London, Academic Press.

Hennigar, C.R, MacLean, D.A., Porter, K.B., and Quiring, D.T. 2007. Optimized harvest planning under alternative foliage-protection scenarios to reduce volume losses to spruce budworm. Can. J. For. Res., 37(9):1755-1769. DOI: 10.1139/X07-001.

Higdon, J.W., MacLean, D.A., Hagan, M.J., and Reed, J.M. 2005. Evaluating vertebrate species risk on industrial forest landscape. For. Ecol. and Manage., 204(2-3):279-296. DOI: 10.1016/j.foreco.2004.09.018.

Honer, T.G., Ker, M.F., and Alemdag, I.S. 1983. Metric timber tables for the commercial tree species of central and eastern Canada. Marit. For. Res. Cent. Inf. Rep. M-X-140.

Husch, B., Miller, C.I., and Beers, T.W. 1972. Forest Mensuration. Ronald, New York, 410 pp.

Innes, J.C., North, M.P., and Williamson, N. 2006. Effect of thinning on prescribed fire restoration treatments on woody debris and snag dynamics in a Sierran old-growth,

mixed-conifer forest. Can. J. For. Res., 36(12):3183-3193. DOI: 10.1139/x06-184.Jonsell, M. 2007.

Jonsell, M. 2007. Effects on biodiversity of forest fuel extraction, governed by processes working on a large scale. Biomass Bioenergy, 31(10):726–732. doi: 10.1016/j.biombioe.2007.06.018.

Jonsell, M., Weslien, J., and Ehnström, B. 1998. Substrate requirements of red-listed saproxylic invertebrates in Sweden. Biodiversity and Conservation, 7(6):749-764.

Jonsell M., Hansson, J., and Wedmo, L. 2007. Diversity of saproxylic beetle species in logging residues - comparisons between tree species and diameters. Biol. Conserv., 138(1-2):89-99. DOI: 10.1016/j.biocon.2007.04.003.

Kerr, G. 1999. The use of silvicultural systems to enhance the biological diversity of plantation forests in Britain. Forestry, 72(3):191-205. DOI: 10.1093/forestry/72.3.191.

Lang, G. E. 1985. Forest turnover and the dynamics of bole wood litter in subalpine balsam fir forest. Can. J. For. Res., 15:262-268.

MacLean, D.A., Dracup, E., Gandiaga, F., Haughian, S.R., MacKay, A., Nadeau, P., Omari, K., Adams, G., Frego, K.A., Keppie, D., Moreau, G., and Villard, M-A. 2015. Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. For. Chron., 91:161-175.

Maser, C., Tarrant R.F., Trappe, J.M. and Franklin, J.F. 1988. From the forest to the sea: a story of fallen trees. USDA For. Serv. Gen. Tech. Rep. PNW-229.

McCarthy, B.C., and Bailey, R.R. 1994. Distribution and abundance of coarse woody

debris in managed forest landscape in the central Appalachians. Can. J. For. Res., 24(7):1317-1329. DOI: 10.1139/x94-172.

Minitab Inc. 2010. Minitab 17 statistical software. State College, Pennsylvania. Available from www.minitab.com.

Montigny, M.K., and MacLean, D.A. 2006. Triad forest management: Scenario analysis of forest zoning effects on timber and non-timber values in New Brunswick, Canada. For. Chron., 82(4):496-511. DOI: 10.5558/tfc82496-4.

Muller, R.N., and Liu, Y. 1991. Coarse woody debris in an old-growth deciduous forest on the Cumberland Plateau, southeastern Kentucky. Can. J. For. Res., 21:1567-1572.

Nadeau, P., Majka, C.G., and Moreau, G. 2015. Short-term response of Coleopteran assemblages to thinning-induced differences in dead wood volumes. For. Ecol. Manage., 336:44-51.

Nyland, R. D. 2002. Silviculture: concepts and applications. Second edition. McGraw-Hill, New York.

Pelletier, G., and Pitt, D.G. 2008. Silvicultural responses of two spruce plantations to midrotation commercial thinning in New Brunswick. Can. J. For. Res., 38(4):851-867.DOI: 10.1139/X07-173.

R Core Team. 2015. The *R* foundation for statistical computing platform: x86_64-w64-mingw32/x64 (64-bit). Version 3.1.3.

Raile, G.K. 1982. Estimating stump volume. USDA For. Serv. Res. Pap. NC-224.

Ranius, T., Kindvall, O., Kruys N., and Jonsson, B.G. 2003. Modelling dead wood in Norway spruce stands subject to different management regimes. For Ecol.

Manage., 182(1-3):13-29. DOI: 10.1016/S0378-1127(03)00027-6.

Rouvinen, S., Kuuluvainen, T., and Karjalainen, L. 2002. Coarse woody debris in old *Pinus sylvestris* dominated forests along a geographic and human impact gradient in boreal Fennoscandia. Can. J.of For. Res., 32(12):2184-2200. DOI: 10.1139/x02-144.

Rudolphi, J., and Gustafsson, L. 2005. Effects of forest-fuel harvesting on the amount of deadwood on clear-cuts. Scand. J. For. Res., 20(3):235-242. DOI:10.1080/02827580510036201.

Russell, M.B., Kenefic, L.S., Weiskittel, A.R., Puhlick, J.J., and Brissette, J.C. 2012. Assessing and modeling standing deadwood attributes under alternative silvicultrual regimes in the Acadian Forest region of Maine, US. Can. J. For. Res., 42(11):1873-1883. DOI: 10.1139/x2012-131.

Russell, M.B., Woodall, C.W., Fraver, S., D'Amato, A.W., Domke, G.M., and Skog, K.E. 2014. Residence times and decay rates of downed woody debris biomass/carbon in eastern US forests. Ecosystems, 17(5):765-777. DOI :10.1007/ s10021-014-9757-5.

Seedre, M., Taylor, A.R., Chen, H.Y., and Jõgiste, K. 2013. Deadwood desnity of five boreal tree species in relation to field-assigned decay class. For. Sci., 59(3):261-266. Http://dx.doi.org/10.5849/forsci.11-157.

Seymour, R. S., and Hunter, M.L. 1999. Principles of ecological forestry. Pp. 22-61. In: M.L. Hunter, Jr. (Ed.). Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK.

Siitonen, J. 2001. Forest management, coarse woody debris and saproxylic organisms:

Fennoscandia boreal forests as an example. Ecol. Bull., 49:11-41.

Siitonen, J., Martikainen, P., Punttila, P., and Rauh, J. 2000. Coarse woody debris and stand characteristics in mature managed and old-growth boreal mesic forests in southern Finland. For. Ecol. Manage., 128 (3):211-225. DOI: 10.1016/S0378-1127(99)00148-6.

Sippola A.-L., Siitonen, J., and Kallio, R.. 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland.Scand. J,. For. Res., 13(1-4):204-214. DOI:10.1080/02827589809382978.

Söderström, L. 1988. Sequence of bryophytes and lichens in relation to substrate variables of decaying coniferous wood in Northern Sweden. Nord. J.Bot., 8(1):89-97. DOI: 10.1111/j.1756-1051.1988.tb01709.x.

Sturtevant B.R., Bissonette, J.A., Long, J.N., and Roberts, D.W. 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. Ecol. Applic., 7:702-713.

Taylor, S.L., and MacLean, D.A. 2007. Dead wood dynamics in declining balsam fir and spruce stands in New Brunswick. Can.J. For. Res., 37(4):750-762. DOI: 10.1139/X06-272.

Thiffault, E., Hannam, K.D., Paré, D., Titus, B.D., Hazlett, P.W., Maynard, D.G., and Brais, S. 2011. Effects of forest biomass harvesting on soil productivity in boreal and temperate forests -A review. Environ. Rev., 19:278-309. DOI: 10.1139/A11-009.

Van Deusen, P., C., and Gove, J.H. 2011. Sampling coarse woody debris along spoked transects. Forestry, 84:93-98. DOI:10.1093/forestry/cpq041.

Vincent, M., Krause, C., and Zhang, S.Y. 2009. Radial growth response of black spruce roots and stems to commercial thinning in the boreal forest. Forestry, 82:557-571. DOI: 10.1093/forestry/cpp025.

Zelazny, V. Martin, G.L., Toner, M., Gorman, M., Colpitts, M., Veen, H., Godin, B., McInnis, B. Steeves, C., and Roberts, M. 2003. Our landscape heritage: the story of ecological land classification in New Brunswick. New Brunswick Department of Natural Resources, Fredericton, NB, Canada.

Table 2.1. Volume of deadwood, including coarse woody debris (CWD) and standing dead trees (snags) in different forest types and under various silvicultural treatments.

Forest type and Region	Age (years)	Silvicultural treatment	Mean CWD (m^3/ha)	Mean snag (m^3/ha)	Reference
Mixed-conifer, U.S.A.[a]	Old-growth	Unthinned	223.9	145.2	Innes et al. (2006)
		Shelterwood	127.2	185.9	
		40% canopy cover	144.8	256.2	
Trembling aspen, Canada[a,b]	81	Unthinned	116.1		Harvey & Brais (2007)
		67% basal area	97.8		
		33% basal area	87.3		
Appalachian hardwood, U.S.A.[a,c]	68	Unthinned		75.1	Graves et al. (2000)
		75% relative density		43.9	
		60% relative density		24.2	
Scots pine, Fennoscandia		45% relative density		22.5	
		Natural forest	20.0		Rouvinen et al. (2002)
Boreal forest, Sweden		Selectively logged	18.7		
		Managed	4.5		
	Old-growth	Unthinned	25.7	46.8	Gibb et al. (2005)
Balsam fir and fir-black spruce,	74-144	Past selective logging	9.3	14.1	
Canada		Clear cut	8.3	5.3	
	36	Second growth	32.3		Sturtevant et al. (1997)
Chestnut oak, U.S.A.	58	Second growth	15.2		
North. boreal, Sweden	80	Second growth	78.1		Harmon et al. (1986)
Hemi-boreal			132		Fridman & Walheim (2000)
Temperate			7.7	2.0	
Fir-spruce, Canada			2.1	1.5	Taylor & MacLean (2007)
Declining fir-spruce			2.3	1.7	
Declining spruce-fir	72-81		30	45	Böhl & Brändli (2007)
Conifer, Switzerland	70-128		140	50	

Mixed conifer	83-140		80	39	
Pure broadleaf			15.1	4.9	Fraver et al. (2002)
Mixed broadleaf			18.4	8.6	
Acadian forest, central Maine, USA			20.3	5.4	Russell et al. (2012)
Acadian forest, central Maine, USA			21.9	10.2	
			108.9		
		Unmanaged		29.4	
		Selection system[d]		3.1	

[a]Canopy cover, basal area, and relative density refer to amounts retained after thinning removal
[b]Results 6 years after treatment
[c]Results 15 years after the treatment
[d]5-year cutting cycle

Table 2.2. Mean diameter at breast height (DBH, 1.3 m), basal area (BA), density of live stems, and mean volume of downed coarse woody debris (CWD) before (2010) and 3 years after thinning (2013) in young white spruce plantations.

Plantation	Treat-ment	DBH (cm)		BA (m^2/ha)		Density (stems/ha)		CWD (m^3/ha)	
		2010	2013	2010	2013	2010	2013	2010	2013
Roussel Brook	UT	15.1	16.9	33.1	41.1	1750	1745	45.4	45.4
	SQ	14.5	17.6	34.0	27.7	1915	1075	49.5	62.5
	BR	14.2	16.8	33.5	28.5	2030	1240	19.5	21.9
	ES	15.5	18.4	34.8	29.5	1755	1065	18.7	24.0
Brown Brook	UT	14.7	16.3	34.5	42.3	1910	1890	17.1	17.1
	SQ	13.7	17.4	30.6	27.1	1895	1090	34.4	36.8
	BR	13.7	16.9	33.5	27.1	2140	1190	44.8	47.3
	ES	12.5	15.6	29.2	25.2	2230	1265	54.5	59.1
Yellow Brook	UT	13.5	15.0	36.9	43.7	2385	2305	44.1	44.1
	SQ	13.8	16.8	39.0	28.0	2430	1205	4.9	7.0
	BR	14.5	18.1	37.8	26.9	2125	1010	22.7	23.4
	ES	13.4	16.6	40.7	28.3	2730	1260	10.5	14.9
Airstrip	UT	10.7	11.9	35.3	41.5	3615	3465	1.2	1.4
	SQ	12.5	14.3	30.3	21.0	2285	1220	1.1	7.7
	BR	13.8	15.1	39.2	23.9	2470	1250	31.5	34.0
	ES	11.5	14.7	33.1	20.7	2885	1120	1.7	5.1
Canton	UT	14.6	16.3	31.7	38.4	1800	1770	9.7	9.7
	SQ	14.3	18.2	28.8	22.8	1675	845	16.6	20.3
	BR	14.1	17.1	31.8	22.8	1945	960	4.0	4.4
	ES	14.2	17.9	30.2	23.0	1850	905	23.4	27.6
Paget	UT	13.5	15.5	25.2	32.5	1595	1585	22.3	22.3
	SQ	11.9	15.2	31.0	24.4	2385	1240	18.7	25.1
	BR	13.2	16.0	27.0	26.2	1780	1205	26.8	27.8
	ES	13.5	16.9	27.3	24.3	1730	995	66.0	67.7

Note: UT, unthinned; SQ, status quo thinned; BR, biomass removal thinned; ES, enhanced structure thinned.

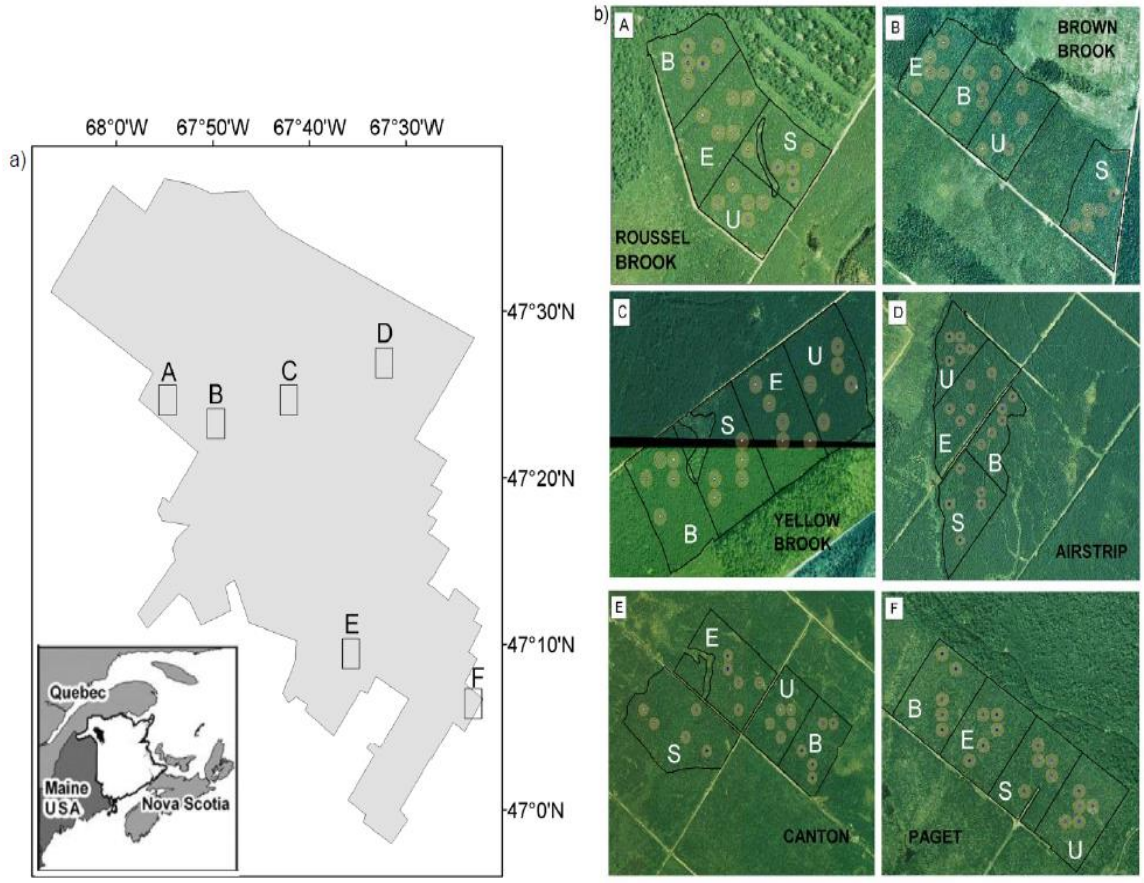

Fig. 2.1. (a) Map of New Brunswick showing the Black Brook District and (b) plantation treatment blocks and plot locations in the Black Brook District. U, S, B, and E (white text in (b)), represent unthinned, status quo, biomass removal, and enhanced structure treatments, respectively.

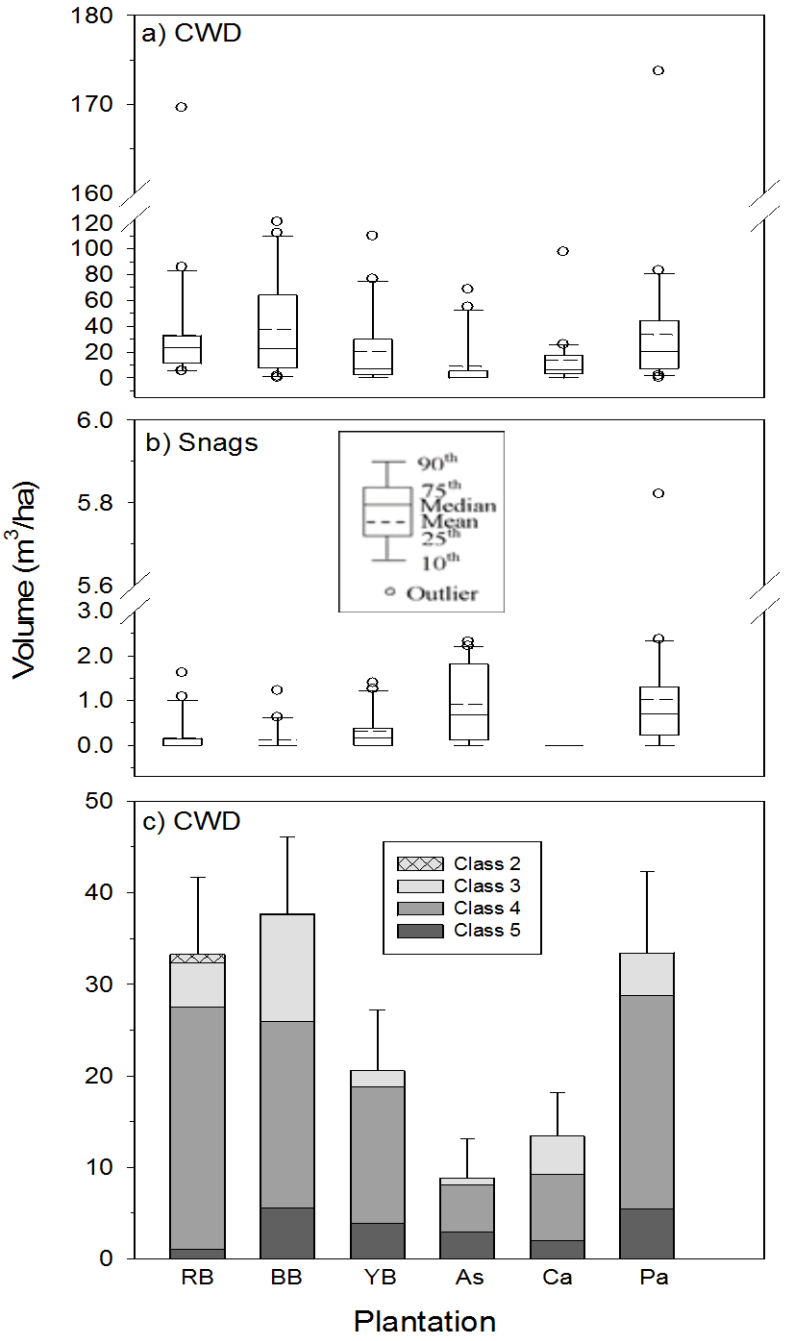

Fig. 2.2. Volume of prethinning deadwood in 20 plots in each of six spruce plantations: (a) downed coarse woody debris (CWD), (b) snags, and (c) mean CWD by decay class. RB, BB, YB, As, Ca, and Pa represent Roussel Brook, Brown Brook, Yellow Brook, Airstrip, Canton, and Paget plantations, respectively.

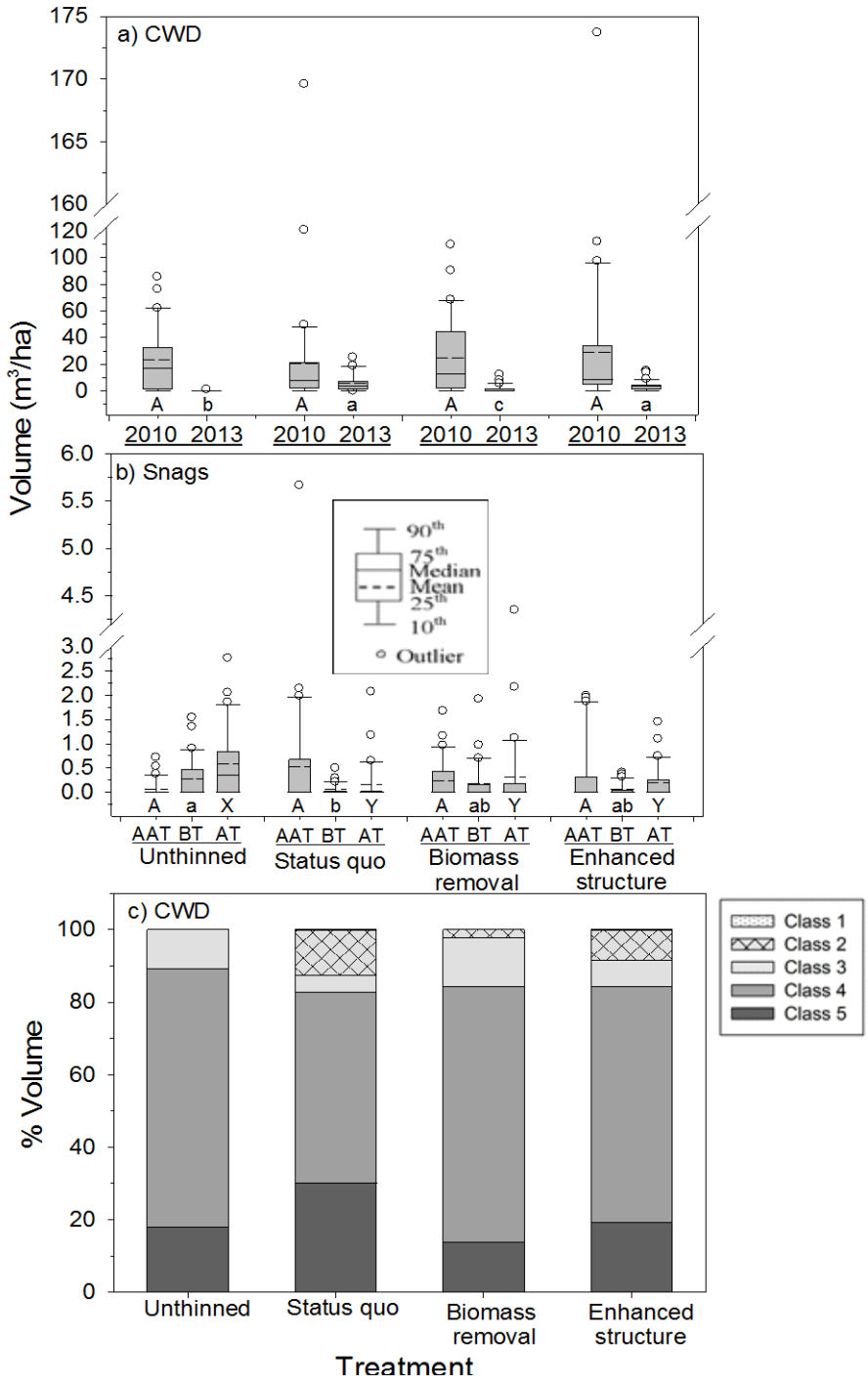

Fig. 2.3. Volume of deadwood in unthinned, status quo, biomass removal, and enhanced structure treatments (30 plots each): (a) downed CWD present prior to thinning (2010) and new CWD added by the 2013 post-thinning remeasurement; (b) snags present before

thinning but absent after thinning (AAT), snags present before thinning and retained after thinning (BT), and snags added after thinning (AT); (c) CWD decay classes 2 years after thinning. Comparisons are among treatments for each year (a) and for each response variable separately (b). Means with the same letter are not significantly different.

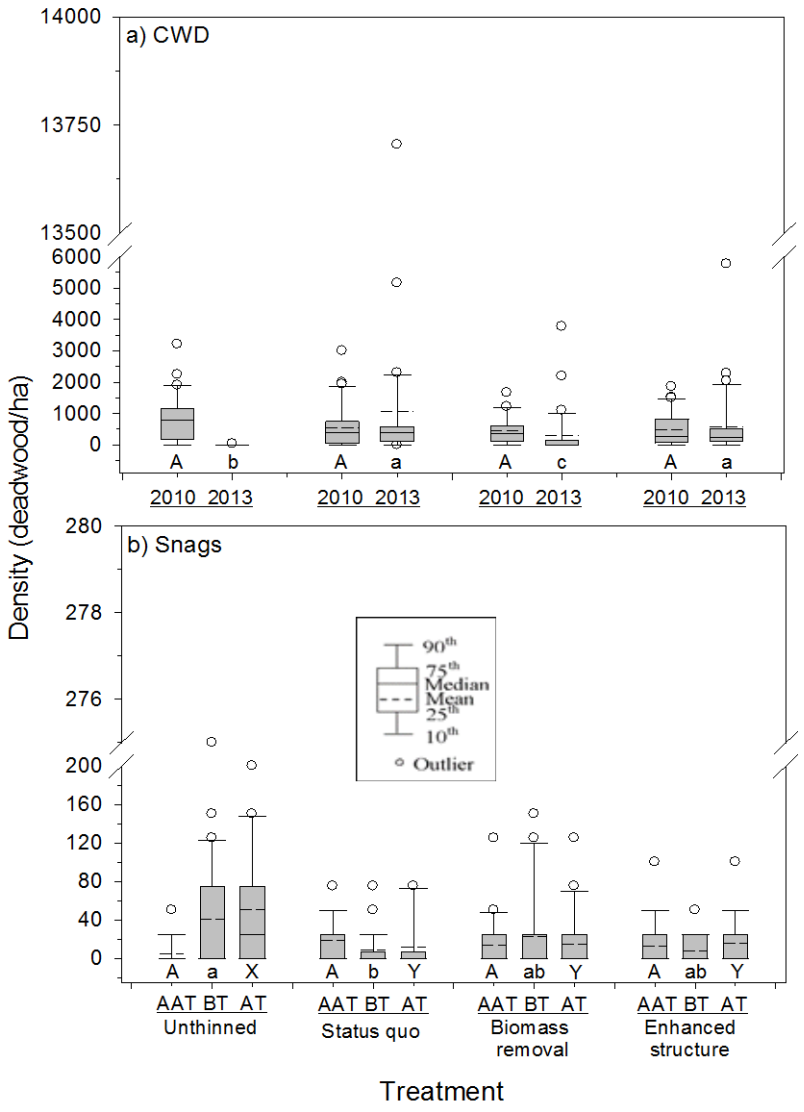

Fig. 2.4. Density of deadwood in 30 plots each of unthinned, status quo, biomass removal, and enhanced structure treatments: (a) downed CWD present prethinning (2010) and new CWD added by the 2013 post-thinning remeasurement; (b) snags present before thinning but absent after thinning (AAT), snags present before thinning and retained after thinning (BT), and snags added after thinning (AT). Comparisons are among treatments for each year (a) and for each response variable separately (b). Means with the same letter are not significantly different.

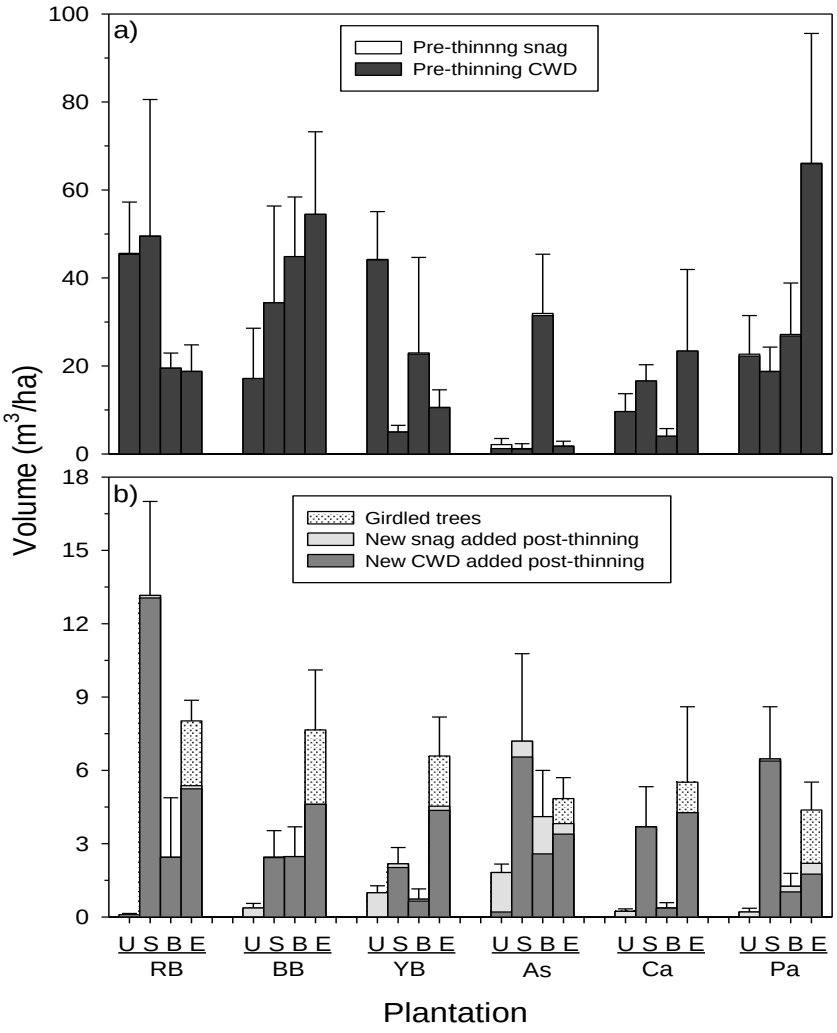

Fig. 2.5. Mean volume of all deadwood (snags and coarse woody debris (CWD)) (a) present before thinning and retained after thinning and (b) new additions after thinning in five plots in each of four treatments in six spruce plantations. Volume of girdled trees is the sum of the volumes of trees girdled in 2011 and planned future to-be-girdled trees in 2016. Treatments: U, unthinned; S, status quo; B, biomass removal; E, enhanced structure commercial thinning. Plantations: RB, Roussel Brook; BB, Brown Brook; YB, Yellow Brook; As, Airstrip; Ca, Canton; Pa, Paget. Stumps of cut trees are excluded here but averaged 4.6-4.9 m^3 ha^{-1} in the thinned treatment plots.

CHAPTER 3: EFFECT OF LOCAL STAND STRUCTURE ON LEAF AREA, GROWTH, AND GROWTH EFFICIENCY FOLLOWING THINNING OF WHITE SPRUCE

Paper published as:

Omari, K., MacLean, D.A., Lavigne, M.B., Kershaw, J.A. Jr., and Adams, G.W. 2016. Effect of local stand structure on leaf area, growth, and growth efficiency following thinning of white spruce. For. Ecol. Manage., 368:55-62.

3.1 Abstract

We examined the influence of stand structure surrounding individual dominant and codominant trees on leaf area, tree growth, and growth efficiency (stem growth per unit leaf area) in young white spruce (*Picea glauca* (Moench) Voss) plantations. Objectives were to (i) test the hypothesis that individual tree volume increment and growth efficiency increase with increasing growing space, and (ii) determine the relative importance of growth efficiency and leaf area to stem volume increment in young spruce following thinning. Growing space was expressed as area potentially available (APA) to each tree. Relative current annual volume increment (annual increment divided by the mean increment for the 3 years immediately preceding thinning) increased linearly with increasing APA 2 and 3 years after thinning, supporting our hypothesis that tree volume increment increases with APA. Growth efficiency however, was not related to APA. Leaf area was positively related to APA 3 years after thinning, and current annual volume increment was related to leaf area. Leaf area per tree increased from 17.8 m^2 to 29.8 m^2 over the 3 years (2011-2013) following thinning and was 16.5-18.7 m^2 for unthinned trees over the same period. Growth efficiency decreased from 1.35 to 0.64 $dm^3\ m^{-2}$ for thinned trees and from 0.74 to 0.55 $dm^3\ m^{-2}$ for unthinned trees from 2010 to 2013. Growth efficiency did not differ between thinned and unthinned trees, but it was significantly lower in year 3 than year 1 after thinning ($p = 0.0178$) and significantly lower than the prethinning growth efficiency ($p = 0.0034$). Our results show that thinning increased individual tree volume increment by increasing leaf area of remaining trees and not by increasing their growth efficiency.

3.2 Introduction

Tree growth is a function of the amount of foliage, the rate of photosynthesis per unit of foliage, allocation of photosynthate to components and conversion rates to new structural matter (Brix, 1983). The unit leaf area rate or net assimilation rate, i.e. the dry weight increase per unit of foliage over time (Briggs et al., 1920; Evans, 1972), can be used as a surrogate for photosynthesis and conversion rates because these are difficult to measure for entire plants over long periods of time (Brix, 1983). For forestry purposes, growth efficiency, defined as stem wood growth per unit of foliage by Waring et al. (1980), can be used instead of net assimilation rate. The amount of foliage is strongly correlated with absorbed photosynthetic active radiation (Binkley et al., 2010; Gspaltl et al., 2013) and can be regarded as the potential production capacity of a tree (Brix, 1983). Growth efficiency is a measure of resource use efficiency (Brix, 1983; Gspaltl et al., 2013) and tree vigor (Waring et al., 1980).

Several studies have reported on the relative importance of leaf area and growth efficiency in determining tree growth response to thinning. Average rates of stem growth per tree were 3-8 times greater in thinned than in unthinned balsam fir (*Abies balsamea* (L.) Mill.) stands, and stem growth was correlated with foliar weight , however, growth efficiency of dominant and codominant trees in thinned stands were similar to those of similar trees in unthinned stands (Lavigne, 1988). Over a 7-year period, mean annual stemwood biomass increment was 34% greater for thinned Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) than unthinned trees, and leaf biomass increased by 0.58 kg year^{-1} for thinned trees compared to a decrease of 0.03 kg year^{-1} for unthinned trees (Brix, 1983). Stem growth per unit leaf area was only 14% greater for the thinned than

unthinned trees indicating that the major growth response to treatment was caused by an increase in the amount of foliage (Brix, 1983). Five-year stem growth and leaf area per tree were greater at intermediate spacings (4.0 -5.2 m) in thinned Douglas-fir plantations and, in contrast to other studies, stem growth per unit leaf area generally increased with increasing spacing (Binkley and Reid, 1984). Determining the relative role of leaf area and growth efficiency on stand treatment responses is important, because it may account for much of the variation found among treatments or between studies on different sites, and may allow more precise predictions of growth responses (Binkley and Reid, 1984).

Each individual tree in a stand has a finite amount of growing space, which can be approximated by its crown projection area (Assmann, 1970) or leaf area (O'Hara, 1988). The use of crown projection area to represent growing space assumes that trees are limited only by horizontal or lateral competition (Assmann, 1970; O'Hara, 1988). However, as stands develop and trees differentiate, a dominant tree can increase in height and intercept the sunlight of a nearby suppressed tree without lateral expansion, and the suppressed tree with limited growth due to the reduced light may decline in growth without a reduction in horizontal growing space (O'Hara, 1988). Leaf area includes a vertical dimension of growing space (O'Hara, 1988; Gspaltl et al., 2012) and provides a better measure of growing space occupancy than crown projection area (O'Hara, 1988). However, allocation of growing space by leaf area is more difficult operationally than crown projection area. Individual tree growing space can be expressed as area potentially available (APA) (Assmann, 1970), which is defined as the area of an irregular polygon constructed around a subject tree (Brown, 1965; Moore et al., 1973). The APA also has been suggested as a surrogate measure of the degree of

potential root spread, available belowground resource pool, and/or degree of crown crowding (Mainwaring and Maguire, 2004). Thus APA may be operationally more practical than allocating growing space by leaf area (Mainwaring and Maguire, 2004), and may have merit in analysis of growth response to thinning, where residual trees remaining following thinning respond to suddenly increased growing space and light conditions. Trees in closed-canopy stands fully occupy their APA but trees in recently thinned stands may not, and the relative occupancy may be related to increase of leaf area per tree in thinned versus unthinned stands. This may introduce a time since thinning effect on growth per tree. Therefore APA may provide a quantitative basis for relating thinning intensity to individual tree growth (Moore et al., 1973).

Mainwaring and Maguire (2004) found a decrease of volume growth per APA with increasing APA for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and lodgepole pine (*Pinus contorta* Dougl. ex. Loud.). Similarly, Sterba (2005) found that tree growth per crown projection area decreased with increasing crown projection area for a given social class in mixed stands of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). Studies on the influence of APA on leaf area and growth per unit leaf area, which may account for the increased growth of residual trees following thinning, are needed. Knowledge of the relationship among volume increment, growth efficiency, foliage amount, and APA can help forest managers design silvicultural treatments that can potentially optimize both foliage distribution among trees and growth efficiency, and, thereby, increase tree growth. Growth models that use resource use efficiency could also benefit from data on the relationship between efficiency of individual trees and their growing space (APA). Application of such

relationships in models may lead to better growth predictions than using an average stand growth efficiency that does not account for differences between individual trees.

We examined effects of APA on leaf area, volume increment, and growth efficiency for 3 years after commercial thinning in young white spruce plantations. Objectives of this paper were to: (i) test the hypotheses that individual tree volume increment and growth efficiency increase with APA in young white spruce plantations; and (ii) determine the relative importance of growth efficiency and leaf area to stem volume increment in young spruce trees following thinning. This forms part of a larger study that determined effects of alternative commercial thinning treatments on stand growth, deadwood, and plant and animal response (MacLean et al., 2015; Omari and MacLean, 2015).

3.3 Materials and methods

3.3.1 Study area

The study was carried out in the Black Brook District, a 220 000 ha forest, owned by J.D. Irving, Limited (JDI) in northern New Brunswick, Canada (47°9′51″-67°55′27″). The Black Brook District is located in the Southern Uplands Ecoregion, which is underlain by meta-sedimentary and calcareous sedimentary bedrock, and drained to the South and West by tributaries of the Saint John River (New Brunswick Department of Natural Resources and Energy (NBDNRE), 1998). Elevation ranges from 180 to 600 m, increasing from South to North. The Black Brook district contains some of the most intensively managed forests in Canada with over 85 000 ha of primarily

spruce plantations. Clearcuts are generally replanted within one year of harvest, with mechanical site preparation before planting and herbicide application 1-3 years after planting, if required. Plantations are often cleaned at 10-15 years, commercially thinned at 20-40 years, and final harvesting is done between ages 35-55 years old. Further details on the study area can be found in Omari and MacLean (2015).

3.3.2 Study design

The commercial thinning installations described in Omari and MacLean (2015) were used in this study. Six >20 ha white spruce plantations aged between 22 and 30 years, selected on the basis of similar stand characteristics, were commercially thinned in the fall of 2010 or winter of 2011. Each plantation was divided into four blocks (minimum block size of ~5 ha) and randomly assigned one of four treatments: (1) an unthinned control, and three 40% basal area removal thinning treatments; with (2) slash and tops remaining on site (status quo); (3) branches and tops extracted from the site (biomass removal); and (4) 11-12 clumps of unthinned trees left per treatment block, and one-half of the trees in each clump girdled to create snags (enhanced structure). Five 0.04 ha circular permanent sample plots (PSPs) were randomly located in each treatment block. Approximately 12% of each thinned treatment block area was harvested as trails. Harvest trail width and spacing were approximately 3.5 m and 23 m, respectively.

3.3.3 Data collection

Two of the plantations (Roussel Brook and Canton) were randomly selected, and

one plot randomly selected in each of the unthinned and status quo thinned treatments of each plantation. In the surrounding area of each selected plot, dominant and codominant trees were marked and measured for diameter at breast height (DBH), total height, and crown width before destructive sampling in fall 2013. Three trees were selected in each unthinned plot and 12 trees in each status quo thinned plot. Trees in the thinned treatment were selected based on number of trees removed around each tree and proximity of the tree to an extraction trail. The eight or nine closest surrounding trees around each tree selected for destructive sampling (subject tree) were measured for DBH as well as azimuth and distance to the subject tree. Twenty additional trees, five trees from each of the status quo thinned and unthinned treatments of Roussel Brook and Canton plantations, were also destructively sampled to develop allometric equations.

After trees were destructively sampled, tree height and crown length were measured. The crown base was defined as the lowest whorl with living branches (contiguous live branches from that whorl to the top of the tree). The crown was divided into three sections, all branches in each crown section were removed, and fresh weight measured for each crown third. Six branches per tree, two from each crown section, were weighed and taken for further analysis in the laboratory. Stem disks were taken at stump height, breast height, every 1 m from breast height to crown base, crown base and mid-crown. Fresh weight of stems and disks were also measured, and the disks brought to the laboratory for further analysis.

In the laboratory, we measured the inside and outside bark diameters of each disk. Growth rings were measured for five disks per tree taken from breast height, 2 and 4 m above breast height, crown base, and mid-crown. The growth rings were measured

for each disk along four radii spaced at 90° using WinDENDRO (Regent Instruments Inc., QC, Canada). Leaf area was measured for 100-needle samples (current year and ≥ 3 years old age classes measured separately, representing 3 years after thinning and before thinning, respectively) from the upper, middle, and lower crown sections using WinSEEDLE (Regent Instruments Inc., QC, Canada). Needle samples were taken from six destructively sampled trees in the unthinned treatment and from 23 trees in the thinned treatment. Disks and branches were oven dried at 70° C for at least 48 hours, and the oven dry weight of disks and needle and twig samples measured.

3.3.4 Data analysis

Mean annual height increment was calculated for each tree (total tree height divided by tree age when destructively sampled (27 years old) in both plantations), and used to estimate total tree height for the years prior to destructive sampling. Length of the leading shoots were not measured while processing destructively sampled trees, hence we estimated height increments in recent years as equalling mean annual height increment. We recognize that some error is introduced but believe that this error is similar for all of the dominant and codominant trees being analyzed in this study. Conversion ratios were developed for each treatment within a plantation for fresh to dry weight and total branch weight to needle weight. Specific leaf area (leaf area of fresh needles per unit dry weight) was determined for each crown section per treatment for each plantation, and used to convert foliage dry weight per tree to area. Live crown ratio (LCR; live crown length divided by total tree height) was also calculated for each tree.

3.3.4.1 Estimation of leaf area prior to destructive sampling

We developed a non-linear mixed effect model of leaf area versus crown base inside bark diameter, with plantation as a random effect, to predict leaf area for the 3 years before the trees were destructively sampled (2010-2012). Including treatment as a random factor nested within plantation resulted in a model that was not statistically different from the one without the treatment term; therefore we excluded the treatment term.

For the thinned trees, crown recession was assumed not to have occurred from the year of thinning to 3 years after thinning. Inside bark crown base diameters for the thinned trees were obtained from ring width measurements of the crown base disk, and used to predict leaf area for years 2010-2012. For unthinned trees LCR was assumed to be constant for each tree from year of thinning (2010) to 3 years after thinning (2013). The error associated with the assumption of a constant LCR is expected to be marginal for the short duration of this study. We calculated crown length of unthinned trees for the 3 years before trees were destructively sampled by multiplying LCR by total tree height in a given year, and consequently estimated height to crown base. Crown base inside bark diameter was predicted for years 2010-2013 from tree height, DBH, and height to crown base using species-specific stem taper equations for the Acadian region (Li et al., 2012). The 2013 measured crown base inside bark diameter was divided by the 2013 predicted crown base inside bark diameter. The resulting ratio was multiplied by the predicted crown base inside bark diameters so that the 2013 predicted values were

same as the measured values, and the predicted values for years 2010-2012 adjusted accordingly. The crown base inside bark diameter of unthinned trees was used to predict leaf area for years 2010-2012. Leaf area predictions for thinned and unthinned trees were also adjusted, as described above for crown base inside bark diameters, using an adjusting ratio of 2013 measured leaf area to 2013 predicted leaf area.

3.3.4.2 Annual stem volume increment and growth efficiency

Current annual volume increment (CAI) was calculated based on the following geometric assumptions: top of tree to mid-crown considered as a cone, breast height to ground surface as a cylinder, and sections between stem disks as frustums of cones. When the crown base disk did not have a (measured) growth ring for a particular year prior to destructive sampling, the top of the tree to the disk height below where a (measured) growth ring existed for that year was considered as a cone. Mensurational formulae appropriate for each stem section were used to calculate its volume (Husch et al., 2003).

We calculated relative CAI as CAI per year postthinning divided by the mean of the 3 years (2008-2010) prethinning CAI. Growth efficiency was calculated for each year after thinning:

$$\text{Growth efficiency} = \frac{Vol_2 - Vol_1}{LA_2} \quad (1)$$

where Vol_2 -Vol_1 represents the current annual volume increment and LA_2 is total tree leaf area for the current year.

3.3.4.3 Area potentially available (APA) and ratio of maximum crown area to APA

Distances and azimuths of surrounding trees were used to create a Thiessen polygon around each subject tree using ArcGIS (ESRI, Redlands, CA), such that the boundaries of the polygon were at points equidistant between the subject tree and each of its surrounding trees. The area of each polygon was assumed to represent the APA. We tried weighting APA by tree sizes (DBH of subject and surrounding trees), and found similar relationships when leaf area or growth efficiency were plotted against weighted or unweighted APA. Relative CAI showed a stronger relationship with unweighted than weighted APA. Also for the period immediately after thinning when residual trees have yet to use their additional growing space, using weighted APA could lead to an overestimation of a subject tree's growing space if it is surrounded by smaller trees. Therefore, unweighted APA is used throughout this paper.

A nonlinear 0.99 quantile regression of crown diameter versus crown length (power function) was developed for each plantation to predict maximum crown diameter for each tree. The maximum crown radius of each tree was used to calculate the crown projection area. The ratio of crown projection area inside the APA to APA was calculated in ArcGIS (ESRI, Redlands, CA) to estimate the extent to which trees use the growing space available to them.

3.3.4.4 Statistical analyses

Inside bark DBH before and 3 years after thinning, and height at the time of destructive sampling were compared between thinned and unthinned trees using a mixed

model analysis of variance (ANOVA), with treatment as a fixed factor and plantation as a random factor. Differences in growth efficiency were tested between the fixed factors: thinning treatments, year after thinning (years 0 (2010)-3 (2013) after thinning), and treatment and year after thinning interaction, with tree size (DBH inside bark) as a covariate and plantation as random a factor. A power variance function structure with fitted values as the variance covariate (Pinheiro and Bates, 2000, pp. 206-211; Zuur et al., 2009, pp. 71-84) was used to accommodate heteroscedasticity when testing for differences in growth efficiency. Tukey's test was applied to determine which years after thinning differed significantly in growth efficiency.

A linear mixed effect regression model was fitted to the relationships between each of the dependent variables: relative CAI, leaf area, and growth efficiency versus APA, as well as between CAI versus leaf area. We also developed a linear mixed model for relative CAI versus APA and total tree leaf area for current or previous year. In each of these models, plantation and treatment nested within plantation were used as random factors. Equivalence tests (paired t-test for equivalence) were used to determine if model predictions were dissimilar between postthinning years. For each equivalence test, values for magnitude of the region of similarity of 0.25 and 0.5, corresponding to strict and liberal tests, respectively (Wellek, 2003, p.12) were used.

An alpha level of 0.05 was used for ANOVA comparisons and equivalence tests. All statistical analyses were performed using *R* statistical software (R Core Team, 2015).

3.4 Results

3.4.1 Sample tree characteristics

Characteristics of dominant and codominant trees destructively sampled in the thinned and unthinned treatments of Roussel Brook and Canton plantations are summarized in Table 3.1. Density of unthinned plots was 1750 and 1800 stems ha^{-1} in 2010 in Roussel Brook and Canton plantations, respectively, versus 1745 and 1770 stems ha^{-1} in 2013. Prethinning density for the status quo thinned plots were 1915 and 1675 stems ha^{-1} in 2010 in Roussel Brook and Canton plantations, respectively, and 1075 and 845 stems ha^{-1} 3 years after thinning (2013). Mean inside bark DBH before thinning (year 2010) did not differ significantly between thinned and unthinned trees. Three years after thinning, mean inside bark DBH and height were 18.9 cm and 12.6 m for thinned versus 17.8 cm and 12.1 m for unthinned trees. There were significant differences in DBH and height between plantations ($p < 0.0001$) but not between thinned and unthinned trees 3 years after thinning. Crown diameter 3 years after thinning differed between plantations ($p < 0.0001$), but not between treatments. Leaf area was 60% greater for thinned (29.8 m^2) than for unthinned trees (18.7 m^2), and the amount of growing space (APA) covered by the maximum tree crown area ranged from 64-100% for the thinned and 90-100% for unthinned trees 3 years after thinning.

3.4.2 Stem growth response to thinning

The relationship between relative CAI and APA changed within the 3-year postthinning period (Fig. 3.1). Although APA stays the same for each tree, relative CAI varies from one year to the next in this analysis. In the first year after thinning (Fig.

3.1a), the slope of the regression was not significantly different from zero (p = 0.300). The slopes were significantly different from zero in years 2 (Fig. 3.1b; p = 0.0004) and 3 (Fig. 3.1c; p = 0.0002) after thinning. There was a large increase in the regression slope from year 1 (0.006 ± 0.006; slope ± standard error) to year 2 (0.037 ± 0.009) and an additional increase from year 2 to year 3 (0.045 ± 0.010) following thinning (Fig. 3.1d). Equivalence tests, both liberal and strict tests, showed that relative CAI predictions from APA differed between the first, second, and third years after thinning (Fig. 3.1d).

When relative CAI was expressed as a linear function of APA and leaf area (Table 3.2), APA had a significant effect on relative CAI in years 2 (p = 0.0015) and 3 (p = 0.0010) after thinning and current year total tree leaf area was significant in years 1 (p = 0.0440) and 2 (p = 0.0075). Substituting previous year total tree leaf area in the model (Table 3.2) resulted in APA being significant 2 (p = 0.0011) and 3 (p = 0.0008) years after thinning, and previous year leaf area was significant only in year 2 (p = 0.0200).

3.4.3 Leaf area and growth efficiency relationships with APA

Leaf area increased with increasing APA over the 3 years following thinning (Fig. 3.2). The regression slope was not significantly different from zero in year 1 (Fig. 3.2a), and in year 2 (Fig. 3.2b) after thinning but in the third year after thinning (Fig. 3.2c) the slope differed significantly from zero (p = 0.0396). There was a trend of increasing leaf area for a given APA, from years 1 and 2 after thinning to the third year following thinning with regression slopes increasing from 0.68 ± 0.49 and 1.15± 0.61

in the first and second years after thinning, respectively, to 1.60 ± 0.73 in the third year following thinning (Fig. 3.2d). For example, at APA values of 10 m^2 and 15 m^2, leaf area for the population average was 19.1 m^2 and 22.5 m^2 in year 1 after thinning, 25.0 m^2 and 30.7 m^2 in year 2, and 30.9 m^2 and 38.9 m^2 in year 3 (Fig. 3.2d). Equivalence tests, both liberal and strict tests, showed that leaf area predictions from APA differed between the first, second, and third years after thinning (Fig. 3.2).

There was no apparent relationship between growth efficiency and APA (Fig. 3.3a-c). Growth efficiency decreased from 1.35-0.64 dm^3 m^{-2} for thinned trees and from 0.74-0.55 dm^3 m^{-2} for unthinned trees from years 2010-2013. There were no significant differences in growth efficiency between thinned and unthinned trees and between year since thinning and thinning treatment interaction but growth efficiency was significantly lower in year 3 compared to year 1 after thinning ($p = 0.0178$) and compared to prethinning growth efficiency ($p = 0.0034$).

3.4.4 Effect of leaf area and growth efficiency on stem growth response

CAI was positively, linearly related to leaf area each year after thinning (Fig. 3.4a-c). Regression slopes varied from 0.38 to 0.45 in the 3 years after thinning (Fig. 3.4d) and were all significantly different from zero ($p < 0.0001$). Equivalence tests, both liberal and strict tests, showed that CAI predictions from leaf area differed between the first, second, and third years after thinning (Fig. 3.4d). Mean CAI of thinned trees was greater than those of unthinned trees in each year. In addition mean CAI was greater in years 2 and 3 (17.0-17.4 dm^3/tree) than in year 1 (14.2 dm^3/tree) in the thinned stand but

not significantly different among years in the unthinned plantations (10.4-11.8 dm^3/tree). Leaf area averaged 16.5-18.7 m^2 for unthinned trees compared to 17.8-29.8 m^2 for thinned trees over the 3 years following thinning.

3.5 Discussion

3.5.1 Volume increment, leaf area, and APA

Thinning reduces competition between residual trees and thereby maintains or enhances growth rates, or prevents them from declining as quickly as they would without intervention (Smith et al., 1997; Nyland, 2002). Stem growth response to thinning increased during the 3 years of this study as crowns of thinned trees expanded to take increasing advantage of the additional APA provided to them by thinning. The consistent, linear relationship between light interception and individual tree crown leaf area (Binkley et al., 2013) shows that by investing in their crown leaf area, the thinned trees increased light interception over the 3 years following thinning, and consequently increased stem volume growth. Our results are consistent with the findings of Brix (1983), who reported that as much as 80% of the dry matter response to thinning for Douglas-fir trees could be accounted for by an increase in foliage amount over a 7-year period.

We also found a positive linear trend of CAI versus leaf area for each year after thinning. Strong, positive and linear relationships between tree growth and leaf area have also been reported for overstory and main canopy redwood trees (*Sequoia sempervirens* (D. Don) Endl.) (Berrill and O'Hara, 2007), Douglas-fir trees (Binkley

and Reid, 1984) and for loblolly pine (*Pinus taeda* L.) (Teskey et al., 1987). The predictive power of absorbed photosynthetic radiation was either as good or only marginally superior to tree leaf area in predicting bole volume growth for Norway spruce (Gspaltl et al., 2013). Stem growth response to thinning increased as crowns expanded to take advantage of the additional APA provided to them by thinning by increasing leaf area.

3.5.2 Growth efficiency and volume increment

Growth efficiency showed no apparent trend with APA for each of the 3 years following thinning. This is a similar result to several thinning studies. Using leaf area as a measure of growing space, O'Hara (1988) found that there was no apparent linear relationship between growth efficiency and sapwood basal area (surrogate for leaf area) for thinned and unthinned Douglas-fir trees from four crown classes. There were also no significant differences in growth efficiency among crown classes in stands with relatively heavy removals during early thinnings and very light removals in later thinnings, or in stands where thinnings maintained a constant residual basal area (O'Hara, 1988). Dry matter per absorbed photosynthetic active radiation was not affected by thinning for Sitka spruce (*Picea sitchensis* (Bong.) Carrière) (Wang 1988), while for a given tree size, trees from unthinned Norway spruce plots were more efficient than thinned trees in immature and pole-stage stands (Gspaltl et al., 2013). Our results did not support the hypothesis that growth efficiency increases with APA in young thinned spruce plantations. However, a tree's efficiency is a dynamic function

that results from interactions with other trees and may vary over time (Gspaltl et al., 2012).

Our study provides evidence that higher tree productivity of dominant and codominant trees 3 years after thinning, expressed in terms of annual stem volume increment, does not result from increase in growth efficiency following thinning. While growth efficiency was generally constant with increasing APA 3 years after thinning, positive linear relationships occurred between leaf area and relative CAI versus APA as well as CAI versus leaf area. These results demonstrate that individual tree volume increment following thinning was driven by increase in potential production capacity (leaf area) and not by an increase in growth efficiency.

3.6 Conclusions

We examined the mechanism of tree growth response to thinning in young spruce plantations by examining the influence of available growing space (APA) on leaf area, tree growth and growth efficiency. Tree growth increased with increasing APA in the second and third years after thinning, but growth efficiency was not related to APA. Leaf area was positively related to APA, and CAI was related to leaf area. Mean leaf area increased by 85% over the 3 years following thinning compared to a 13% increase over 3 years for unthinned trees. Growth efficiency did not differ significantly between thinned and unthinned trees and between thinning treatment and year since thinning interaction but was significantly lower 3 years after thinning than prethinning (p = 0.0034) or 1 year after thinning (p = 0.0178). Increase in leaf area, and not growth

efficiency, was responsible for the increased tree growth following thinning.

3.7 Acknowledgements

This research was funded by J.D. Irving, Limited and by a Natural Sciences and Engineering Research Council of Canada Collaborative Research and Development grant to a team led by D.A. MacLean. Kwadwo Omari was funded by a NSERC Industrial Post-graduate Scholarship. We thank the staff at J.D. Irving, Limited for their input and assistance with the project.

3.8 References

Assmann, E. 1970. The principles of forest yield study. Pergamon Press Ltd., Oxford. 506 p.

Berrill, J-P., and O'Hara, K.L., 2007. Patterns of leaf area and growing space efficiency in young even-aged and multiaged coast redwood stands. Can. J. For. Res. 37:617-626. doi:10.1139/X06-271.

Binkley, D., and Reid, P., 1984. Long-term responses of growth and leaf area to thinning and fertilization in a Douglas-fir plantation. Can. J. For. Res., 14:656-660.

Binkley, D., Laclau, J-P., and Sterba, H., 2013. Why one tree grows faster than another: patterns of light use and light use efficiency at the scale of individual trees and stands. For. Ecol. Manage. 288:1-4. http://dx.doi.org/10.1016/j.foreco.2012.08.009.

Binkley, D., Stape, J.L., Bauerle, W.L., and Ryan, M.G., 2010. Explaining growth of

individual trees: Light interception and efficiency of light use by *Eucalyptus* at four sites in Brazil. For. Ecol. Manage. 259:1704-1713. doi:10.1016/j.foreco.2009.05.037.

Briggs, G.E., Kidd, F., and West, C. 1920. A quantitative analysis of plant growth. Part II. Ann. App. Biol., 7:202-223.

Brix, H., 1983. Effects of thinning and nitrogen fertilization on growth of Douglas-fir: relative contribution of foliage quantity and efficiency. Can. J. For. Res., 13:167-175.

Brown, G.S., 1965. Point density in stems per acre. For. Res. Inst., N.Z. For. Serv. No. 38.

Evans, G.C., 1972. The quantitative analysis of plant growth. University of California, Berkeley.

Gspaltl, M., Bauerle, W., Binkley D., and Sterba, H., 2013. Leaf area and light use efficiency patterns of Norway spruce under different thinning regimes and age classes. For. Ecol. Manage., 288:49-59. doi:10.1016/j.foreco.2011.11.044.

Gspaltl, M., Sterba, H., and O'Hara, K.L., 2012. The relationship between available area efficiency and area exploitation index in an even-aged coast redwood (*Sequoia sempervierns*) stand. Forestry, 85:567-577. doi:10.1093/forestry/cps052.

Husch, B., Beers, T.W., and Kershaw, J.A., Jr. 2003. Forest mensuration. Wiley.

Lavigne, M.B., 1988. Growth and net assimilation rates in thinned and unthinned stands of balsam fir. Can. J. For. Res., 18:1205-1210.

Li, R., Weiskittel, A., Dick, A.R., Kershaw. J.A. Jr., and Seymour, R.S., 2012. Regional stem taper equations for eleven conifer species in the Acadian region of North

America: development and assessment. North. J. Appl. For., 29:5-14.

MacLean, D.A., Dracup, E., Gandiaga, F., Haughian, S.R., MacKay, A., Nadeau, P., Omari, K., Adams, G., Frego, K.A., Keppie, D., Moreau, G., and Villard, M-A., 2015. Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. For. Chron., 91:161-175.

Mainwaring, D.B., and Maguire, D.A., 2004. The effect of local stand structure on growth and growth efficiency in heterogeneous stands of ponderosa pine and lodgepole pine in central Oregon. Can. J. For. Res., 34:2217-2229.

Moore, J.A., Budelsky, C.A., and Schlesinger, R. C., 1973. A new index representing individual tree competitive status. Can. J. For. Res., 3:459-500.

NBDNRE. 1998. Ecological land classification for New Brunswick: ecoregion, ecodistrict, and ecosite levels. New Brunswick Department of Natural Resources and Energy, Fredericton, NB, Canada.

Nyland, R.D., 2002. Silviculture: concepts and applications. 2nd ed. McGraw-Hill, New York.

O'Hara, K.L., 1988. Stand structure and growing space efficiency following thinning in an even-aged Douglas-fir stand. Can. J. For. Res., 18:859-866.

Omari, K., and MacLean D.A., 2015. Do biomass removal and structure-enhancing treatments influence deadwood characteristics following commercial thinning in spruce plantations in New Brunswick, Canada? Can J. For. Res., 45:1407-1418.

Pinheiro J., and Bates, D., 2000. Mixed effects models in S and S-Plus. Springer-Verlag, New York, USA.

R Core Team, 2015. The *R* foundation for statistical computing platform: x86_64-w64-mingw32/x64 (64-bit). Version 3.1.2.

Smith, D.M., Larson, B.C., Kelty, M.J., and Ashton, P.M.S., 1997. The practice of silviculture: applied forest ecology. 9th ed. John Wiley & Sons, Inc., New York.

Sterba, H., 2005. Is there an optimum individual tree crown coverage - a contribution to individual tree growth theory. Austrian J. For. Sci., 2:55–68.

Teskey, R. O., Bongarten, B. C., Cregg, B. M., Dougherty, P. M., and Hennessey, T. C., 1987. Physiology and genetics of tree growth response to moisture and temperature stress: an examination of the characteristics of loblolly pine (*Pinus taeda* L.). Tree Physiol., 3:41-61.

Wang, Y.P., 1988. Crown structure, radiation absorption, photosynthesis and transpiration. Ph.D. thesis, University of Edinburgh, College of Science and Engineering, School of GeoSciences.

Waring R.H., Thies, W.G., and Muscato, D., 1980. Stem growth per unit of leaf area: a measure of tree vigor. For. Sci., 26:112-117.

Wellek, S. 2003. Testing statistical hypotheses of equivalence. Chapman and Hall/CRC. 284 p.

Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., and Smith, G.M., 2009. Mixed effects models and extensions in ecology with R. Springer, New York. 574 p.

Table 3.1. Mean (± standard error) tree dimensions, area potentially available (APA) and crown metrics for white spruce trees destructively sampled from Roussel Brook and Canton plantations 3 years after thinning. DBHs are diameter inside bark.

Plantation	Roussel Brook		Canton	
Treatment	Unthinned	Thinned	Unthinned	Thinned
n	3	12	3	12
$DBH_{before\ thin.}$ (cm)	17.2±0.3	16.6±0.6	16.0±0.6	17.7±0.6
$DBH_{after\ thin.}$ (cm)	18.5± 0.3	18.1±0.8	17.1±0.5	19.6±0.6
Height (m)	12.6± 0.2	12.8±0.3	11.5±0.2	12.3±0.2
Crown length (m)	4.4± 0.2	5.2±0.3	3.8±0.3	4.7±0.3
Crown width (m)	3.3± 0.2	3.2±0.2	3.0±0.3	3.6±0.1
Leaf area (m^2)	20.7± 3.3	26.6±4.6	16.7±2.6	33.4±4.3
APA (m^2)	5.7±0.6	7.5±0.7	6.8±1.3	10.0±1.3
$CA_{inside\ APA}/APA$[a]	0.99±0.01	0.93 ±2.9	0.96±0.03	0.92±4.1

[a] Ratio of maximum crown area inside the APA to APA.

Table 3.2. Linear mixed regression models (fixed effect coefficient ± standard error) for relative current annual volume increment (current annual volume increment (CAI) divided by the mean increment for the last 3 years before thinning) versus area potentially available (APA) and total tree leaf area for previous (Previous leaf area) or current (Current leaf area) year during 3 years after thinning for thinned and unthinned white spruce trees.

	Relative CAI by years after thinning		
	1	2	3
Previous leaf area	0.004 ± 0.002	**0.008 ±0.003**	0.005 ± 0.003
APA	0.003 ± 0.002	**0.032 ± 0.008**	**0.040 ± 0.010**
Intercept	**1.058 ± 0.061**	**0.917 ± 0.103**	**0.775 ± 0.136**
Current leaf area	**0.004 ± 0.002**	**0.007 ± 0.002**	0.005 ± 0.002
APA	0.003 ± 0.005	**0.030 ± 0.008**	**0.039 ± 0.010**
Intercept	**1.049 ± 0.057**	**0.914 ± 0.095**	**0.765 ± 0.130**

Bold font indicates parameter estimates that were significantly different from zero ($\alpha = 0.05$).

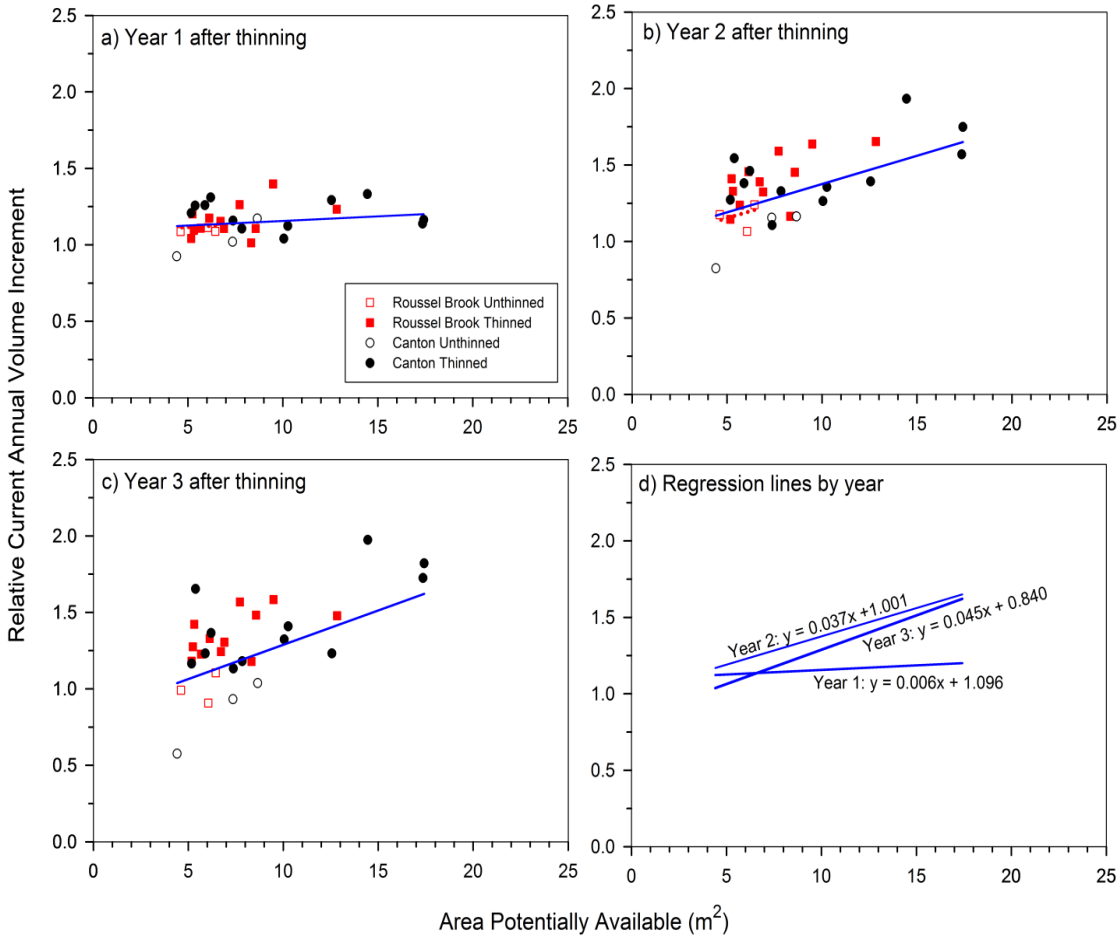

Fig. 3.1. Relationship between relative current annual volume increment (calculated as annual increment divided by the mean increment for the last 3 years before thinning (2008-2010)) and area potentially available for 30 thinned and unthinned white spruce trees in Roussel Brook and Canton plantations.

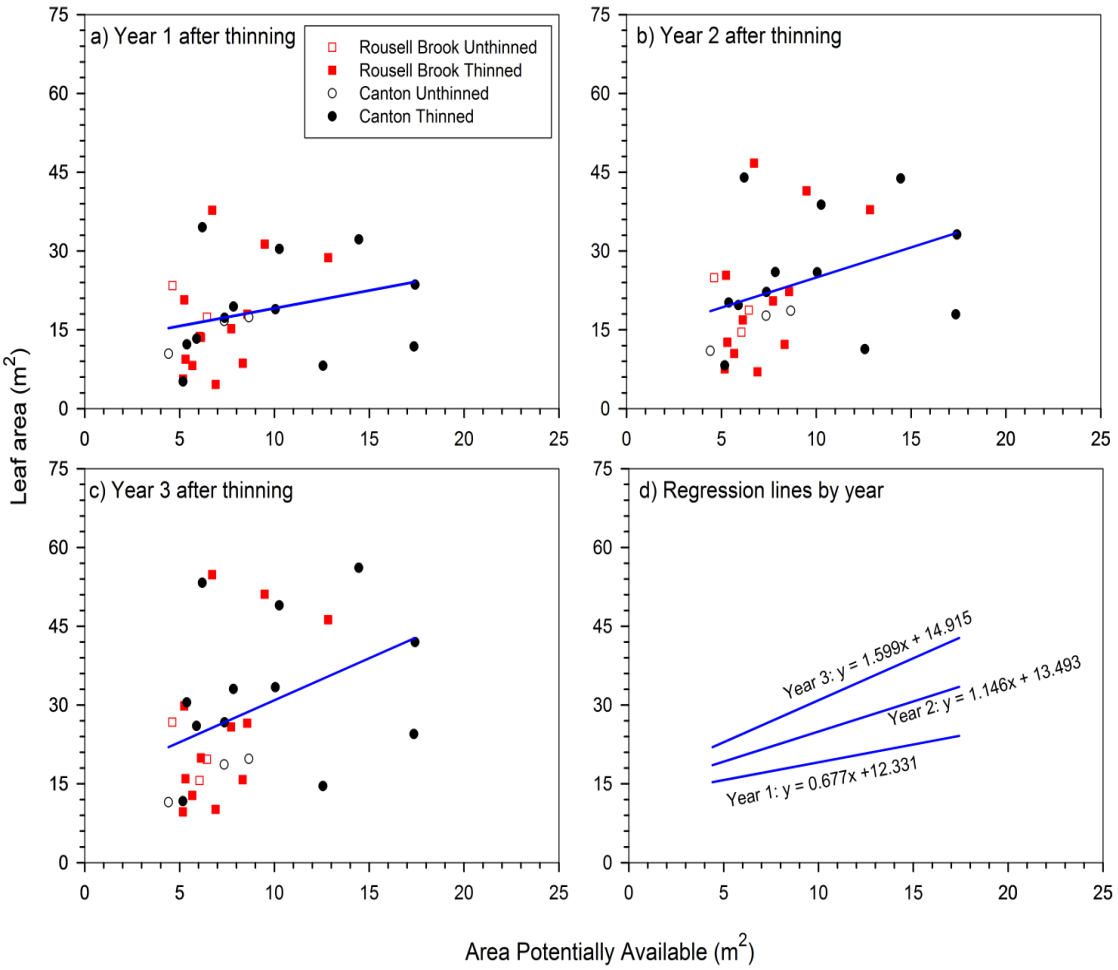

Fig. 3.2. Relationship between leaf area versus area potentially available during 3 years after thinning for 30 thinned and unthinned white spruce trees in Roussel Brook and Canton plantations.

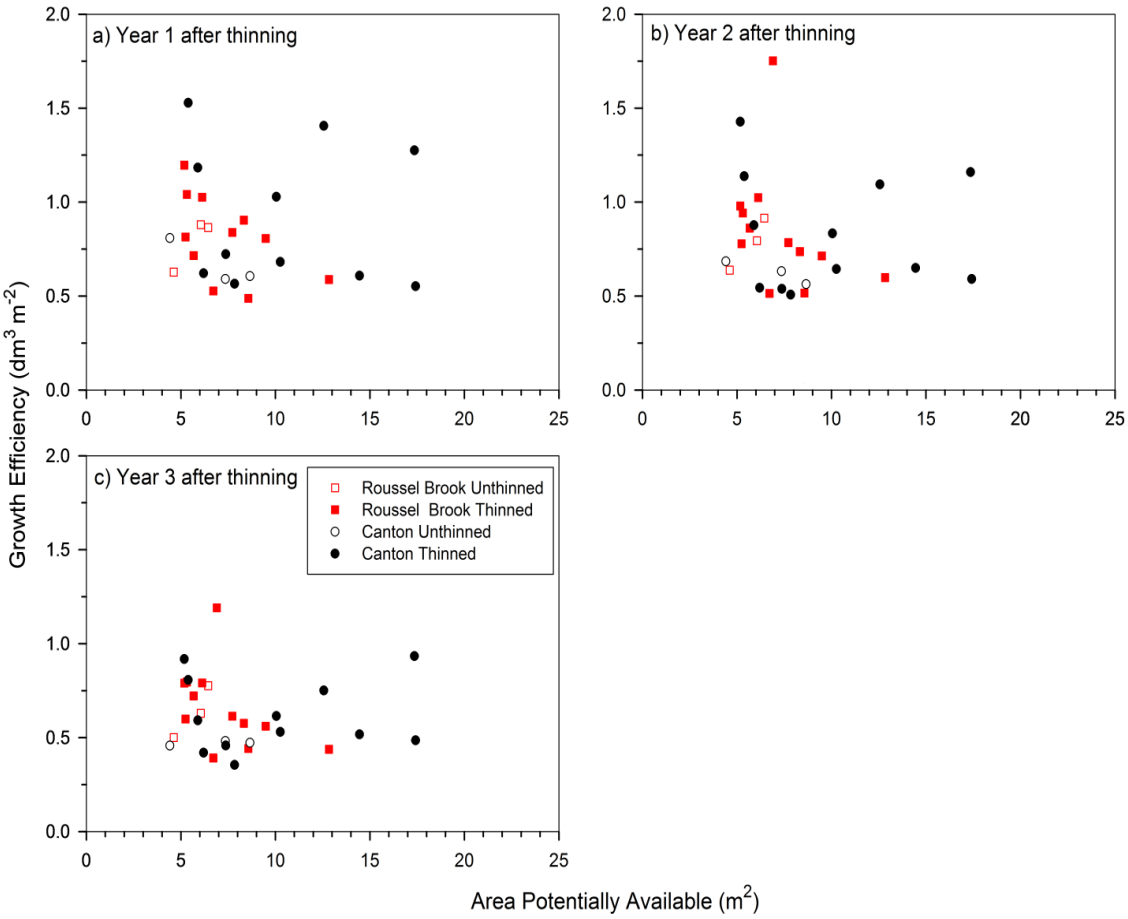

Fig. 3.3. Relationship between growth efficiency and area potentially available during 3 years after thinning for 30 thinned and unthinned white spruce trees in Roussel Brook and Canton plantations.

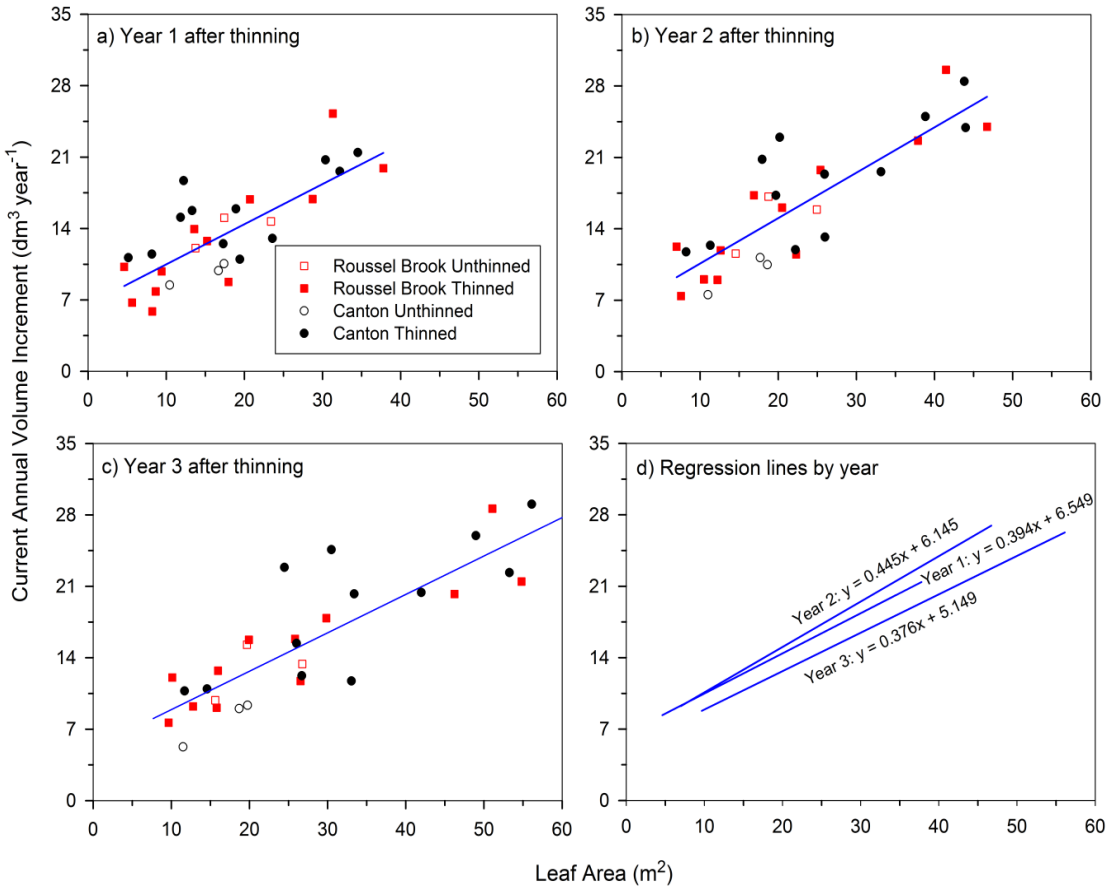

Fig. 3.4. Relationship between current annual volume increment and leaf area during 3 years after thinning for 30 thinned and unthinned white spruce trees in Roussel Brook and Canton plantations.

CHAPTER 4: EFFECT OF COMMERCIAL THINNING OF WHITE SPRUCE ON PHOTOSYNTHESIS, PHOTOSYNTHETIC EFFICIENCY AND FOLIAR NITROGEN

Paper planned for submission as:

Omari, K., MacLean, D.A., Lavigne, M.B., Kershaw, J.A. Jr., and Adams, G.W. 2016. Effect of commercial thinning of white spruce on photosynthesis, photosynthetic efficiency and foliar nitrogen. Planned for submission to Forest Ecology and Management.

4.1 Abstract

Effects of thinning on light-saturated photosynthetic rates, photosynthetic quantum efficiency (mole of CO_2 fixed per mole of incident light), and foliar nitrogen concentration were evaluated 1 and 3 years after commercial thinning of white spruce (*Picea glauca* (Moench) Voss) plantations. Objectives were to (i) determine effects of thinning on photosynthetic quantum efficiency of upper and lower crown portions of white spruce trees, and (ii) test if thinning increases photosynthetic rates and foliar nitrogen concentration of the upper and lower crown foliage. For unthinned trees, light-saturated net photosynthetic rates were greater for upper than lower crowns, and differences between upper and lower crowns were greater 1 year than 3 years after thinning. Thinned trees had higher light-saturated net photosynthetic rates in their lower crowns than unthinned trees, and after thinning, light-saturated net photosynthetic rates of new foliage in lower crowns equalled those in upper crowns. Foliar nitrogen concentration and photosynthetic quantum efficiency did not differ significantly between upper and lower crowns of thinned and unthinned trees. Crown length was 13% and 19% greater for thinned than unthinned trees 1 and 3 years after thinning. In unthinned plots, leaf area index (LAI) was 7% greater for shade than sun foliage, but 3 years after thinning, LAI of sun foliage was 1.5 times greater than for shade foliage. In thinned plots, light-saturated gross photosynthetic rate was 65% greater for sun than for shade foliage but in unthinned plots only 11% greater for sun than shade foliage. Basal area increment at the plot level was positively correlated with upper canopy (sun foliage) light-saturated gross photosynthetic rates, and increased nonlinearly with LAI. Growth response of trees in thinned stands resulted from increased crown size and greater ability

of lower crown foliage to photosynthesize in high light, particularly in the first year after thinning, and not from increases in foliar nitrogen concentration or photosynthetic quantum efficiency.

4.2 Introduction

Thinning reduces the number of trees in a stand, thereby improving supplies of light, water, and nutrients available to the residual trees (Aussenac, 2000; Zeide, 2001). Trees respond to increased growing space over time with changes in crown size, physiological behaviour, and growth (Aussenac, 2000). For example, 2 years after thinning of 8-year old loblolly pine (*Pinus taeda* L.) stands, thinned trees had 51% greater stem diameter growth and over 78 cm larger crown diameter than unthinned trees (Ginn et al., 1991). Light-saturated photosynthetic rate of thinned trees in the lower crown equalled that of the upper crown, but for unthinned trees, upper crown light-saturated photosynthetic rate was significantly greater than the lower crown (Gin et al., 1991). The increased crown size and higher physiological activity of the lower crown foliage were likely the major factors responsible for the increased growth after thinning (Ginn et al., 1991). Net photosynthetic rates increased with thinning intensity in 9- to 13-year old paper birch (*Betula papyrifera* Marsh.) stands 2 years after thinning, and this increase was attributed to increase in light and foliar nitrogen concentration (Wang et al., 1995). Thinning can increase nutrient supply per tree because of a reduction in the number of competing individuals, even if nutrient availability per unit area remains unchanged (Carlyle, 1995). Higher nutrient supply to trees could increase foliar nitrogen concentration, which can influence photosynthetic rates by altering levels of photosynthetic enzymes (Reich et al., 1994; Kozlowski and Pallardy, 1997). Thinning, however, did not affect leaf nitrogen content per unit leaf area of black walnut (*Juglans nigra* L.) trees 2 years after thinning (Gauthier and Jacobs, 2010). The contribution of foliar nitrogen concentration to growth response following thinning requires

investigation for individual species.

Thinning increases light intensity within a stand, which can increase the photosynthetic quantum efficiency (efficiency with which light is used for fixing carbon - Lambers et al., 2008) of the whole crown (Han, 2012). Photosynthetic quantum efficiency showed a greater increase over time in thinned than in unthinned black walnut trees (Gauthier and Jacobs, 2010). Light use efficiency, expressed as annual aboveground biomass or stemwood growth per unit of light intercepted, is an ecological measure related to photosynthetic quantum efficiency, and it varies among species in response to thinning. In young *Eucalyptus nitens* (Deane and Maiden) Maiden, thinning increased aboveground biomass growth of the 200 largest-diameter sawlog crop trees by 34%, increased light use efficiency by 13%, and increased rates of photosynthesis (Forrester et al., 2013). However, thinning did not affect light use efficiency of Sitka spruce (*Picea sitchensis* (Bong.) Carrière) (Wang, 1988). Knowledge of the effects of silvicultural treatments on resource availability and hence on physiology and morphology of tree crowns, can help to develop mechanistic models of the functioning of forest stands (Medhurst and Beadle, 2005). Understanding the physiological response of trees to thinning also provides a functional approach to resolve thinning problems rather than relying on manipulation of stand density alone (Aussenac, 2000).

Three years after commercial thinning of 22-30 years old white spruce plantations, trees in thinned stands had 27-42% greater basal area increment and 20-30% greater crown diameter than unthinned trees (MacLean et al., 2015). Current annual volume increment and leaf area were 65% and 60%, respectively, greater for thinned than unthinned dominant and codominant trees 3 years after thinning (Omari et al.,

2016). In the current study, we examined the same plantations evaluated by MacLean et al. (2015) and Omari et al. (2016) to elucidate mechanisms underlying the observed increase in tree growth, specifically effects on light-saturated photosynthetic rates, photosynthetic quantum efficiency, and foliar nitrogen concentration. Objectives were to (i) determine the effect of thinning on photosynthetic quantum efficiency of upper and lower crowns of spruce trees and (ii) test if thinning increases photosynthetic rates and foliar nitrogen concentration of the upper and lower crown foliage.

4.3 Materials and methods

4.3.1 Study area

The study was conducted in the Black Brook District, an intensively managed forest owned by J.D. Irving, Limited (JDI) in northern New Brunswick, Canada (47° 9′ 51″ to 67° 55′ 27″). The Black Brook District is located in the Southern Uplands Ecoregion, which is underlain by meta-sedimentary and calcareous sedimentary bedrock, and drained to the south and west by tributaries of the Saint John River (New Brunswick Department of Natural Resources and Energy (NBDNRE), 1998). Elevation ranges from 180 to 600 m, increasing from south to north.

The Black Brook District includes 85 000 ha of primarily spruce plantations. Clearcuts are generally replanted within one year of harvest, with mechanical site preparation before planting and herbicide application 1-3 years after planting, if required. Plantations are often cleaned at 10-15 years, commercially thinned at 20-40 years, and final harvesting is done between ages 35-55 years old. Further details on the

study area can be found in Omari and MacLean (2015).

4.3.2 Experimental design

Six >20 ha white spruce plantations, aged 22-30 years old, were selected for experimental commercial thinning based on having similar stand characteristics. Each plantation was divided into four blocks with a minimum size of ~ 5 ha. Blocks were commercially thinned in the fall of 2010 and winter of 2011. Three of the blocks in each plantation received 40% basal area removal commercial thinning treatments, with varying amount of deadwood left on site after thinning, and one block was unthinned. Five 0.04 ha circular permanent sample plots (PSPs) were randomly located in each treatment block.

4.3.3 Data collection

In the summer and fall of 2011, one year after thinning, three plantations, Roussel Brook, Brown Brook and Yellow Brook, were chosen and one plot selected in each of unthinned and status quo thinned (40% basal area removal with slash and tops left on the site) treatments. Three codominant trees were selected for measurements of net photosynthetic rates from each thinned and unthinned plot in each plantation, and measured for diameter at breast height (DBH), height, and crown length. One foliage-bearing twig was clipped, using pole pruners, from each of the upper and lower one-third crown sections for measurements of net photosynthetic rates. The twigs were clipped immediately before measurement, and the twig end was recut under water and

placed in a bottle of water to ensure that needles received water during gas exchange measurement. One current year shoot was measured for light-saturated net photosynthetic rates, i.e. rate of net photosynthesis at high light (photosynthetic active radiation (PAR) was 1500 μmol photons m^{-2} s^{-1}). Rates of net photosynthesis were measured using a LI-6400 (Li-Cor, Inc., Lincoln, NE, USA) and climate-controlled conifer chamber equipped with a red-blue light-emitting diode (LED) light source (model 6400-18, Li-Cor, Inc.). CO_2 entering the chamber was maintained at 400 μmol m^{-2} s^{-1} and temperature and humidity inside the chamber were maintained at constant levels during the measurement period. Photosynthetic rates were recorded when readings were stable.

Shoots were stored on ice and transported to the laboratory following gas exchange measurements. All needles were removed from the shoots, a 50-needle subsample was selected, leaf area was measured using a WinSEEDLE (Regent Instruments Inc., QC, Canada), remaining needles per shoot were counted, and fresh weight was determined. Needles were then oven dried at 60°C for at least 48 hours and weighed. Specific leaf area (leaf area per unit dry weight) per shoot was calculated by multiplying average needle area from the 50-needle sample by the total number of needles per shoot, and dividing by weight per shoot. The needles were finely ground and foliar nitrogen concentration of each shoot measured for net photosynthetic rate was determined using a Leco CNS-2000 Analyzer (Leco Corporation, St. Joseph, MI).

Gas exchange measurements were also made 3 years after thinning, in the summer and fall of 2013. One codominant tree was selected from each of the unthinned and status quo thinned treatments in all six plantations. Foliage-bearing twigs were

collected from upper and lower crown thirds, and prepared for measurement as described above. Light response curves were measured for one current year shoot, from each of the upper and lower crowns of each tree, by using the light source attached to the conifer chamber to adjust incoming PAR between 0-1800 µmol photons m^{-2} s^{-1}. Eight to 9 light levels were measured per shoot. Two to four additional trees, from each of unthinned and status quo thinned plots in four plantations (Yellow Brook, Airstrip, Canton, and Paget) were also selected and light-saturated net photosynthetic rates were measured at a PAR level of 1200 µmol photons m^{-2} s^{-1} for one current year shoot from each of the upper and lower crown sections. Light-saturated net photosynthetic rates were compared between thinned and unthinned tress and between crown sections for each of years 1 and 3 after thinning. Therefore, the different high light levels at which light-saturated net photosynthetic rates were measured for year 1 (1500 µmol photons m^{-2} s^{-1}) and year 3 (1200 µmol photons m^{-2} s^{-1}) after thinning do not affect conclusions of the study.

4.3.4 Data analysis

Tree attributes (DBH, height, crown length, basal area, and basal area increment), light-saturated net photosynthetic rates, foliar nitrogen concentration, and specific leaf area were compared between thinned and unthinned trees using a mixed model analysis of variance (ANOVA). Thinning treatment was used as the fixed factor and trees nested in plots and plots nested in plantations as random factors. Light-saturated net photosynthetic rates, foliar nitrogen concentration, and specific leaf area

were also compared between crown sections of thinned and unthinned trees in the same way, but with crown section as the fixed factor. In all statistical comparisons, means were considered significantly different at $p < 0.05$.

Light response curve parameters were estimated using nonlinear least squares regression of a nonrectangular hyperbola (Marshall and Biscoe, 1980):

$$A_{net} = \frac{\Phi PAR + A_{max} - \sqrt{(\Phi PAR + A_{max})^2 - 4\theta\Phi PAR(A_{max})}}{2\theta} - R_d \qquad (1)$$

where A_{net} and A_{max} are light-saturated net and gross photosynthetic rates, respectively, Φ is photosynthetic quantum efficiency (expressed as apparent quantum yield, i.e. mole of CO_2 fixed per mole of incident PAR), R_d is diurnal dark respiration rate and θ is curve convexity. Light compensation point (LCP) was estimated form the x-axis intercept of the light response curves. Differences in photosynthetic light response curve parameters were also compared between crown sections and thinning treatments as described above.

4.3.4.1 Canopy photosynthesis

Rates of canopy photosynthesis were estimated for 92 plots, which had ≥ 75% of basal area comprised of white spruce. Leaf area index (total leaf area per plot divided by plot area; LAI) was used to scale photosynthetic rates from shoot to canopy level (Norman, 1993). Leaf area of white spruce was predicted using a linear relationship between the natural logarithms of leaf area versus DBH derived from destructively sampled trees in the study area:

$$\text{LN(Leaf area)} = -6.335 + 3.1572\ \text{LN(DBH)} \qquad (2)$$

The back-transformed model predictions were multiplied by a correction factor

(CF=1.10921) to account for the bias when natural logarithm is back-transformed to arithmetic units. The CF was given by the following equation:

$$CF = \exp\left(\frac{\hat{\sigma}^2}{2}\right) \quad (3)$$

where $\hat{\sigma}^2$ is the sample variance of the log transformed regression model (Baskerville, 1972; Parresol, 1999). For the other species on the plots, foliage biomass was predicted using the Canadian national tree aboveground biomass equations (Lambert et al., 2005). Leaf area was calculated by multiplying the foliage biomass by specific leaf area (Bond-Lamberty et al., 2002) expressed on a projected or one-sided leaf area basis: black spruce (*Picea mariana* (Mill.) BSP) (Goudiaby et al., 2011), balsam fir (*Abies balsamea* (L.) Mill.) (Boyce, 1993), red maple (*Acer rubrum* L.) (Anderson and Ryser, 2015), sugar maple (*Acer saccharum* Marsh.) (Burton et al., 1991), trembling aspen (*Populus tremuloides* Michx.) (Bond-Lamberty et al., 2002), yellow and white birch (*Betula spp.*) and pin cherry (*Prunus pennsylvanica* L.) (Khomik et al., 2014), and willow (*Salix spp.*) (Tharakan et al., 2005).

Proportions of sun and shade foliage were used to quantify effects of thinning on gross primary production. Leaf area index for sun foliage was calculated as:

$$LAI_{sun} = [1 - \exp(-K\,LAI)] / K \quad (4)$$

where LAI_{sun} is the LAI for sun foliage and K is the extinction coefficient (Norman, 1993). An extinction coefficient of 0.5, which is used in most top-down mechanistic models (Weiskittel et al., 2011) was used. Light-saturated gross photosynthetic rates per portion of canopy were calculated for thinned and unthinned plots as the product of mean light-saturated gross photosynthetic rate for upper crown (per m^2 of foliage) ×

LAI_{sun} and mean light-saturated gross photosynthetic rate for lower crown × LAI_{shade}. Furthermore, LAI_{shade} was calculated by difference: LAI-LAI_{sun} (Norman, 1993).

Annual basal area increment at the plot level was related to upper canopy light-saturated gross photosynthetic rates. Growth efficiency (3-year plot basal area increment divided by plot leaf area) was also related to canopy-weighted light-saturated gross photosynthetic rates (proportions of plot LAI in upper and lower canopies were used to weight upper and lower crown light-saturated gross photosynthetic rates from the light response curves). A mixed effect regression model (quadratic function) was fitted to the relationship between plot basal area increment versus LAI, with plantation and treatment nested in plantation as random factors. Statistical analyses were done using *R* statistical software (R Core Team, 2015).

4.4. Results

4.4.1 Tree characteristics

Characteristics of thinned and unthinned sample trees measured for photosynthetic rates and foliar nitrogen concentration are summarized in Table 4.1. DBH and height were 15.4 cm and 10.4 m for thinned versus 13.7 cm and 10.3 m for the unthinned trees in year 1 after thinning, due in part to the removal of smaller trees through thinning. Three years after thinning, mean DBH and height were 17.3 cm and 11.7 m for thinned and 15.9 cm and 11.1 m for unthinned trees. DBH and height did not differ significantly between the thinned and unthinned trees.

4.4.2 Tree level photosynthesis, specific leaf area, and foliar nitrogen concentration

of current year foliage

One year after thinning, mean light-saturated net photosynthetic rate of current year foliage was significantly higher ($p = 0.0001$) for the upper (13.0 µmol CO_2 m^{-2} s^{-1}) compared with the lower crown foliage of unthinned trees (8.3 µmol CO_2 m^{-2} s^{-1}) (Fig. 4.1a). For thinned trees, light-saturated net photosynthetic rate did not differ significantly between the upper (13.0 µmol CO_2 m^{-2} s^{-1}) and lower (12.2 µmol CO_2 m^{-2} s^{-1}) crown foliage 1 year after thinning (Fig. 4.1b). Upper crown light-saturated net photosynthetic rate did not differ significantly between thinned and unthinned trees but the lower crown light-saturated net photosynthetic rate of thinned trees was significantly higher than that of the unthinned trees 1 year after thinning ($p = 0.0496$).

Specific leaf area of the lower crown (52.9 cm^2 g^{-1} for unthinned and 39.9 cm^2g^{-1} for thinned) was significantly higher ($p = 0.0009$ and 0.0081) than the upper crown (36.3 cm^2 g^{-1} and 34.6 cm^2 g^{-1}, respectively), 1 year after thinning, for both unthinned and thinned trees. Specific leaf area of upper and lower crowns did not differ significantly between unthinned and thinned trees. Foliar nitrogen concentration averaged 1% of the leaf dry weight for the lower and upper crowns of thinned and unthinned trees 1 year after thinning (Fig. 4.2a and b), and did not differ significantly between crown sections of thinned and unthinned trees.

Three years after thinning, patterns of light-saturated net photosynthetic rates between crown sections (Fig. 4.3) were similar to those 1 year following thinning. For unthinned trees, light-saturated net photosynthetic rate was significantly ($p = 0.0005$) greater in upper (15.4 µmol CO_2 m^{-2} s^{-1}) than in lower crowns (11.1 µmol CO_2 m^{-2} s^{-1}) (Fig. 4.3a), but photosynthetic rates of upper and lower crowns, 14.7 and 15.6 µmol CO_2

m^{-2} s^{-1}, respectively, did not differ significantly for the thinned trees (Fig. 4.3b). Light-saturated net photosynthetic rate in upper crowns did not differ significantly between thinned and unthinned trees but it was significantly higher in lower crowns of thinned than unthinned trees 3 years after thinning ($p = 0.0281$). Specific leaf area of the lower crown of unthinned trees (38.2 cm^2 g^{-1}) was significantly higher ($p = 0.0003$) than the upper crown (26.8 cm^2 g^{-1}) but for thinned trees specific leaf area of the lower and upper crowns, 31.2 and 28.5 cm^2 g^{-1}, respectively, did not differ significantly 3 years after thinning. Specific leaf area of upper and lower crowns did not differ significantly between unthinned and thinned trees.

4.4.3 Light response curves, leaf area index and plot level photosynthesis

Light response curve parameters, light-saturated gross photosynthetic rate, photosynthetic quantum efficiency, diurnal dark respiration, and light compensation point, did not differ significantly between upper and lower crowns of thinned and unthinned trees 3 years after thinning (Fig. 4.4; Table 4.2a and b).

In unthinned plots, LAI was 7% greater for shade than sun foliage. In contrast, 3 years after thinning, LAI of sun foliage was 1.5 times greater than for shade foliage (Fig. 4.5a). Consequently, plot level light-saturated gross photosynthetic rate in thinned plots, calculated as shoot-level gross photosynthetic rate multiplied by plot LAI, was 65% greater for sun than for shade foliage (30.3 versus 18.4 μmol CO_2 m^{-2} s^{-1}; $p < 0.0001$) but in unthinned plots, only 11% greater for sun than shade foliage (34.6 versus 31.3 μmol CO_2 m^{-2} s^{-1}; $p = 0.0047$). Basal area increment increased nonlinearly with LAI

(Fig. 4.5b).

Basal area increment at the plot level was positively correlated (r = 0.78) with upper canopy (sun foliage) light-saturated gross photosynthetic rate (Fig. 4.6) but growth efficiency was not related to gross photosynthetic rate (Fig. 4.7).

4.5. Discussion

4.5.1 Growth and photosynthetic rates

Thinning increases the amount of available growing space and consequently the resource supply to residual trees. Changes in resource availability influence crown processes and are ultimately reflected in changes in tree growth (Medhurst and Beadle, 2005). For the same plantations as in this study, thinned codominant and dominant trees had 60% greater leaf area and 65% greater current annual volume increment than unthinned codominant and dominant trees 3 years after thinning (Omari et al., 2016). The increased growth of thinned trees was associated with greater rates of light-saturated net photosynthesis of the lower crown foliage in comparison to similar trees in unthinned stands. Specific leaf area of upper crown foliage was similar among thinned and unthinned trees, but for lower crown foliage, it was 22-33% less for thinned than unthinned trees 1 and 3 years after thinning. Plants growing in high light generally develop thick leaves with a low specific leaf area (Björkman, 1981), which is partly due to extra layers of palisade or longer palisade cells (Hanson, 1917). This increases the number of chloroplasts and amount of photosynthetic enzymes, thereby enhancing the

photosynthetic capacity per unit leaf area (Evans and Poorter, 2001). The lower specific leaf area of lower crown foliage of thinned than unthinned trees showed that more light was reaching the lower crowns of thinned trees, and this, coupled with larger crowns, increased tree growth. This is consistent with results of Ginn et al. (1991) who reported that the increase in crown size and physiological ability of the lower crown foliage to utilize increased light following thinning (as evidenced by greater lower crown light saturated photosynthetic rates and needle conductance after thinning) were likely the major factors responsible for the increased growth of thinned loblolly pine trees. The capability of lower crown foliage to photosynthesize at high rates, if given light, allows lower crown foliage to contribute to the tree's carbon economy soon after exposure to higher light levels from thinning (Ginn et al., 1991).

We also found that plot basal area increment was positively correlated with upper canopy light-saturated gross photosynthetic rates, and increased nonlinearly with increasing LAI. As trees in thinned stands increase their crown leaf area to occupy the increased growing space (Omari et al., 2016), tree and stand growth would increase until mutual shading substantially increases, at which point photosynthetic and growth rates would be similar to those in unthinned stands. Juodvalkis et al. (2005) reported that due to extensive crown growth in thinned deciduous stands, total crown area after 4-7 years often equalled or exceeded that of unthinned controls. For loblolly pine, Peterson et al. (1997) found that during years 5 and 6 after thinning, lower crowns of thinned stands were equally shaded and exhibited gas exchange characteristics similar to those of unthinned stands.

4.5.2 Foliar nitrogen concentration and photosynthetic efficiency

Increased light could lead to preferential allocation of nitrogen to foliage in areas of high irradiance (Field, 1983; Givnish, 1988). This, however, was not found for the current study. Foliar nitrogen concentration was similar for the upper and lower crowns of thinned and unthinned trees, averaging 1% 1 year after thinning. Similar results were found in other thinning studies. For ponderosa pine (*Pinus ponderosa* Dougl. ex. Laws), nitrogen concentration of current year leaves did not differ significantly among thinning treatments, tree size classes and their interaction 1 year after thinning (Skov et al., 2004). Two years after thinning, there was still no significant difference in foliar nitrogen content between thinned and unthinned trees (Skov et al., 2004). Nitrogen content of current year foliage of thinned and unthinned loblolly pine did not differ significantly 1 or 2 years after thinning (Ginn et al., 1991). Thinned trees, however, showed a lower concentration of foliar nutrients, including nitrogen, 2 years after thinning, indicating the possibility of dilution due to the greater growth of the thinned trees (Ginn et al., 1991). Our study showed that the increased growth following thinning did not result from increased foliar nitrogen concentration, at least for the first year after thinning. The study area, Black Brook District, is underlain by fertile soils, and foliar nitrogen content after thinning may not be limiting for tree growth.

The total growth of a stand is determined largely by the combination of greater light use and higher light use efficiency of the larger trees (Binkley et al., 2013). On our study site, dominant and codominant trees in thinned plots had 65% and 60% greater current annual volume increment and leaf area, respectively, compared with unthinned trees 3 years after thinning (Omari et al., 2016). However, photosynthetic quantum

efficiency, a measure of light use efficiency, did not differ significantly between the upper and lower crown foliage of thinned and unthinned trees. Growth efficiency was also not related to light-saturated canopy-weighted gross photosynthetic rates for thinned and unthinned plots. Photosynthetic quantum efficiency did not vary with thinning for black spruce or jack pine (*Pinus banksiana* Lamb.) (Goudiaby et al., 2011), and in immature and pole-stage Norway spruce (*Picea abies* (L.) Karst), for a given tree size, light use efficiency of unthinned trees was higher than thinned trees (Gspaltl et al., 2013).

Our results showed that growth response of codominant and dominant white spruce trees to thinning was not determined by an increase in photosynthetic quantum efficiency or foliar nitrogen concentration but rather by the increase in crown size, and consequently increased light acquisition, as well as the greater ability of the lower crown to photosynthesize at high light compared to unthinned trees.

4.6 Acknowledgements

This study was funded by J.D. Irving, Limited and by Natural Sciences and Engineering Research Council of Canada (NSERC) Collaborative Research and Development Grant CRDPJ 373858-2008 to a team led by D.A. MacLean. Kwadwo Omari was funded by a NSERC Industrial Post-graduate Scholarship. We appreciate the input and assistance of staff at J.D. Irving, Limited and Gretta Goodine of Canadian Forestry Service-Atlantic Forestry Centre, towards this project.

4.7 References

Anderson, R., and Ryser, P. 2015. Early autumn senescence in red maple (*Acer rubrum L.*) is associated with high leaf anthocyanin content. Plants, 4:505-522.

Aussenac, G. 2000. Interactions between forest stands and microclimate: ecophysiological aspects and consequences for silviculture. Ann. For. Sci., 57:87-301.

Baskerville, G.L., 1972. Use of logarithmic regression in the estimation of plant biomass. Can. J. For. Res., 2:49-53.

Binkley, D., Laclau, J-P., and Sterba, H. 2013. Why one tree grows faster than another: patterns of light use and light use efficiency at the scale of individual trees and stands. For. Ecol. Manage., 288:1-4.

Björkman, O. 1981. Responses to different quantum flux densities. In Physiological Plant Ecology I. Responses to the Physical Environment (Eds. O.L. Lange, P.S. Nobel, C.B. Osmond and H. Ziegler). Encyclopedia of Plant Physiology, New Series, Vol. 12A, pp. 57–107. Springer-Verlag, Berlin.

Bond-Lamberty, B., Wang, C., Gower, S.T., and Norman, J. 2002. Leaf area dynamics of a boreal black spruce fir chronosequence. Tree Physiol., 22:993-1001.

Boyce, R.L. 1993. A comparison of red spruce and balsam fir shoot structures. Tree Physiol., 12:217-230.

Burton, A.J., Pregitzer, K.S., and Reed, D.D. 1991. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. For. Sci., 37:1041-1059.

Carlyle, J.C. 1995. Nutrient management in a *Pinus radiata* plantation after thinning: the

effect of thinning and residues on nutrient distribution, mineral nitrogen fluxes, and extractable phosphorus. Can. J. For. Res., 25:1278-1291.

Evans, J., and Poorter, H. 2001. Photosynthetic acclimation of plants to growth irradiance: the relative importance of specific leaf area and nitrogen partitioning in maximizing carbon gain. Plant, Cell, Environ., 24:755-767.

Field, C. 1983. Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. Oecologia, 56:341–347.

Forrester, D.I., Collopy, J.J., Beadle, C.L., and Baker, T.G. 2013. Effect of thinning, pruning and nitrogen fertiliser application on light interception and light-use efficiency in a young *Eucalyptus nitens* plantation. For. Ecol. Manage., 288:21-30.

Gauthier, M.-M., and Jacobs, D.F. 2010. Ecophysiological responses of black walnut (*Juglans nigra*) to plantation thinning along a vertical canopy gradient. For. Ecol. Manage., 259:867-874.

Ginn, S.E., Seiler, J.R., Cazell, B.H., and Kreh, R.E. 1991. Physiological and growth responses of eight-year-old loblolly pine stands to thinning. For. Sci., 37:1030-1040.

Givnish, T.J. 1988. Adaption to sun and shade: a whole-plant perspective. Aust. J. Plant Physiol., 15:63–92.

Goudiaby, V., Brais, S., Grenier, Y. and Berninger, F. 2011. Thinning effects on jack pine and black spruce photosynthesis in eastern boreal forests of Canada. Silva Fennica, 45:595–609.

Gspaltl, M., Bauerle, W., Binkley D., and Sterba, H. 2013. Leaf area and light use efficiency patterns of Norway spruce under different thinning regimes and age

classes. For. Ecol. Manage., 288:49-59.

Han, Q. 2012. Leaf photosynthetic responses to thinning. In Applied Photosynthesis (Ed. M.M. Najafpour). InTech, Rijeka, pp. 215-228.

Hanson, H.C. 1917. Leaf-structure as related to environment. Am. J. Bot., 4:533-560.

Juodvalkis, A., Kairiukstis, L., and Vasiliauskas, R. 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. Eur. J. For. Res., 124: 187-192.

Khomik, M., Williams, C.A., Vanderhoof, M.K., MacLean, R.G., and Dillen, S.Y. 2014. On the causes of rising gross ecosystem productivity in a regenerating clear cut environment: leaf area vs. species composition. Tree Physiol., 34:686-700.

Kozlowski, T.T., and Pallardy, S.G. 1997. Physiology of Woody Plants. Academic Press, Inc., San Diego, CA.

Lambers, H., Chapin III, F.S., and Pons, T.L. 2008. Plant Physiological Ecology. 2nd Edition. Springer, New York.

Lambert, M.-C., Ung, C.-H., and Raulier, F. 2005. Canadian national tree above ground biomass equations. Can. J. For. Res., 35:1996-2018.

MacLean, D.A., Dracup, E., Gandiaga, F., Haughian, S.R., MacKay, A., Nadeau, P., Omari, K., Adams, G., Frego, K.A., Keppie, D., Moreau, G., and Villard, M-A. 2015. Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. For. Chron., 91:161-175.

Marshall, B., and Biscoe P.V. 1980. A model for C3 leaves describing the dependence of net photosynthesis on irradiance. I. Derivation. J. Exp. Bot., 31:29-39.

Medhurst, J.L., and Beadle, C.L. 2005. Photosynthetic capacity and foliar nitrogen distribution in *Eucalyptus nitens* is altered by high-intensity thinning. Tree Physiol., 25:981-991.

NBDNRE. 1998. Ecological land classification for New Brunswick: ecoregion, ecodistrict, and ecosite levels. New Brunswick Department of Natural Resources and Energy, Fredericton, NB, Canada.

Norman, J.M. 1993. Scaling processes between leaf and canopy levels. In Scaling physiological processes: leaf to globe (Eds. J.R. Ehleringer, and C.B. Field). Academic Press, San Diego. Pp. 41-76.

Omari, K., and MacLean D.A. 2015. Do biomass removal and structure-enhancing treatments influence deadwood characteristics following commercial thinning in spruce plantations in New Brunswick, Canada? Can J. For. Res., 45:1406-1417.

Omari, K., MacLean, D.A., Lavigne, M.B., Kershaw, J.A. Jr., and Adams, G.W. 2016. Effect of local stand structure on leaf area, growth, and growth efficiency following thinning of white spruce. Ecol. Manage., 368:55-62.

Parresol, B.R. 1999. Assessing tree and stand biomass: a review with examples and critical comparisons. For. Sci., 45:573–593.

Peterson, J.A., Seiler, J.R., Nowak, J., Ginn S.E., and Kreh, R.E. 1997. Growth and physiological responses of young loblolly pine stands to thinning. For. Sci., 43: 529-534.

R Core Team, 2015. The *R* foundation for statistical computing platform: x86_64-w64-mingw32/x64 (64-bit). Version 3.2.2.

Reich, P.B., Walters, M.B., Ellsworth, D.S., and Uhl, C. 1994. Photosynthesis-nitrogen

relations in Amazonian tree species. I. Patterns among species and communities. Oecologia, 97:62-72.

Skov, K.R., Kobl, T.E., and Wallin, K.F. 2004. Tree size and drought affect ponderosa pine physiological response to thinning and burning treatments. For. Sci., 50:81-91.

Tharakan, P.J., Volk, T.A., Nowak, C.A., and Abrahamson, L.P. 2005. Morphological traits of 30 willow clones and their relationship to biomass production. Can. J. For. Res., 35:421-431.

Wang, J.R., Simard, S.W., and Kimmins, J.P. 1995. Physiological responses of paper birch to thinning in British Columbia. For. Ecol., Manage. 73:177–184.

Wang, Y.P. 1988. Crown structure, radiation absorption, photosynthesis and transpiration. Ph.D. thesis, University of Edinburgh, College of Science and Engineering, School of GeoSciences.

Weiskittel, A.R., Hann, D.W., Kershaw, J.A., and Vanclay, J.K. 2011. Forest growth and yield modelling. John Wiley and Sons, Ltd., UK.

Zeide, B. 2001. Thinning and growth. J. For., 99:20-25.

Table 4.1. Attributes (mean ± standard error) of unthinned and thinned white spruce trees measured for rates of photosynthesis and foliar nitrogen concentration, 1 and 3 years after thinning.

	1 year after thinning		3 years after thinning	
	Unthinned	Thinned	Unthinned	Thinned
DBH (cm)	13.7±0.9	15.4±0.7	16.1±0.6	17.3±0.7
Height (m)	10.3±0.5	10.4±0.2	11.1±0.2	11.7±0.3
Crown length	4.1±0.5	4.7±0.3	4.2±0.2	5.0±0.4
Basal area (cm^2)	152.7±20.1	188.5±17.4	204.8±15.5	239.7±18.8
BAI (cm^2)[a]	16.6±2.2	17.4±3.0	38.9±4.8	47.5±5.8

[a]Basal area increment (BAI) is cumulative (2010-2013) for 3 years after thinning.

Table 4.2a. Estimate ± standard error of light saturated gross photosynthetic rate (A_{max}), diurnal dark respiration rate (R_d), photosynthetic quantum efficiency (Φ), and light compensation point (LCP) from photosynthetic light response curves of 12 thinned and unthinned white spruce trees. RB, BB, YB, As, Ca and Pa represent Roussel Brook, Brown Brook, Yellow Brook, Airstrip, Canton and Paget plantations, respectively.

Planta-	Treat-	Upper Crown				Lower crown			
tion	ment	A_{max}	R_d	Φ	LCP	A_{max}	R_d	Φ	LCP
RB	Unthin	20.5±2.6	2.9±0.6	0.030±0.007	100	20.8±2.2	2.5±1.1	0.09±0.040	30
	Thin	26.8±3.4	2.7±0.6	0.046±0.012	65	26.5±1.5	2.7±0.3	0.062±0.010	50
BB	Unthin	23.7±0.9	2.0±0.55	0.053±0.006	38	18.9±0.6	1.7±0.3	0.052±0.005	34
	Thin	22.6±1.1	3.2±0.2	0.031±0.002	110	17.4±0.7	1.9±0.4	0.057±0.009	36
YB	Unthin	14.6±0.8	1.3±0.4	0.055±0.011	24	12.1±0.1	1.0±0.1	0.044±0.002	23
	Thin	20.0±0.5	1.4±0.1	0.041±0.003	36	21.3±1.2	1.2±0.4	0.042±0.005	30
As	Unthin	20.4±0.2	1.2±0.1	0.039±0.001	32	18.7±0.2	1.40±0.1	0.037±0.001	39
	Thin	19.1±0.2	1.4±0.1	0.029±0.001	51	15.3±0.2	1.0±0.1	0.036±0.002	28
Ca	Unthin	27.7±1.7	2.5±0.5	0.070±0.013	39	24.6±1.2	1.5±0.5	0.03±0.003	51
	Thin	25.0±2.8	2.3±0.6	0.060±0.019	44	15.7±1.9	0.2±1.1	0.036±0.013	6
Pa	Unthin	20.9±1.6	2.3±0.5	0.033±0.006	71	8.7±0.7	-	0.013±0.002	-
	Thin	22.7±.04	1.4±0.1	0.035±0.001	40	25.2±1.2	2.2±0.3	0.04±0.004	57

Missing values (-) could not be estimated from the data.

Table 4.2b. ANOVA of differences in shoot-level gross photosynthetic rate (A_{max}), diurnal dark respiration rate (R_d), photosynthetic quantum efficiency (Φ), and light compensation point (LCP) between upper and lower one-third crown sections for unthinned and thinned white spruce trees, and differences between unthinned and thinned trees for upper and lower crown sections.

	Differences between upper and lower crowns				Differences between unthinned and thinned			
	Unthinned		Thinned		Upper crown		Lower crown	
Factor	F_{df}-value	*P*-value	F_{df}-value	*P*-value	F_{df}-value	*P*-value	F_{df}-value	*P*-value
A_{max}	$5.012_{1,5}$	0.0753	$1.8461_{1,5}$	0.2323	$0.870_{1,5}$	0.3938	$0.907_{1,5}$	0.3846
R_d	$3.439_{1,4}$	0.1373	$1.549_{1,5}$	0.2685	$0.038_{1,5}$	0.8528	$0.300_{1,4}$	0.6133
Φ	$0.030_{1,5}$	0.8694	$0.715_{1,5}$	0.4364	$1.332_{1,5}$	0.3006	$0.033_{1,5}$	0.8622
LCP	$1.239_{1,4}$	0.3280	$3.434_{1,5}$	0.1230	$0.180_{1.5}$	0.6889	$0.020_{1,4}$	0.8949

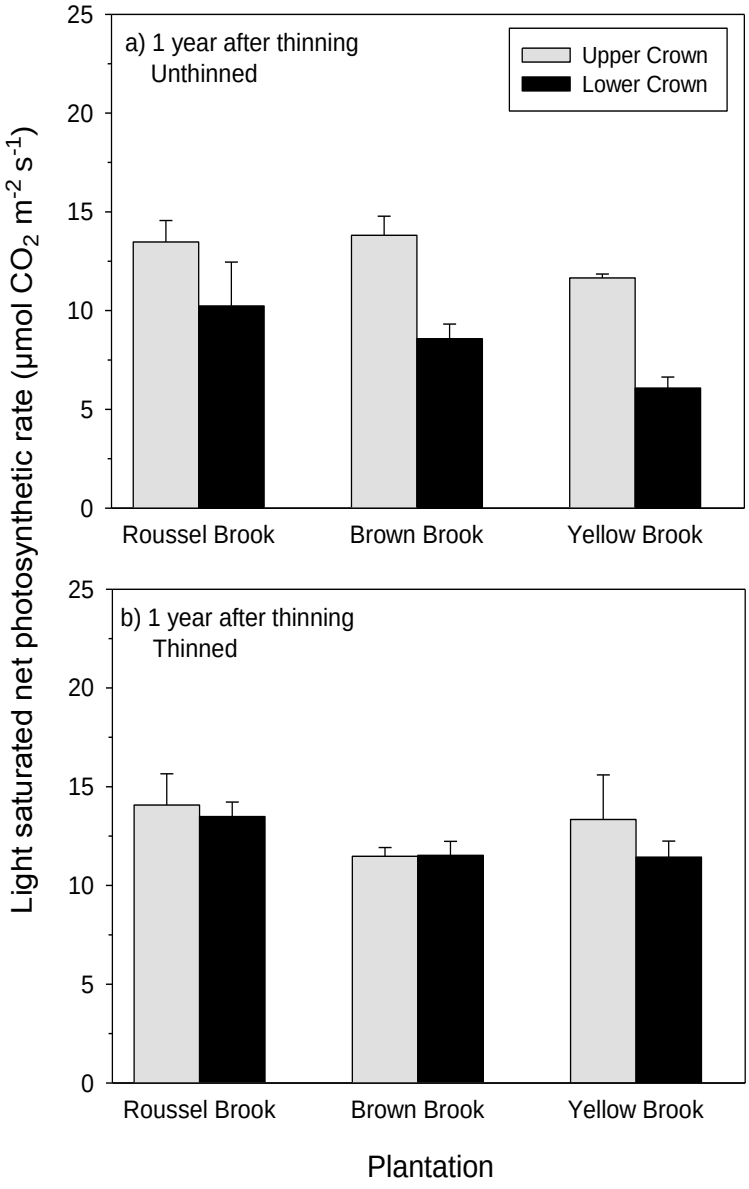

Fig. 4.1. Light-saturated net photosynthetic rates per leaf area of white spruce shoots from upper and lower crown thirds of 18 unthinned and thinned codominant trees 1 year after thinning.

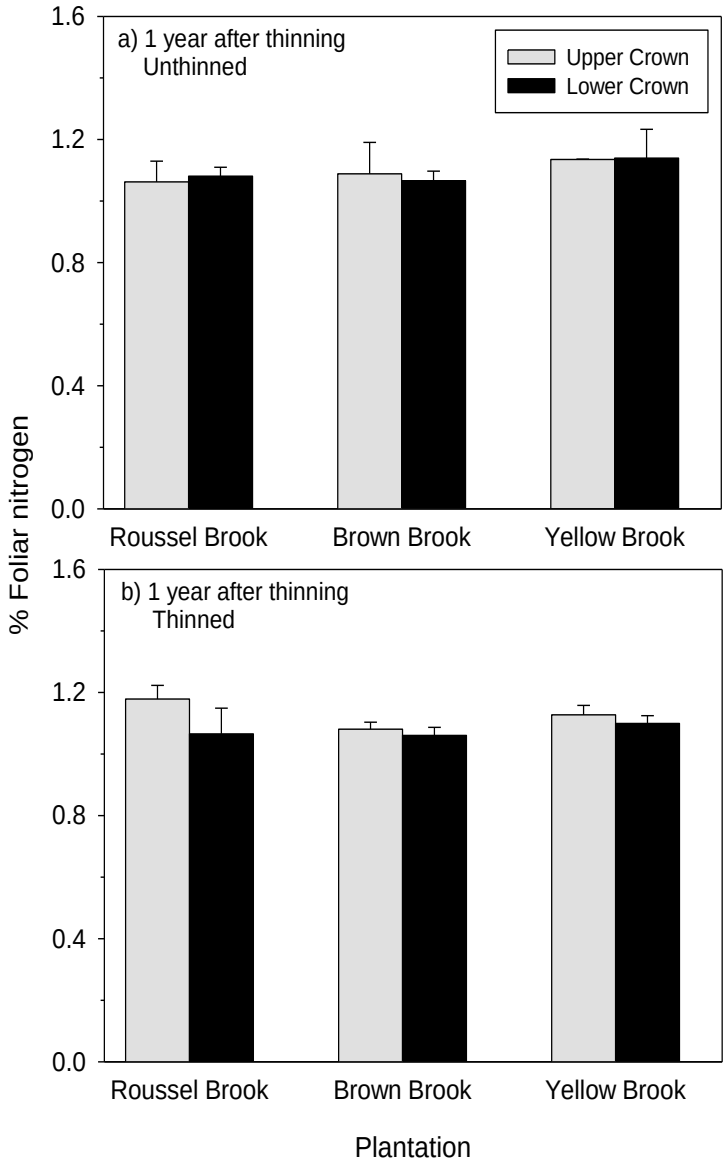

Fig. 4.2. Foliar nitrogen concentration of white spruce shoots from the upper and lower crown thirds of 18 unthinned and thinned codominant trees 1 year after thinning.

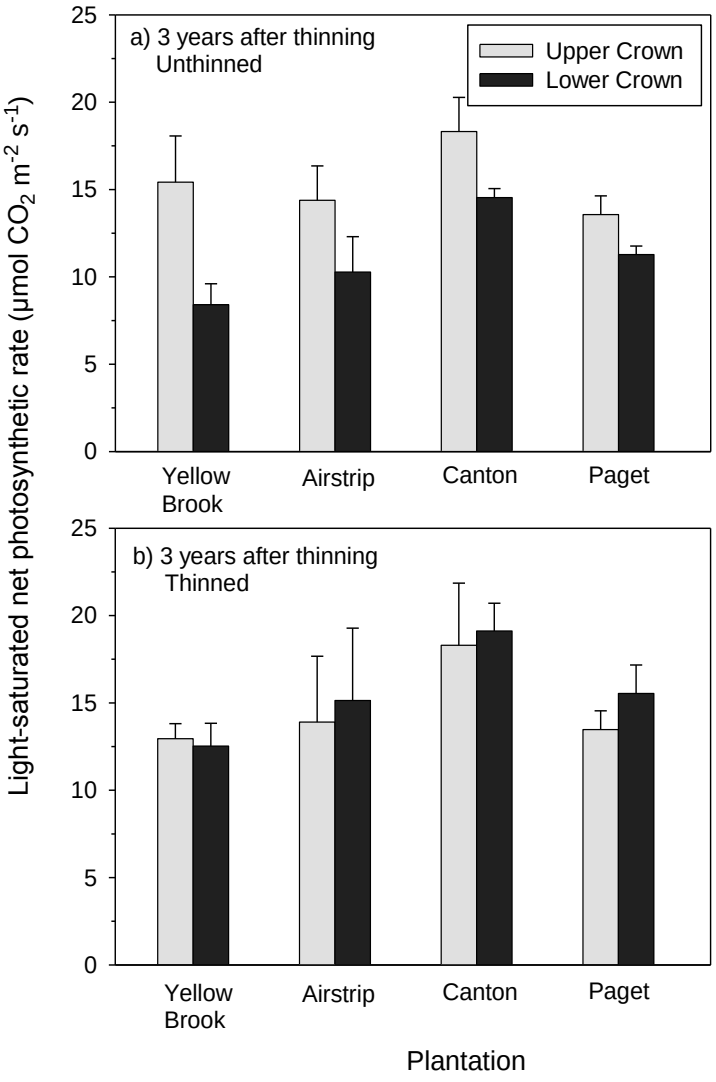

Fig. 4.3. Light-saturated net photosynthetic rates per leaf area of white spruce shoots from upper and lower crown thirds of 24 unthinned and thinned codominant trees 3 years after thinning.

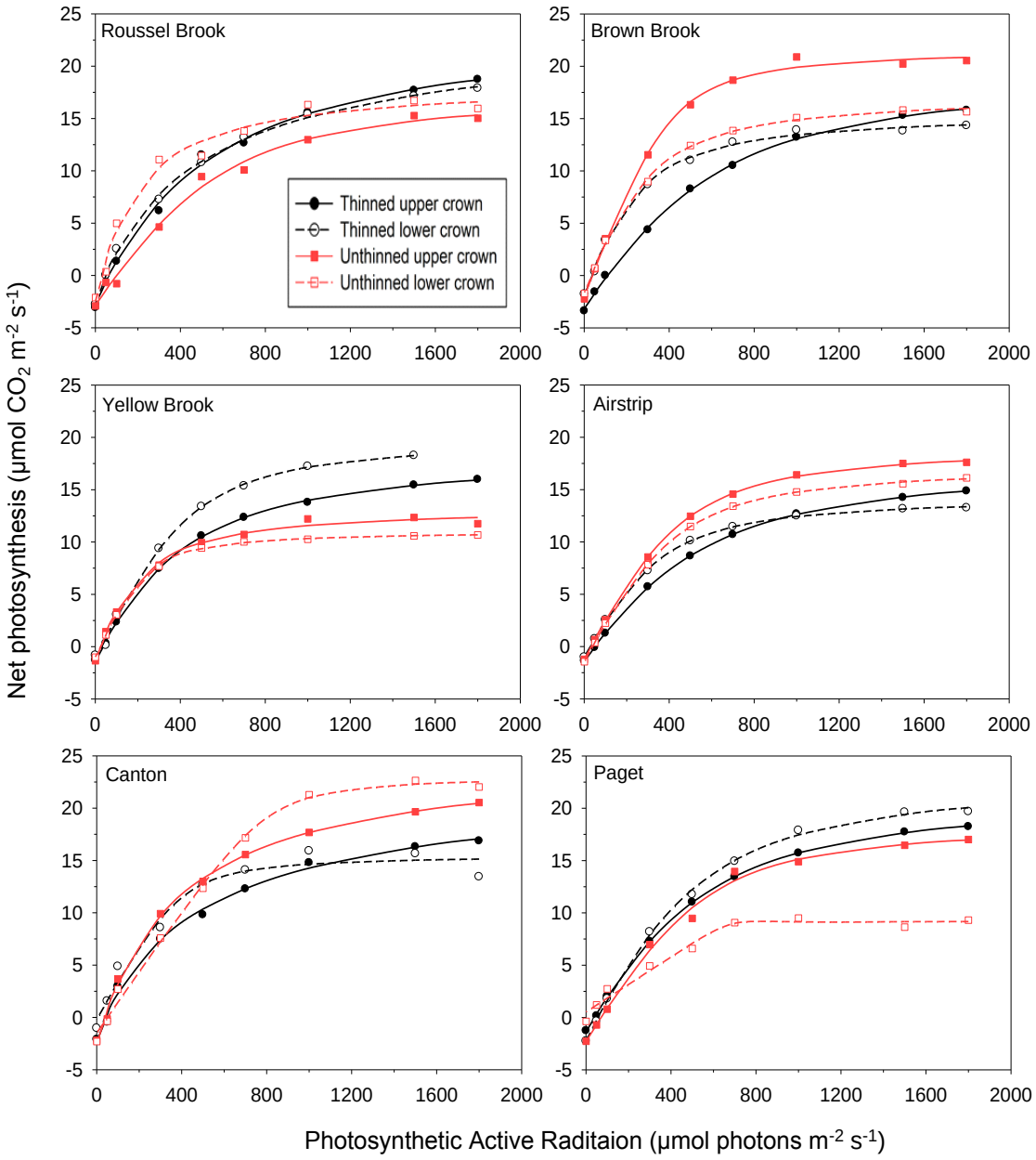

Fig. 4.4. Photosynthetic light response curves of white spruce shoots from upper and lower thirds of 12 unthinned and thinned trees 3 years after thinning. Curves were fit using a non-linear least square regression of a nonrectangular hyperbola. Photosynthetic parameter estimates are given in Table 4.2a.

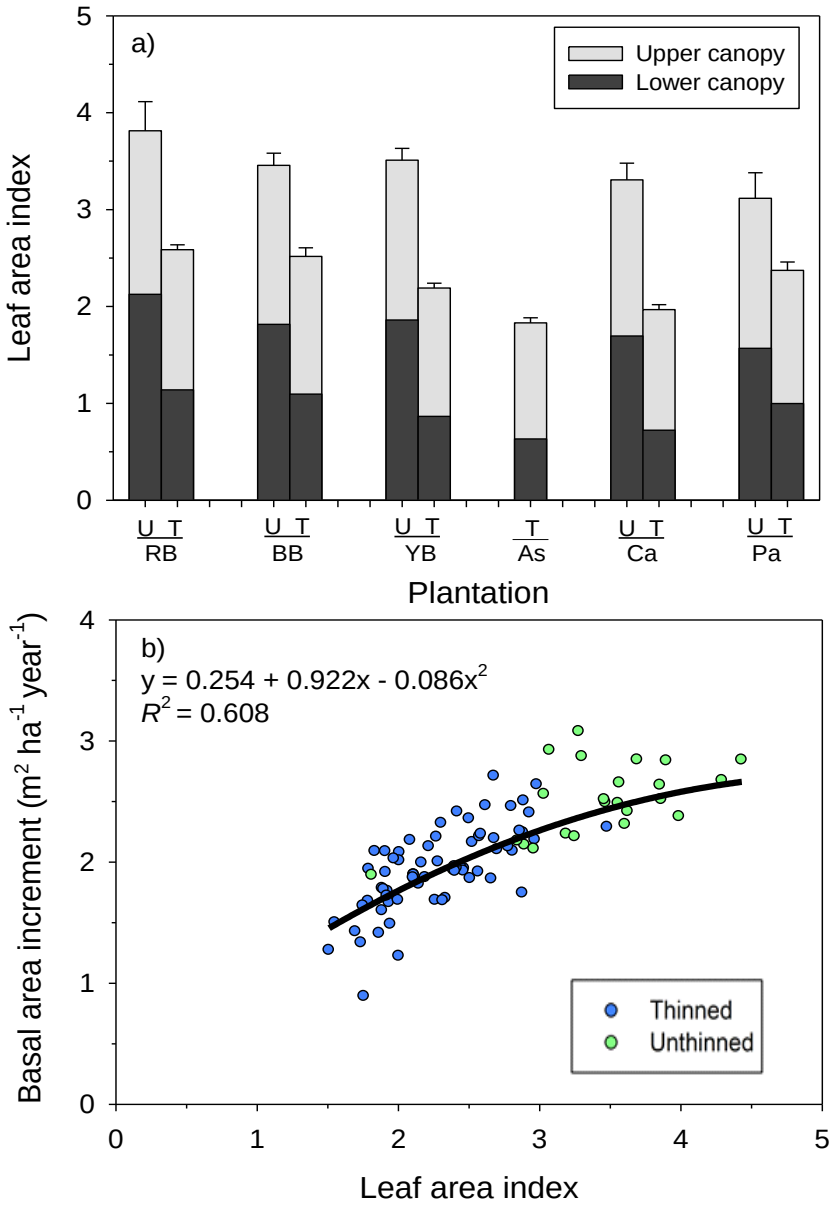

Fig. 4.5. (a) Leaf area index of upper (sun foliage) and lower (shade foliage) canopy 3 years after thinning, and (b) basal area increment versus leaf area index 3 years after thinning for 92 thinned and unthinned plots in 6 white spruce plantations. Abbreviations: U unthinned, and T thinned treatments; RB Roussel Brook, BB Brown Brook, YB Yellow Brook, As Airstrip, Ca Canton, and Pa Paget plantations.

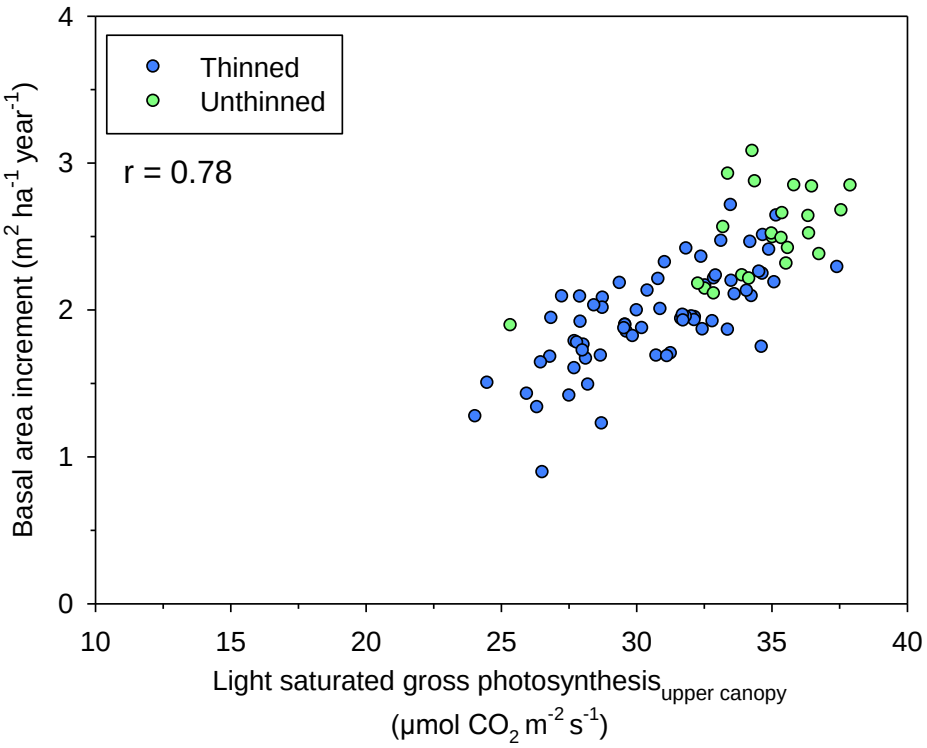

Fig. 4.6. Relationship between basal area increment and upper canopy light-saturated gross photosynthetic rates for 92 unthinned and thinned white spruce plots.

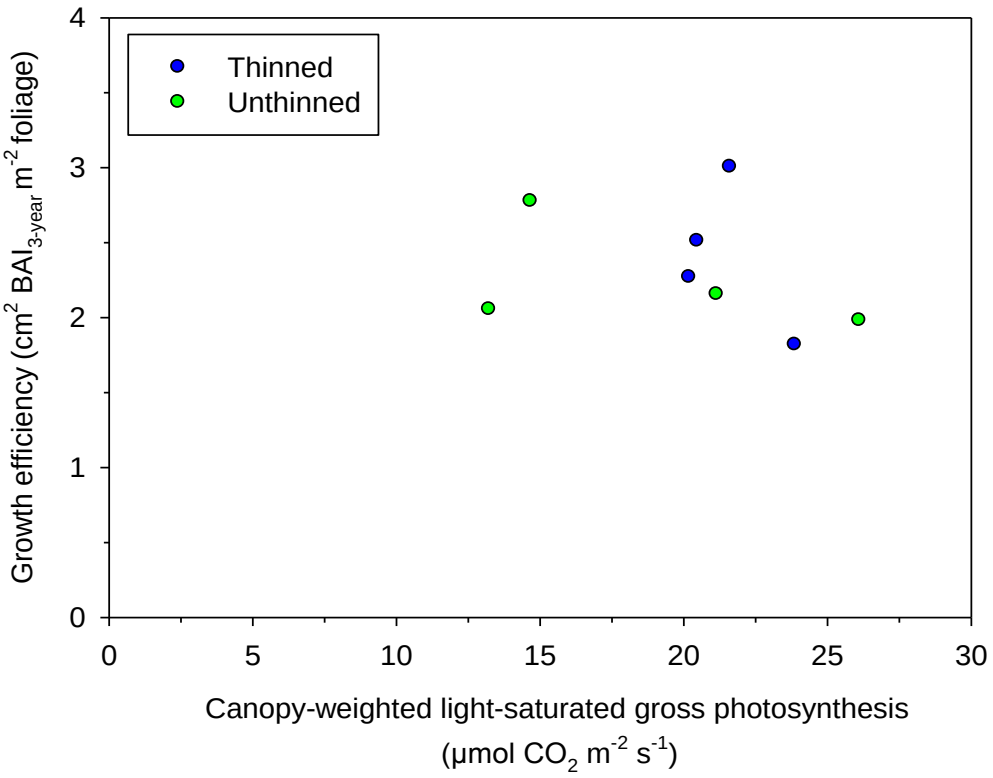

Fig. 4.7. Relationship between growth efficiency (3-year post-thinning plot basal area increment divided by leaf area) and canopy-weighted light-saturated gross photosynthetic rates for thinned and unthinned white spruce plots. White spruce plots (≥ 75% basal area comprising of white spruce) with light-response curve measurements were used.

CHAPTER 5: GENERAL DISCUSSION AND CONCLUSIONS

5.1 Introduction

Over the past decades, emphases on forest management have shifted from solely managing for wood production to include management for habitat and biodiversity (Secretariat of the Convention on Biological Diversity, 2009). There exists a growing agreement between forest managers and conservation biologists about the importance of incorporating maintenance of deadwood in forest management (Bütler et al., 2004). This thesis examined the effect of commercial thinning on both the living (live trees) and dead (CWD and snags) components of the stand structure of 22-30 years old white spruce plantations. The study provides guidelines on how management objectives relating to living (tree growth) and non-living (CWD and snag maintenance) components of stand structure can be achieved in intensively managed forests. The study also elucidates mechanisms underlying the observed increase in tree growth following thinning, which are essential to develop and improve mechanistic models to simulate tree growth response to thinning. This Chapter presents a general discussion of the results and conclusions of this study and discusses the applications and limitations.

5.2 Summary of results

5.2.1 Deadwood dynamics following thinning

Chapter 2 (Omari and MacLean, 2015) focused on effects of commercial thinning on CWD and snag dynamics. Objectives were to (i) quantify the prethinning amount of CWD and snag deadwood, and its decay status; (ii) determine effects of

commercial thinning on amount and type of deadwood; and (iii) determine effects of biomass removal and enhanced structure commercial thinning treatments on deadwood dynamics. The main findings of this study were:

- Commercial thinning produced small-diameter CWD, which were within early to intermediate stages of decay 3 years after thinning, and the new snag volume resulting from the girdling treatment (current and planned future to-be-girdled trees) increased new deadwood by up to 50% in the enhanced structure treatment. However, volume of total deadwood (CWD, snag, girdled trees, and future to-be-girdled trees) did not differ significantly between the thinned and unthinned treatments 3 years after thinning.
- Large CWD, mostly of decay class 4, which were carried over from the previous stand contributed the most to total deadwood volume in the commercially thinned stands.

The results indicated that commercial thinning produced fine debris but had little effect on overall deadwood amount.

5.2.2 Effect of local stand structure on leaf area, tree growth, and growth efficiency

Chapter 3 (Omari et al., 2016) examined influences of stand structure surrounding individual dominant and codominant trees on leaf area, tree growth, and growth efficiency. This study tested the hypothesis that individual tree volume increment and growth efficiency increase with increasing growing space (area

potentially available; APA), and also determined the relative importance of growth efficiency and leaf area to stem volume increment following thinning. The main findings of this study were:

- In the first year after thinning, trees did not expand their crowns sufficiently to take advantage of the increasing growing space made available to them through thinning. This was evidenced by the slopes not significantly different from zero in the relationship between leaf area and tree growth versus APA 1 year after thinning.
- From years 1 and 2 after thinning to year 3 after thinning, leaf area increased annually with increasing APA, resulting in a significant relationship between tree growth and APA 2 and 3 years after thinning.
- Current annual volume increment increased linearly with leaf area over the 3 years after thinning, and leaf area was positively related to APA 3 years after thinning. However, growth efficiency was not related to APA and was significantly lower in year 3 compared to year 1 after thinning ($p = 0.0178$) and compared to the prethinning growth efficiency ($p = 0.0034$).

The results showed that increasing APA through thinning increased tree growth by its positive effect on potential production capacity (leaf area) and not by any effect on growth efficiency.

5.2.3 Effect of thinning on photosynthesis, photosynthetic efficiency, and foliar

nitrogen

Three years after commercial thinning of 22-30 years old white spruce plantations, thinned trees had 27-42% greater basal area increment and 20-30% greater crown diameter than unthinned trees (Appendix 1; MacLean et al., 2015). Chapter 4 examined the mechanisms underlying this observed increase in tree growth, by determining effects of thinning on light-saturated photosynthetic rates, photosynthetic quantum efficiency, and foliar nitrogen concentration. The main findings of the study were:

- Light-saturated net photosynthetic rates in the lower crowns of thinned trees were similar to those in the upper crowns of thinned and unthinned trees. Light-saturated net photosynthetic rates were significantly less in the lower crown of unthinned trees than in the upper crowns.
- Foliar nitrogen concentration and photosynthetic quantum efficiency did not differ significantly between the upper and lower crowns of thinned and unthinned trees.
- Basal area increment at the plot level increased nonlinearly with leaf area index, and was positively correlated with upper canopy (sun foliage) light-saturated gross photosynthetic rates. Growth efficiency was not related to canopy-weighted light-saturated gross photosynthetic rates.

The results indicated that growth response of trees in the thinned stands resulted from increased crown size and the greater ability of the lower crown foliage to photosynthesize at high light, and not from increases in foliar nitrogen concentration,

growth efficiency, or photosynthetic quantum efficiency compared to unthinned trees.

5.3 Applications of study results

5.3.1 Commercial thinning and deadwood maintenance

A component of sustainable forest management is biodiversity conservation, which is included in international agreements and in the certification of forest operations (Brockerhoff et al., 2001). The combination of both wood production and biodiversity conservation remains a challenge for plantation forestry (Spellerberg and Sawyer, 1996). Omari and MacLean (2015; this thesis, Chapter 2) showed that commercial thinning did not have an overall effect on total deadwood volume. Commercial thinning does produce fine woody debris, and small mammal species responded both positively (red-backed voles) and negatively (woodland jumping mice) to thinning treatments, but areas dominated by plantations had negative effects on voles (MacLean et al. 2015; Dracup et al. 2015). Girdling trees during commercial thinning, at intensities similar to the one used in this study (11-12 clumps of unthinned trees in an area ≥5 ha in each of 6 plantations, with 10 trees (mean DBH 14 cm) per clump, and one-half of the trees in each clump girdled), is unlikely to produce sufficient snags for all deadwood-requiring wildlife. Girdling larger or more trees would increase overall deadwood volume but in young plantations this will not produce large-sized deadwood. These results indicate that incorporation of ecological forestry principles (Franklin et al., 2007) in intensively managed forests will provide the best strategy to enhance biodiversity values. Leaving

trees, either current snags or live trees to produce future snags, during the harvest preceding plantation establishment would be a feasible means to ensure retention of sufficient large-diameter snags. This will provide habitat for cavity-nesting wildlife species and a near future supply of large CWD on the forest floor (McCarthy and Bailey, 1994) as habitats for cryptogams (Fraver et al., 2002), small mammals (Fauteux et al., 2012), and other saproxylic organisms.

Leaving large trees to die, to become future snags or CWD, will lead to timber production losses. This would be counterproductive to the increased tree value (tree growth and form, and economic value) achieved through thinning. However, such production costs incurred from deadwood maintenance could be recovered through forest certification programs, for example by the Forest Stewardship Council. Trees which are certified as coming from sustainably managed forests, where at least threshold amounts of deadwood are maintained in the forests, can benefit from price premiums and a wider access to market (de Camino and Alfaro, 1998).

5.3.2 Influence of growing space on post-thinning tree growth

The substantial contribution of dominant trees to stand growth (Waring et al., 1980; Binkley et al., 2010) should spur further work on thinning to increase growth and lengthen rotations for dominant trees (Binkley et al., 2010). A major question remains about how much space dominant trees need (Binkley et al., 2013). Omari et al. (2016; this thesis, Chapter 3) explored relationships between volume increment and growth efficiency versus growing space (APA). For dominant and codominant white spruce

trees, growth efficiency was unrelated to APA but tree growth increased linearly with increasing APA. The relationship developed between tree growth and APA (Fig. 3.1) could be used by forest managers to determine how much growth could be expected from dominant or codominant white spruce trees in the short-term by thinning them to a particular stand structure. For example, at a planting spacing of 1.8 m × 1.8 m in the study plantations, a subject tree with all of its immediate 8 surrounding trees present had an APA of 3.2 m^2 (Fig. 5.1a; Table 5.1) and an increase in volume increment of 12% after 2 years of growth (Fig. 3.1). In contrast, if all 8 surrounding trees were removed, the APA would increase to 11.9 m^2 and volume increment after 2 years of growth would increase by 44%. A tree adjacent to an extraction trail, 3.6 m wide (Fig. 5.1b), has APA of 4.9 m^2 and an 18% increase in volume increment 2 years after thinning. Positions of the immediate surrounding trees removed, relative to the subject tree, also affect the amount of available growing space and consequently tree growth. Tree removals in the cardinal directions (i.e., 0º, 90º, 180º, 270º) around a subject tree result in higher APA and growth than removing the same number of immediate surrounding trees in the diagonal directions (i.e. 45º, 135º, 225º, 315º) of the subject tree (Table 5.1). For example, removing four trees in the cardinal directions around a subject tree resulted in APA 6.5 m^2 and a 15% increase in volume increment, compared to an unthinned tree, 3 years after thinning. In contrast, removing four trees in the diagonal directions around the subject tree resulted in APA 4.5 m^2 and 6% increase in volume increment (Table 5.1 and Fig. 5.1a). Removing two immediate surrounding trees in cardinal directions around a subject tree adjacent to an extraction trail resulted in APA 8.5 m^2 and 24% increase in

volume increment, compared to an unthinned tree, 3 years after thinning, which was greater than the resulting APA (7.1 m^2) and 18% increase in volume increment when 1 tree in a cardinal direction plus 2 trees in diagonal directions were removed (Table 5.1; Fig. 5.1b). These results can help forest managers to understand effects of alternative thinning prescriptions on resulting growing space and expected growth increment needed to fulfill management objectives. Table 5.1 can also help to explore effects of alternative trail widths and removal intensities in between trails.

5.3.3 Application of mechanism of growth response following thinning in epsilon growth models

Empirically based growth and yield models have been calibrated and used for stand growth simulations. However as stand management intensifies and environmental conditions alter as result of climate change, empirically based growth and yield models may become less useful for scenario analyses and projection of probable forest growth (Landsberg et al., 2001). Detailed process-based models need to be simplified to generate growth relationships, soundly based on biophysical processes yet accessible to practitioners and scientists (Landsberg and Waring, 1997). Such models include light-use efficiency models (epsilon growth models), e.g. the StandLeap bioclimatic model (Girardin et al., 2008) and 3-PG model (Landsberg and Waring, 1997). These models predict gross primary production from absorbed photosynthetically active radiation and a radiation use efficiency coefficient.

Improvement of epsilon growth models to simulate forest growth and yield following thinning would require that the mechanisms of growth response to thinning be accurately represented in the models. In this study, it was shown that individual tree growth efficiency did not differ significantly between thinned and unthinned trees, and was unrelated to the amount of available growing space to each tree (Omari et al., 2016; this thesis, Chapter 3). Similarly, photosynthetic quantum efficiency was not significantly different between the upper and lower canopies of thinned and unthinned trees (Chapter 4). Tree growth after thinning was driven by an increase in leaf area, and consequently increased light absorption (Omari et al., 2016; this thesis, Chapter 3), and higher photosynthetic rates of new foliage in lower crowns of thinned trees (Chapter 4). Stand growth was also positively correlated with sun-foliage photosynthetic rates, and increased with increasing stand leaf area following thinning, but stand growth efficiency was not related to canopy-weighted photosynthetic rates (Chapter 4). These results show that when simulating white spruce growth response to thinning in epsilon growth models, using individual tree-level resource use efficiency to account for changes in growing space after thinning will not result in more accurate growth predictions. Changes in leaf area (or absorbed photosynthetic active radiation) at the tree and stand level following thinning must be accurately accounted for in the model, as tree and stand growth increased with increasing leaf area following thinning.

As the slope of the relationship between leaf area versus growing space increased from 0.68 ± 0.49 (slope ± standard error) in year 1 to 1.60 ± 0.73 in year 3 after thinning, growth efficiency 3 years after thinning was significantly less than 1 year after

thinning and the prethinning growth efficiency (Omari et al., 2016; this thesis, Chapter 3). Therefore, modifiers that modulate changes in resource use efficiency over time in epsilon growth models should account for the decrease in resource use-efficiency as leaf area increases following thinning. This will help improve these models to explain and predict growth response to thinning.

5.4 Limitations of the study

This study determined changes in growth, as well as morphology and physiology of tree crowns in the short term, i.e., up to 3 years following thinning. Generalizations of results beyond the 3 post-thinning years considered in this study are difficult. For example, Ginn et al. (1991) found that in 8 years old loblolly pine, thinning increased light-saturated photosynthetic rates of the lower crown to the level of the upper crown foliage 2 years after thinning. However in the same plantations during years 5 and 6 after thinning, measured light levels showed that the lower crowns of thinned stands were equally shaded and exhibited photosynthetic rates similar to those of unthinned stands (Peterson et al., 1997). In the current study, lower crown light-saturated net photosynthetic rates of thinned trees equalled that of the upper crown in the first and third years after thinning (Chapter 4). However, this trend can be expected to change over time as trees expand their crowns to utilize the increased growing space made available to them through thinning, resulting in lower crown shading. Changes in photosynthetic rates beyond 3 years after thinning of white spruce should be measured to

allow for accurate simulation of long term photosynthetic rates and growth response to thinning in epsilon growth models.

A tree's efficiency is a dynamic function that results from interactions among trees and probably varies over time (Gspaltl et al., 2012). We found that growth efficiency showed no apparent linear trend with growing space for the first 3 years after thinning (Omari et al., 2016; this thesis Chapter, 3). The relationship between resource use efficiency and growing space over a longer term should be tested empirically to determine if both the long and short term trends are similar. This would provide a more comprehensive understanding of changes in resource use efficiency in response to thinning and would help to improve epsilon growth models to simulate long term growth response to thinning.

5.5 References

Binkley, D., Laclau, J-P., and Sterba, H. 2013. Why one tree grows faster than another: patterns of light use and light use efficiency at the scale of individual trees and stands. For. Ecol. Manage., 288:1-4.

Binkley, D., Stape, J.L., Bauerle, W.L., and Ryan, M.G. 2010. Explaining growth of individual trees: light interception and efficiency of light use by *Eucalyptus* at four sites in Brazil. For. Ecol. Manage., 259:1704-1713.

Brockerhoff, E.G., Ecroyd, C.E., and Langer, E.R. 2001. Biodiversity in New Zealand plantation forests: policy trends, incentives, and the state of our knowledge. New

Zeal. J. For., 46:31-37.

Bütler, R., Angelstam, P., and Schlaepfer, R. 2004. Quantitative snag targets for the three-toed woddpecker *Picoides tridactylus*. Ecol. Bull., 51:219-232.

de Camino, R., and Alfaro, M. 1998. Certification in Latin America: experience to date. Rural Development Forestry Network, Paper 23c.

Dracup, E.C., Keppie, D.M., and Forbes, G.J. 2015. Woodland mouse and vole response to increased structural diversity following midrotation commercial thinning in spruce plantations. Can. J. For. Res., 45:1121-1131.

Fauteux, D., Imbeau, L., Drapeau, P., Mazerolle, M.J. 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. For. Ecol. Manage., 266:194-205.

Franklin, J.F., Mitchell, R.J., and Palik, B.J. 2007. Natural disturbance and stand development principles for ecological forestry. USDA For. Serv. Gen. Tech. Rep. NRS-19.

Fraver, S., Wagner, R.G., and Day, M. 2002. Dynamics of coarse woody debris following gap harvesting in the Acadian forest of central Maine, U.S.A. Can. J. For. Res., 32:2094-2105.

Ginn, S.E., Seiler, J.R., Cazell, B.H., and Kreh, R.E. 1991. Physiological and growth responses of eight-year-old loblolly pine stands to thinning. For. Sci., 37:1030-1040.

Girardin, M.P., Raulier, F., Bernier, P.Y., and Tardif, J.C. 2008. Response of tree growth to a changing climate in boreal central Canada: A comparison of empirical,

process-based, and hybrid modeling approaches. Ecol. Model., 213:209-228.

Gspaltl, M., Sterba, H., and O'Hara, K.L. 2012. The relationship between available area efficiency and area exploitation index in an even-aged coast redwood (*Sequoia sempervierns*) stand. Forestry, 85:567-577.

Landsberg, J.J., and Waring, R.H. 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and portioning. For. Ecol. Manage., 95:209-228.

Landsberg, J.J., Johnsen, K.H, Albaugh, T.J., Allen, L.H., and McKeand, S.E. 2001. Applying 3-PG, a simple process-based model designed to produce practical results, to data from loblolly pine experiments. For. Sci., 47:43-51.

MacLean, D.A., Dracup, E., Gandiaga, F., Haughian, S.R., MacKay, A., Nadeau, P., Omari, K., Adams, G., Frego, K.A., Keppie, D., Moreau, G., and Villard, M-A. 2015. Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. For. Chron., 91:161-175.

McCarthy, B.C., and Bailey, R.R. 1994. Distribution and abundance of coarse woody debris in managed forest landscape in the central Appalachians. Can. J. For. Res., 24:1317-1329.

Omari, K., and MacLean D.A. 2015. Do biomass removal and structure-enhancing treatments influence deadwood characteristics following commercial thinning in spruce plantations in New Brunswick, Canada? Can J. For. Res., 45:1407-1418.

Omari, K., MacLean, D.A., Lavigne, M.B., Kershaw, J.A. Jr., and Adams, G.W. 2016.

Effect of local stand structure on leaf area, growth, and growth efficiency following thinning of white spruce. For. Ecol. Manage., 368:55-62.

Peterson, J.A., Seiler, J.R., Nowak, J., Ginn, S.E., and Kreh, R.E. 1997. Growth and physiological responses of young loblolly pine stands to thinning. For. Sci., 43:529-534.

Secretariat of the Convention on Biological Diversity. 2009. Sustainable forest management, biodiversity and livelihoods: a good practice guide. Montreal, 47p.

Spellerberg, I.F., and Sawyer, J.W.D. 1996. Standards for biodiversity: a proposal based on biodiversity standards for forest plantations. Biodivers. Conserv., 5:447–459.

Waring, R.H., Thies, W.G., and Muscato, D. 1980. Stem growth per unit of leaf area: a measure of tree vigor. For. Sci., 26:112-117.

Table 5.1. Area potentially available (APA) and percent difference in increase in volume increment from an unthinned tree for each year after thinning, for a subject dominant or codominant tree in the study plantations by number and position of its immediate surrounding trees removed. Tree removals are based on Fig. 5.1; diagonals and cardinals represent immediate surrounding trees in the diagonal or cardinal directions of the subject tree.

Tree removal			Increment above unthinned (%)[2]		
Number[1]	Position	APA (m^2)	Year 1	Year 2	Year 3
	Away from extraction trail				
1	1 cardinal	4.1	0.5	3.3	4.1
2	1 diagonal, 1 cardinal	4.5	0.8	4.8	5.9
	2 cardinals	4.9	1.0	6.3	7.7
3	3 diagonals	4.5	0.8	4.8	5.9
	2 diagonals, 1 cardinal	4.9	1.0	6.3	7.7
	1 diagonal, 2 cardinals	5.3	1.3	7.8	9.5
	3 cardinals	5.8	1.6	9.6	11.7
4	4 diagonals	4.5	0.8	4.8	5.9
	2 diagonals, 2 cardinals	5.7	1.5	9.3	11.3
	4 cardinals	6.5	2.0	12.2	14.9
	Beside extraction trail				
1	1 diagonal	4.9	1.0	6.3	7.7
	1 cardinal	6.7	2.1	13.0	15.8
2	2 diagonals	4.9	1.0	6.3	7.7
	1 diagonal, 1 cardinal	7.1	2.3	14.4	17.6
	2 cardinals	8.5	3.2	19.6	23.9
3	2 diagonals, 1 cardinal	7.1	2.3	14.4	17.6
	1 diagonal, 2 cardinals	8.8	3.4	20.7	25.2
	3 cardinals	9.3	3.7	22.6	27.5
4	2 diagonals, 2 cardinals	9.3	3.7	22.6	27.5
	1 diagonal, 3 cardinals	10.7	4.5	27.8	33.8

[1] Number of trees around the subject trees that were removed in the thinning.
[2] Percent volume increment above unthinned represents the percent difference between thinned and unthinned dominant or codominant trees in increase in volume increment. Increase in volume increment was calculated by substituting APA for each tree removal scenario in the equations given in Fig. 3.1d for each year after thinning. Removing 1 or 2 immediate surrounding trees in the diagonal directions of a subject tree away from an extraction trail gives the same APA (3.2 m^2) as an unthinned tree, and are therefore not shown in the Table.

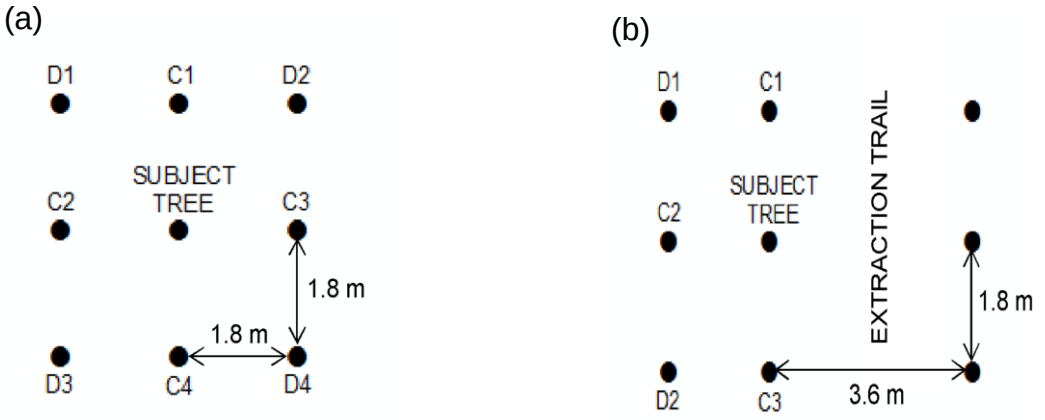

Fig. 5.1. Diagrammatic representation of planting spacing in the study plantations for a subject tree (a) away from or (b) adjacent to an extraction trail. The area potentially available to the subject tree by number and position (C and D represent trees in cardinal or diagonal directions) of its immediate surrounding trees removed is shown in Table 5.1.

APPENDIX 1: EXPERIMENTAL MANIPULATION OF HABITAT STRUCTURES IN INTENSIVELY MANAGED SPRUCE PLANTATIONS TO INCREASE THEIR VALUE FOR BIODIVERSITY CONSERVATION

Paper published as:

MacLean, D.A., Dracup, E., Gandiaga, F., Haughian, S.R., MacKay, A., Nadeau, P., Omari, K., Adams, G., Frego, K.A., Keppie, D., Moreau, G., and Villard, M-A., 2015. Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. For. Chron., 91:161-175.

Abstract

Six intensively managed white spruce (*Picea glauca* (Moench) Voss) plantations located in three general landscape contexts (plantation dominated, hardwood dominated, and mixed hardwood and plantation) in northern New Brunswick underwent alternative commercial thinning (CT) treatments: (1) an unthinned control; and three 40% basal area CT removals, with (2) slash and tops remaining on site (status quo CT), (3) branches and tops extracted from the site (biomass removal CT), and (4) clumps of unthinned trees left, and one-half girdled to create snags (enhanced structure CT). We examined responses of taxa that have a clear connection to deadwood and thinning response: beetles and bird species that are directly dependent upon deadwood, ground vegetation species sensitive to disturbance, and small mammal species that have been observed to have low density in planted stands. Results 3 years post-thinning showed that crown width and tree growth responded positively to CT, and herbaceous vegetation diverged from reference stands and unthinned treatments with CT, but greatest compositional change was associated with biomass removal CT. Beetles responded positively to the CT, small mammal species responded both positively (red-backed voles) and negatively (woodland jumping mice) to CT, but areas dominated by plantations had negative effects on voles. Effects of CT on songbirds were unclear and their quantification would require larger treated blocks, but maintenance of habitat at the landscape level is essential for the conservation of bird species that require deadwood. The experimental biomass removal CT was least similar to both unthinned and older unmanaged stands, and may therefore be detrimental to biodiversity conservation efforts. These results are only the initial 3 years after treatment but set the study up to

permit a long-term legacy of determining long-term responses of taxa over stand development.

Introduction

At least part of Canada's forest will continue the intensification of forest management over the next decades through plantation forestry. A key criticism of plantations is that planted stands are 'sanitized', which reduces structural diversity, species diversity, and volumes of downed and standing deadwood. Concerns are typically most focused on paucity of deadwood and reduced species diversity in the overstory. This research determined the influence of key habitat structures, early in the rotation of planted stands, on animal and plant taxa, and how their improved management can be better incorporated into the overall forest management strategy. We focussed on taxa that have strong connections to deadwood and thinning response, namely invertebrates and birds that are dependent upon deadwood, ground vegetation sensitive to disturbance, and small mammals that have low densities in planted stands (Ramovs and Roberts, 2003; 2005). We experimentally manipulated habitat structure during commercial thinning (CT) treatments in six white spruce (*Picea glauca* (Moench) Voss) plantations, and determined influence and effects of landscape context around sample plantations on selected taxa.

White spruce is an ecologically and economically important species with over 114 000 ha of spruce planted in Canada in 2012 (Canadian Council of Forest Ministers, 2014). CT of plantations occurs when size of thinned trees permits conversion to useable wood products to increase commercial productivity (Nyland, 2002; Pelletier and Pitt, 2008). To contribute to biodiversity conservation while procuring renewable timber (Vincent et al., 2009), traditional silvicultural practices which focus primarily on wood

production may need to be modified.

The ecological contribution of plantations to biodiversity objectives at the landscape scale is not well understood, but is an important topic as forest management intensification occurs. J.D. Irving, Limited, in New Brunswick, has been establishing spruce plantations for over 50 years, and owns one of the most intensively managed forests in Canada. The Irving landscape provides a good test case of effects of plantations on biodiversity.

Intensive forest management may negatively impact biodiversity through (*i*) direct effects of tree removal and site preparation (Freedman et al., 1993; Ross-Davis and Frego, 2002), (*ii*) indirect environmental changes that stem from homogenizing and simplifying stand structure (Ramovs and Roberts, 2003), and (*iii*) reduction of source populations and propagules that may reduce the probability of re-colonization after timber harvesting (Zobel et al., 2006). In particular, intensive management that includes whole-tree or 'biomass' harvesting (using unmerchantable wood as fuel) could increase negative impacts of plantations on biodiversity because it reduces forest structure to a greater extent than conventional harvesting (Freedman et al., 1996, Rudolphi and Gustafsson, 2005). Nonetheless, the one-third greater yield of plantations above conventional forestry in New Brunswick (Erdle and Ward, 2008) has led to increased plantations (Hartley, 2002; Loo and Ives, 2003). If plantations continue to expand and to intensify, it will become increasingly challenging to maintain current levels of biodiversity. Yet, managed forests may have some biodiversity value.

Forest managers may be able to partially compensate for negative impacts of plantations at the landscape scale by integrating principles of natural disturbance

emulation management at the stand scale (Hartley, 2002; French et al., 2008). In some cases, appropriate plantations can be regarded as ecosystem restoration, for example, planting white spruce and red spruce (*Picea rubens* Sarg.) and white pine (*Pinus strobus* L.) in areas where these species have been reduced. As afforestation, reforestation, and forest restoration are key strategies to mitigate climate change, plantation establishment will likely be an important tool in maintaining forest resilience in the face of climate change (e.g., Pawson et al., 2013).

We examined the consequences of changing stand structures on selected taxa during regularly scheduled CT management entries in six 22 to 30-year-old white spruce plantations. Four treatments included (*i*) an unthinned control, and three 40% basal area removal thinning treatments, with (*ii*) slash and tops remaining on site (status quo CT), (*iii*) branches and tops extracted from the site (biomass removal CT), and (*iv*) clumps of unthinned trees left, and one-half girdled to create snags (enhanced structure CT).

In addition to tracking species composition, tree growth, and dead wood response to CT, we evaluated response of four selected groups of taxa for the following reasons: (*i*) *forest floor vascular plants* can be sensitive to anthropogenic disturbance, often showing increased diversity after a disturbance takes place (Paillet et al., 2010) and some species require coarse woody debris (CWD) as substrate (Simard et al., 1998); *(ii) saproxylic invertebrates* are associated with dead and dying wood (Speight 1989), and have been shown to decline in richness in response to thinning in naturally regenerated forest (Klimaszewski et al., 2003) and with practices that reduce deadwood, but we suspected that they may benefit from coarse and fine woody debris (FWD) produced by CT due to the paucity of this resource in plantations; (*iii*) *small mammals* have lower

abundance in intensive spruce plantations than in naturally regenerated softwood (Bowman et al., 2001a; Fuller et al., 2004; Keppie et al., 2005), and large contiguous patches of plantations have been characterized with reduced small mammal abundance (Bowman et al., 2001a); and (*iv*) *forest birds* are tightly linked to stand structure and deadwood, with up to 40% of North American forest birds using cavities for nesting (McComb and Lindenmayer, 1999), and many of those species depend on deadwood as a source of food (e.g., Bütler et al., 2004).

Specific objectives and hypotheses

Herbaceous vegetation: We predicted that the herbaceous vascular plant community in the unthinned control (CO) would be the most similar to that of older, naturally regenerated forests (NAT), whereas that of biomass removal CT (BR) would be least similar as a result of more intense and more recent disturbance (canopy and soil).

Beetles: Recent studies (reviewed in Grove, 2002 and Langor et al., 2008) have shown considerable influence of forest practices on invertebrate communities. We tested the hypothesis that increases in woody debris and canopy openness associated with CT temporarily increase beetle abundance across feeding guilds. For specific guilds, we hypothesized that: (*i*) plant feeder species will rapidly increase in abundance following CT because of increased accessibility and growth of understory vegetation; (*ii*) inner and outer bark saproxylic beetles, which directly depend on woody debris (Speight, 1989), will increase in abundance according to the gradient of dead wood available for one to three years because FWD decays rapidly (Hammond et al., 2001; 2004); and (*iii*) predatory species will increase in abundance as their prey increases following CT.

Because outer bark beetles depend on dead wood preconditioning by inner bark beetles (Hammond et al., 2001; Stokland et al., 2012), they should increase in abundance after inner bark beetles. Because the successive arrival of the beetle guilds can occur over a short period, beetle response to the treatments will be examined within and between seasons.

Small mammals: We hypothesized that red-backed voles (*Myodes gapperi* Vigors) and woodland jumping mice (*Napaeozapus insignis* Miller), being conifer stand specialists (Bondrup-Nielson, 1987; Boonstra and Krebs, 2012), are directly affected by plantation management. We predict CT to enhance small mammal abundance via increasing plantation structural diversity (Carey and Wilson, 2001) and the addition of CWD and FWD accessible to small rodents (Sullivan et al., 2011). We hypothesized that status quo CT would increase and biomass removal CT would decrease small mammal density, and assessed plantations in three surrounding landscape contexts: plantation dominated, hardwood dominated, and mixed hardwood and plantation.

Songbirds: We hypothesized that creating deadwood (both standing and fallen) through alternative CT would increase avian biodiversity by providing foraging substrates. We mapped breeding territories and predicted that species responding positively to thinning treatments would show higher densities within enhanced structure (snags) blocks, whereas species that are not responding to the treatments would establish territories randomly among treatments.

Methods

Study area

Black Brook District is a 220 000 ha landbase in northern New Brunswick owned by J.D. Irving, Limited. It includes arguably the most intensively managed forest in Canada, with over 50 000 ha of primarily spruce plantations, as well as high-value shade tolerant hardwood stands managed for sawlogs and veneer logs by single-tree selection and patch cuts. At Black Brook, clearcuts are generally replanted within one year of the final harvest, and since the 1990s, J.D. Irving, Limited has adopted a variable retention approach where islands of mature trees and clumps of advanced regeneration are maintained to provide structural diversity. Following harvest, mechanical site preparation is used to create favourable seedling microsites and herbicide is often aerially applied to control competing vegetation. About one-half of planted stands are cleaned between ages 10 and 15 years, to release the best crop trees and maintain optimum density. CT is generally prescribed at ages from 20 to 40 years to remove lower quality stems and focus the volume on fewer stems. Planted stands are eligible for final harvest between 35 to 55 years of age.

Plot measurements

The study design consisted of six >20 ha white spruce plantations, 22-30 years old, which underwent CT treatments for this study in fall 2010 or winter 2011**.** Two plantations were located in each of three general landscape contexts: plantation dominated, hardwood dominated, and mixed hardwood and plantation. Effects of landscape context were only analyzed for small mammals in this paper. Plantations were selected on the basis of similar stand characteristics, each plantation was divided into four ~5 ha blocks, with each block subjected to one of four treatments: (*i*) an unthinned

control; and three 40% basal area removal thinning treatments, with (*ii*) slash and tops remaining on site (status quo CT), (*iii*) branches and tops extracted from the site (biomass removal CT), and (*iv*) 11-12 clumps of unthinned trees (10 trees per clump) left, and one-half girdled to create snags (enhanced structure CT). Five 0.04 ha circular permanent sample plots (PSPs) were randomly located in each treatment block (total = 6 plantations × 4 blocks × 5 PSPs = 120 PSPs), measured before and after thinning treatments, and measured 3 years later.

In each PSP, all trees were tagged and DBH and tree density were measured before (in 2010), immediately after CT (2011), and 3 years after CT (2013). Height, height to crown base, and crown radius in four cardinal directions of each tree were measured after the CT. Three years after thinning, a sample of 5-45 trees per plot (calculated based on variability using coefficient of variation from an initial sample and 20% error) was measured for height and crown width.

Herbaceous vegetation

Six plots (10 m × 16.67 m) were randomly distributed throughout each treatment block in each experimental plantation (6 × 4 × 6 = 244 plots). In the summers of 2011 and 2012, percent cover of each herbaceous layer species (< 0.5 m tall) was visually assessed in three 1 × 1 m quadrats per plot, then abundance estimates were pooled by plot. Additional species noted during a systematic search were assigned plot-level abundance of 0.1%.

For comparison with older, more contiguous stands, herbaceous vegetation data were obtained from nearby spruce-dominated stands (M. Roberts and K. Frego,

unpublished data) initiated by clearcut logging in the mid-1960s. These reference stands, (*i*) naturally regenerated (NAT), (*ii*) planted but unthinned (UT), and (*iii*) planted and thinned twice (CT2), were surveyed in 2006 as above (n = 3, 2, 2 stands respectively, each with 40 quadrats but no additional systematic search). Taxonomic resolution was made commensurate by pooling some taxa to form 119 genus- or family-level ecologically similar units (*Amelanchier*, *Aster*, excluding *A. acuminata* and *A. macrophylla*, *Betula*, *Carex*, *Dryopteris*, *Hieracium*, Poaceae, *Prunus*, *Pyrola*, *Ribes*, *Salix*, *Solidago*, and *Viola*).

Beetle sampling

We sampled beetles using flight intercept traps made of two, clear acrylic sheets, 30.5 cm × 61 cm, perpendicularly nested one inside the other. A funnel supporting a plastic glass filled with a solution of 70% ethanol and 2% soap was attached at the base of the sheets. The top of the trap was covered with a circular piece of styrene to reduce input of debris and rain. In each treatment block, traps were placed along a transect parallel to the thinning trails (when present), perpendicular to an extraction road, and at least 200 m from other block edges. On each transect, a trap was set 5, 15, 30, 60, and 120 m (i.e., approximately at treatment block center) away from the road. The traps were suspended between two trees ~1.6 m above the ground. One hundred and thirty-five traps were installed, 20 in each of the six plantations and 5 in each of three coniferous forests, at least 380 ha, left unmanaged for decades. The first year (2011), traps were deployed from June 22-July 5 until August 22-24. In 2012 and 2013, traps were deployed from June 3-6 to August 26-28. Trap content was collected biweekly, and

identification was conducted using current systematic literature. All species were assigned to a feeding guild following Dollin et al. (2008). Greater details about traps, their arrangement, and species identification are provided in Nadeau et al. (2015a).

Small mammals

We trapped small mammals in unthinned, biomass removal CT, and status quo CT treatment blocks during mid-spring and mid to late summer in 2011 and 2012 for five consecutive days. We used a single, square 100-trap grid and medium-sized (7.5 cm × 8.75 cm × 22.5 cm) Sherman galvanized folding live traps spaced 10 m apart to maximize recapture likelihood (Bergeron and Jodoin, 1989; Jorgensen, 2004). Traps were checked twice daily at dawn and late afternoon. Unsalted peanuts were used as bait, and a 25 cm^2 rectangle of cotton was provided during spring and autumn to reduce cold temperature mortality of captured animals. The enhanced structure CT was excluded because trees were girdled in 2011, too late to affect rodent populations noticeably within the study period.

Captured mice and voles were identified to species and uniquely tagged with a small, numbered Monel ear tag applied to one ear for identification. Animal handling followed guidelines set forth by the American Society of Mammalogists (Gannon and Sikes, 2007) and the University of New Brunswick Animal Care Committee, (2011).

We used *Density 4.4* (Efford, 2012) software to calculate density as it assumes that the more an animal moves, the more likely it will be captured (Efford, 2004). This software spatially maps trap locations and records which individuals were caught in which traps and how much each individual moved, which is used to build potential home

range size (Efford, 2004). Home range size was used to calculate capture probability as a decreasing function moving away from home range center, which was then used to calculate population density (Efford, 2004).

Songbirds

We surveyed songbirds using spot mapping (Bibby et al., 2000) where observers walk transects and map bird locations to the nearest 12.5 m. We mapped the territories of eight species (Table 1) in treatment blocks in five plantations. The Paget plantation was omitted due to poor accessibility for early morning surveys. Each plot was surveyed eight times during the breeding season and a territory drawn (Bibby et al., 2000) based on clusters of at least two detections separated by a minimum of 10 days, counter-singing individuals, and territory size estimated from the literature (Table 1).

In the same study area, Guénette and Villard (2005) reported large variation in forest bird tolerance to forest management intensity. Thus, to accurately determine effects of increasing dead wood on birds, we focussed on eight focal species associated with dead wood for foraging, nesting, or both (Table 1). Also, because girdling trees to increase deadwood could decrease the density of nesting or foraging substrates for species that require high densities of live trees, we also included species associated with this structural component. Information about the eight focal species, by category, is summarized in Table 1.

Treatment blocks within plantations were (*i*) relatively small (~ 5 ha) compared to the territories of many songbird (e.g., Boreal Chickadee (*Poecile hudsonicus* Forester) > 5 ha, Ficken et al., 1996) and woodpecker species (e.g., Black-backed Woodpecker

(*Picoides arcticus* Swainson) 150 ha, Tremblay et al., 2009) and (*ii*) spatially adjacent. Therefore, no statistical tests were conducted as territories overlaped treatment blocks. Instead, species maps are presented and patterns of distribution are discussed.

Data analyses

Mean DBH and density, as well as basal area and diameter distribution were calculated for each PSP and treatment block before and after thinning. Mean crown width and live crown ratios were also calculated per PSP and treatment block 3 years post-thinning. Periodic annual increment (PAI) in DBH and basal area increment for each treatment were calculated before (2010) and after (2013) thinning. Statistical comparisons were made for the above stand structural attributes between plantations and treatments using a nested ANOVA with treatment as a fixed factor, plantation as a random factor and plot as a random factor nested in plantation. Where residuals of the data had non-normal distribution or unequal variance, Box-Cox transformations were applied. All significant differences were assessed at $p < 0.05$.

Herbaceous vegetation composition was compared between years and among thinning treatments relative to the reference stands using non-metric multidimensional scaling (NMS) ordination on Bray-Curtis distances and taxa with frequency >1. The optimal number of axes and the stability of resulting axis configurations were achieved from a random starting configuration; the ordination was constructed using a maximum of 50 runs with real data and 250 iterations (randomizations) to evaluate the optimal configuration (*PCORD v5.0,* McCune and Mefford, 2006). The differences in species composition between years and among treatments were compared for experimental

plantations using permutation-based analysis of variance (PERMANOVA), with time and treatment as fixed effects and plantation as a random effect in *Primer v6.0* (Clark and Gorley, 2006). PERMANOVA was applied using Bray-Curtis distances, with 9999 permutations and type III sum of squares; it was followed by permutation-based, pairwise multiple comparison tests (Clark and Gorley, 2006).

Hypotheses about the effects of landscape context, treatments, and their interaction on small mammal densities were tested using repeated-measures ANOVAs (Delaney and Maxwell, 1981). One-way ANOVAs, Shapiro-Wilks tests, or both, were used for post-hoc testing of significant differences. Beetle abundance was analyzed as a function of sampling date and treatment using regression analysis, comparing slopes and intercepts using *R version 2.15.2* (R Core Team, 2012). Values of mean beetle abundance per trap per site per sampling event received a common logarithmic transformation. To account for curvilinear effects, models included a quadratic term. Assumptions regarding normality, linearity and homoscedasticity were met.

Results and Discussion

Tree species composition

Softwood species in the six plantations were primarily planted white spruce, some planted black spruce (*Picea mariana* (Mill) BSP), and naturally regenerated balsam fir. Hardwood species were all naturally regenerated, and included trembling aspen (*Populus tremuloides* Michx.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), white birch (*Betula papyrifera* Marsh.), and yellow birch (*Betula alleghaniensis* Britt.). Pin cherry (*Prunus pensylvanica* L.) and willow (*Salix sp*.) made

up 0.8-1.2% of stem density and contributed little to the overstory, so were excluded from the species composition analysis (Fig. 1).

Prior to CT, white spruce constituted 65-96% of the basal area in each treatment block in the six plantations, except in the Airstrip unthinned, status quo and enhanced structure treatment blocks where white spruce comprised 34-43% and black spruce up to 49% (Fig. 1a). For all six plantations combined, hardwood species made up <3% of basal area. The experimental sites were specifically selected to be conifer-dominated and uniform, so low amounts of hardwood are not surprising.

Three years after CT, species composition was similar to that observed prior to thinning (Fig. 1b). White spruce composed 70-97% of the basal area for treatment blocks in all plantations except for one, which included both white and black spruce. White spruce basal area ranged from 13 m^2 ha^{-1} to 30 m^2 ha^{-1} in the plantations, and balsam fir averaged 11% (4 m^2 ha^{-1}) in the unthinned and 8-11% (2 m^2 ha^{-1} to 3 m^2 ha^{-1}) in the CT treatments. Three years after CT, basal area was 35-37% (14 m^2 ha to 15 m^2 ha) lower than in unthinned while it increased by 15-39% (5 m^2 ha^{-1} to 9 m^2 ha^{-1}) in unthinned plots (Fig. 1b). This was expected, as CT creates the growing space to maximize individual tree growth rates.

Tree and stand responses to CT

Prior to CT, there were no differences in mean DBH between treatments. Three years after thinning, trees in all CT treatments had larger mean DBH (16.6-16.7 cm) compared to the unthinned treatment (15.3 cm) (Fig. 2a). Three years post-thinning, DBH differed between plantations, and mean DBH increment differed between

plantations and among treatments; unthinned (mean 0.51 cm/tree/yr) was less than all CT treatments: biomass removal CT (0.61cm/tree/year), enhanced structure CT (0.68 cm/tree/year), and status quo CT (0.67 cm/tree/year).

Although thinning debris can increase the pool of mineralizable nutrients and potentially influence nutrient supply to the remaining trees (Carlyle, 1995), 3 years post-thinning, CWD resulting from CT showed little to intermediate signs of decay (Omari and MacLean, 2015). Three years post-thinning, CWD volume increased by 14-27% in the status quo and enhanced structure treatments, by 6% after the biomass removal treatment, versus 0.1% in unthinned (Omari and MacLean, 2015). Mean snag volume changed little, less than 1 m^3 ha^{-1} among treatments, and girdled trees in the enhanced structure added only 0.7m^3 ha^{-1} of snags (Omari and MacLean, 2015). Mean volume of cut stumps was similar among treatments, averaging 4.7 m^3 ha^{-1} in the biomass removal and 4.6-4.9 m^3 ha^{-1} in the status quo and enhanced structure CT. Total deadwood volume (CWD plus snags) differed among plantations but not between treatments.

As expected, following CT, density and basal area differed between the unthinned and CT treatments, ranging from 1100-1140 stems ha^{-1} for CT versus 2130 stems ha^{-1} in unthinned plots (Fig. 2b). In all plantations, most trees had DBH of 10-15 cm prior to thinning, versus 15-20 cm 3 years after thinning. Basal area averaged 40 m^2 ha^{-1} in the unthinned treatment, three years post-thinning compared to 25-26 m^2 ha^{-1} in the CT treatments (Figs. 1b, 3a). Mean basal area increment (Fig. 3b) differed between plantations, and was lower in the unthinned treatments (12.6 cm^2/tree/yr) compared to all the CT treatments (16.0-17.9 cm^2/tree/yr). Although 3 years post-thinning, trees in the CT treatments had higher mean DBH and basal area increment than those in the

unthinned, higher tree density resulted in higher basal area in the unthinned treatment. There was a clear growth response to CT.

Mean crown width differed between plantations and treatments 3 years after thinning, averaging 2.0 m in unthinned versus 2.4-2.6 m in CT (Fig. 3c). Live crown ratio 3 years post-thinning differed between plantations but not between treatments, ranging from 39-41% among CT treatments (Fig. 3d). Crown length was also not significantly different among treatments, averaging 4.6 m in unthinned versus 4.7-4.8 m in the thinned treatments. Following thinning, crown expansion occurs over both the short- and long-term, by about 80% in thinned pine and spruce, 200% in aspen, and over 100% in ash and oak (*Quercus robur* L.) (Peterson et al., 1997, Juodvalkis, et al. 2005). As a result, light interception and amount of photosynthetic active radiation absorbed by trees in CT stands increase, and this contributes to increased tree growth. In the current study, crown widths differed between unthinned and all CT treatments, but live crown ratio did not, so CT may increase growth by its positive effect on crown width more so than crown depth.

Herbaceous vegetation

Over 200 herbaceous vascular species were detected from older reference forests (100 taxa) and the two survey years in experimental plantations (179 taxa in 2011, 183 in 2012).

The optimal NMS configuration, reached after 171 iterations, was three-dimensional, with stress = 14.051, instability < 0.00001, and similar variance captured on each of the 3 axes (r^2= 0.235, 0.255 and 0.279 respectively). Axis 3 (Fig. 4a)

primarily captured the variation in species composition among plantations, and between reference and experimental stands (PERMANOVA $P_{plantation} = 0.0001$, df = 5); a major contributor to Axis 3 appeared to be the presence of a well-developed shrub layer in reference stands (e.g., *Viburnum* spp.). Axes 1 and 2 (Fig. 4b) were more relevant in their combined capture of the variation related to treatment effects. Based on the positions of the reference stands, they represent a gradient of increasing disturbance frequency and intensity from lower left to upper right. The experimentally thinned treatments experienced a parallel shift in composition (as shown by vectors) on these axes, away from the compositions of the older naturally regenerated and unthinned reference stands ($P_{treatment}=0.0589$, df=3), however, the magnitude of their changes differed ($P_{plant\times treatment} = 0.0001$, df = 15). Multiple comparison tests confirmed that between-year changes within biomass removal and enhanced structure treatments were significant ($P < 0.03$, df = 5). This shift was positively correlated ($r > 0.38$ on Axes 1 or 2; Fig. 4c) with increasing abundance of rhizomatous forest herbs, wood ferns, regenerating hardwoods and ruderal taxa.

Three trends are worthy of note. First, all young experimental plantations lacked the mid-sized shrub layer (e.g., *Viburnum nudum* L.) that was present in older reference stands; this may be expected to develop with time. Second, plant composition in unthinned experimental treatments (controls) did not change significantly between years and their species composition was the most similar to naturally regenerated and unthinned older stands. Lastly, in spite of the initial compositional differences among experimental plantations, the ground flora of all thinned treatments diverged from that of naturally regenerated and unthinned older stands and the control treatment, with the

greatest change in the biomass removal CT treatments.

Although the primary difference between status quo (SQ) and enhanced structure (ES) treatments versus biomass removal (BR) treatments was the removal of logging debris, the shift in species composition in the latter treatment was likely also related to increased soil disturbance or reduced soil protection. Aikens et al. (2007) found that the degree of change in understory plant communities was greater with both canopy opening and soil disturbance than canopy opening alone. As in our study, this change was characterized by expansion of pre-existing forest herbs and ferns, and invasion of ruderal species. Burke et al. (2008) found the same pattern with higher-intensity thinning treatments that exposed soil. It is likely that the provision of woody debris (or the lack thereof) as a substrate for vascular plant may be less important to forest floor vegetation composition than disruption of the general substrate (Pyle and Brown, 2002). Although it is too early to evaluate the relative merits of thinning with moderate levels of debris creation or retention, removal of woody debris (biomass for pulp or fuel) initially results in a compositional shift away from that found in mature, naturally regenerated forests, and therefore is incompatible with biodiversity conservation objectives; its long-term effects on rare or sensitive species require further study.

Effects of treatments on beetle feeding guilds

We collected 76 212 individual beetles. The list of species recovered in 2011 and 2012 is provided in Nadeau et al. (2015a). Beetle abundance in each feeding guild usually declined throughout the sampling seasons (Fig. 5). Generally, the number of beetles per feeding guild was similar between CT plantations and old forests, while

unthinned plantations supported 5–6 times fewer beetles than old forests and CT plantations (Fig. 5). The slopes and intercepts of the relationships between beetle abundance and time often differed between treatments but these differences usually faded as the time since thinning increased (Fig. 5; Table 2). Trends were similar between the various CT treatments (Fig. 5).

For plant feeder beetles, slopes and intercepts of relationships between beetle abundance and time differed in 2011 because CT plantations exhibited a steeper decline in abundance and supported more beetles than unthinned plantations (Fig. 5a; Table 2). In 2012, a difference in intercept occurred stemming from higher initial abundance in CT than unthinned plantations (Fig. 5a; Table 2). In 2013 no differences between treatments were detected (Table 2). For inner bark beetles, intercepts differed in 2011 because unthinned plantations initially supported fewer beetles than CT plantations (Fig. 5b; Table 2). In 2012, slopes and intercepts differed (Table 2), due to a steeper decline in beetle abundance in old forests than in plantations (Fig. 5b), as well as to higher initial numbers in old forests (Fig. 5b). In 2013, slopes and intercepts differed (Table 2) because of steeper declines in beetle abundance in old forests than in plantations and in CT than in unthinned plantations (Fig. 5b). Unthinned plantations initially supported fewer beetles than CT plantations, and plantations initially supported fewer beetles than old forests (Fig. 5b). For outer bark beetles, no differences in slope occurred but differences in intercept of relationships between beetle abundance and time occurred in all three sampling years (Table 2) because initial outer bark beetle densities were higher in CT than unthinned stands (Fig. 5c). For predatory beetles, intercepts differed between treatments in 2011 (Table 1) because early in the season, unthinned plantations

supported fewer beetles than CT and biomass removal CT plantations supported fewer beetles than status quo CT plantations (Fig. 5d). Intercept also differed in 2012 (Table 2), stemming from a higher initial density being recorded in CT than unthinned plantations (Fig. 5d). No differences between treatments were detected in 2013 (Table 2).

These results support the general hypothesis that changes in woody debris and canopy openness associated with CT of plantations can increase beetle abundance across feeding guilds. Beetle abundance in CT plantations was comparable to that of older naturally regenerated forests in the same area, and was considerably higher than abundance in unthinned plantations. Conversely, our hypotheses for specific feeding guilds were poorly supported because beetle response to the treatments was strong and similar across guilds. Changes in chemical and structural components of dead wood occur over time and should promote beetle species succession (reviewed in Nadeau et al., 2015b), with inner bark species colonizing woody debris first but declining in abundance rapidly because dead wood is only fresh for a short period (Hammond et al., 2001; 2004), and outer bark species colonizing later (Esseen et al., 1992; Vanderwel et al., 2006). However, inner bark species were still abundant in CT areas in 2013, even if they declined from 2012 to 2013. In addition, there was no delay between the increase in abundance of inner and outer bark beetles, both within or between seasons, possibly because outer bark species recovered in this study feed on early succession fungi (Vanderwel et al., 2006). The expected effect on saproxylic beetles of the woody debris gradient produced by the treatments was not observed, in part because girdled trees took two summers to die, suggesting that canopy openness had a greater effect on beetles than

the amount of residual wood, which is consistent with another study of the effect of biomass removal on leaf litter invertebrates (Work et al., 2014). Our hypothesis that plant feeder and predatory species should reach higher abundances in CT plantations because of higher vegetation (Ranius and Jansson, 2000) and prey content (Wermelinger et al., 2002) was supported, as well as our hypothesis that the increase in abundance of predatory species would be delayed. However, the decline of both plant feeder and predatory species in 2013 was not expected as crown closure has not occurred yet.

We conclude that CT can promote occurrence of beetles across different guilds during the first three summers following thinning, but additional sampling seasons will be necessary to determine how long these effects on beetle communities last.

Effects of treatments on small mammals

We completed 36 367 trap nights over 2011 and 2012 totaling 4064 captures. Short-tailed shrews (*Blarina brevicauda* Say) were the most common (8.4/100 trap nights), red-backed voles second (0.91/100 trap nights), woodland jumping mice third (0.84/100 trap nights), and deer mice (*Peromyscus maniculatus* Wager) fourth (0.49/100 trap nights). All other mammal species captured (≤0.13/100 trap nights) were too irregular to track abundance.

Deer mice and short-tailed shrews were not affected by either surrounding landscape composition (two plantations each in plantation-dominated, hardwood-dominated, or mixed plantation-hardwood landscapes) or CT or interactions (Table 3). Woodland jumping mice were not affected by landscape composition, but did express an aversion to CT (Table 3). Woodland jumping mice density averaged 5-6 fold greater in

unthinned (13.8 ha^{-1}) than in CT (2.1 ha^{-1}). Red-backed voles were affected by both landscape and treatment, but there was no interaction (Table 3). Voles were more abundant in status quo CT with debris retained than either unthinned or biomass removal CT. Effect of landscape composition was not significant.

Generally, short-tailed shrews and deer mice do not appear to be affected by CT nor by landscape context; therefore, they likely do not require special management considerations. We found woodland jumping mouse density to be inordinately high in mid-rotation, non-CT plantations within a hardwood dominated landscape when compared to densities within other stand types (Morris, 1955; Bowman et al., 2001a; Fuller et al., 2004; Keppie et al., 2005). Therefore, we advise maintaining some plantations over 25 years of age in a non-CT state and maintaining hardwood stands if present. Further, as hibernation is a significant bottle neck for jumping mice survival, planted non-CT sites with optimal hibernation locations- well-drained or sloped terrain- need to be maintained across the landscape (Ovaska and Herman, 1988). As jumping mice home ranges span 0.4-5.0 ha in these Black Brook plantations (Dracup, 2013), and their linear movements have been reported up to over 600 m (Bowman et al., 2001b), it is likely that if a sloped or well-drained, mid-rotation, non-CT plantation, or mature softwood stand ≥ 5 ha is within 600 m of another such site, jumping mice should be able to move to and populate the adjacent site. Further, riparian buffers facilitate dispersal and residency, so buffer presence may enhance jumping mice movement through a landscape (Ovaska and Herman, 1988).

Vole capture rates in status quo CT within hardwood and mixed hardwood-plantation landscapes were similar to previous results in natural softwood stands (0-

13.5/100 trap nights) (Morris, 1955; Bowman et al., 2001a; Fuller et al., 2004; Keppie et al., 2005). Therefore, plantation CT in hardwood and mixed hardwood-plantation landscapes can improve plantation structure for red-backed voles if debris is retained (i.e., status quo CT). However, our results concur with Bowman et al. (2001a) that large areas of plantations are detrimental to red-backed voles.

As vole density was depressed within plantation-dominated landscapes, special care must be taken when designing these areas so as not to inhibit dispersal. We recommend that large contiguous areas of plantations be broken up by islands of naturally regenerated forest. Voles have been recorded to move up to a maximum of 494 m (Bowman et al., 2001b), and maintain home ranges averaging 0.2-0.5 ha in Black Brook plantations (Dracup, 2013). Patches of untreated forest ≥ 1.0 ha in size are able to maintain internal structural integrity (de Graaf, 2008), and would be able to maintain at least two breeding female voles (Bondrup-Nielson, 1987). Red-backed voles should be able to disperse to and out of these patches if placed ≤ 252 m apart, and maintaining these small patches within plantation-dominated landscapes should allow small populations to establish and enhance colonization of surrounding, less desirable forest space.

Effects of treatments on songbirds

Territory maps for two plantations illustrate the typical patterns observed among plantations and species (Fig. 6). Detections of White-throated Sparrow (*Zonotrichia albicolis*

Gmelin) were mostly concentrated along plantation edges. It is unclear whether this

species responded positively to the addition of FWD because occurrence of sparrows in the enhanced and status quo CT blocks was inconsistent between plantations (Fig. 6a).

As predicted, the Black-backed Woodpecker and Brown Creeper (*Certhia americana* Bonaparte) were virtually undetected. A Black-backed Woodpecker did respond to a playback in one plantation during a single count in the biomass removal CT block that borders a mature spruce forest. The plantation was revisited and repeated playback trials were conducted, but did not produce a second sighting in the plantations. Red-breasted Nuthatch (*Sitta canadensis* L.) and Cape May Warbler (*Setophaga tigrina* Gmelin) were represented only by scattered, mostly peripheral detections and Winter Wren (*Troglodytes hiemalis* Viellot) was absent from all but two sites. Maps were not produced for the Black-backed Woodpecker, Red-breasted Nuthatch or Cape May Warbler due to their scarcity in the plantations. Boreal Chickadee (*Poecile hudsonicus* Forester) territories broadly overlapped treatment blocks, showing no avoidance or preference for any treatment per se (Fig. 6b).

The Bay-breasted Warbler (*Setophaga castanea* Wilson) reached higher occurrences than expected, given the fact that this was not a spruce budworm outbreak year (Fig. 6d). It showed no detectable preference for a given treatment and instead appeared to be avoiding roads and areas directly adjacent to deciduous plots (e.g., Fig. 6d, Roussel Brook plantation).

We detected little evidence for a response to CT by focal bird species. However, the experimental design was not optimal for testing treatment effects on forest birds for three reasons. First, the area of treatment blocks was small relative to the territory size of many bird species, including those most likely to respond negatively to intensive

plantation silviculture (e.g., woodpeckers and Brown Creeper - MacKay et al., 2014). This was obvious when examining territory maps. For instance, it was unclear whether the Boreal Chickadee was using the plantations as their main breeding territory or an extension thereof. High area requirements made these species susceptible to respond to habitat surrounding the plantation sites. Second, treatment blocks were generally adjacent to one another, making it more difficult to detect effects because individuals may nest in one block and forage in another or establish a territory overlapping two treatments. Third, responses by species at the plantation level (e.g., Winter Wren and Bay-breasted Warbler) may confound the detection of eventual responses to treatments within plantations.

Despite obtaining descriptive results with regard to songbirds, we have reason to believe that increasing deadwood through thinning treatments in 22-30 year-old plantations could influence their use by bird species dependent on deadwood over time. Indeed, in the same study site, we compared bird assemblages of commercially mature (40-50 year-old) CT treatment blocks (n = 60) with various amounts of deadwood, with bird assemblages of naturally-regenerated, mature conifer stands (n = 42), and found that stand structure and snag density were important predictors of species assemblage (MacKay et al., 2014). Therefore, benefits of CT treatments that increase deadwood in plantations for songbirds may only become apparent as stands mature.

Conclusions

Our original predicted magnitude of response (high, medium, low; increase or decrease) and speed of response (fast, moderate, slow) are summarized along with the 3-

year study results by treatment in Table 4. Overall results by taxa were as follows:

(1). Tree growth: Three years after CT, tree DBH increment was 20-33% greater in the three CT treatments than in the unthinned plots. Mean crown width was lower in unthinned than in CT plots by 0.4-0.6 m per tree. Live crown ratio did not differ between unthinned and CT, indicating that CT increased basal area growth by its effect on crown width.

(2). Herbaceous vegetation: Composition in unthinned plots changed little between years and remained the most compositionally similar to the older reference stands. The biomass removal CT treatment showed both the greatest magnitude of change and the least similarity to reference and unthinned stands. For herbaceous plants, the conservation merits of all thinning treatments require more time to assess, but in the short-term, biomass removal appears to be detrimental.

(3). Beetles: CT promoted occurrence of beetles across different guilds during the first three summers following thinning. Our results support the general hypothesis that changes in woody debris and canopy openness associated with CT of plantations increase beetle abundance across all feeding guilds. Beetle abundance in CT plantations was comparable to that of older naturally regenerated forests in the same area and was considerably higher than in unthinned plantations. Hypotheses that specifically considered each feeding guild were poorly supported because beetle response to the treatments was strong and similar across guilds.

(4). Small mammals: Short-tailed shrews and deer mice were not affected by either surrounding landscape or CT. Woodland jumping mice were not affected by landscape but averaged 5-6 fold less in CT than unthinned. Red-backed voles were affected by

both landscape and treatment, being more abundant in status quo CT with debris retained than in unthinned or biomass removal CT and less dense in plantation dominated than in either hardwood or mixed landscapes. Recommendations include: (*i*) maintain some plantations > 25 years old in a non-CT state for woodland jumping mice; (*ii*) leave unharvested retention patches to benefit voles; and (*iii*) diversify large planted areas through multiple age class, retention, and regeneration strategies.

(5). Songbirds: There was little evidence for a response to CT by eight focal bird species. However, the experimental design was not optimal for testing treatment effects on forest birds because the treatment block area (~5 ha) was small relative to territory size for many bird species, including those most likely to respond negatively to intensive plantation silviculture. Surveys were conducted too soon after tree girdling in the enhanced structure CT plots because girdled trees had not yet decayed sufficiently to be excavated.

Overall, results showed that crown width and tree growth responded positively to CT; herbaceous vegetation was affected little by status quo CT but was negatively affected by the experimental biomass removal CT; beetles responded positively to CT; small mammal species responded both positively (red-backed voles) and negatively (woodland jumping mice) to CT, but large landscape areas of plantations had negative effects; and the effects of CT on songbirds were unclear and requires larger treated blocks, but deadwood-requiring species require forest patches with high densities of dead wood at the landscape scale. These early results demonstrate the complexity of assessing biodiversity within ecosystems, even within a limited range of sites and treatments. Results from the initial 3 years after treatment of the experimental study sites

really set the study up to permit a long-term legacy of responses of taxa over stand development.

Acknowledgements

This research was supported by a Natural Sciences and Engineering Research Council of Canada Collaborative Research and Development grant and by J.D. Irving, Limited (JDI). We thank current and former staff of JDI, including Jason Killam, Gaetan Pelletier, Pamela Poitras, John Gilbert, and Brian Quirion, as well as JDI Forest Research Advisory Committee members, for considerable input to the project. M. Roberts and K. Frego provided herbaceous plant data for mature reference forests. Andy Whitman and two anonymous reviewers provided review comments which improved the manuscript.

References

Aikens, M.L., Ellum, D., McKenna, J.J., Kelty, M.J., and Ashton. M.S. 2007. The effects of disturbance intensity on temporal and spatial patterns of herb colonization in a southern New England mixed-oak forest. For. Ecol. Manage., 252:144-158.

Animal Care Committee. 2011. Animal Care, Ethics and Safety. University of New Brunswick, Fredericton, NB, Canada.

Bergeron, J., and Jodoin, L. 1989. Patterns of resource use, food quality, and health status of voles (*Microtus pennsylvanicus*) trapped from fluctuating populations. Oecologia, 79:306-314.

Bibby, C.J., Burgess, N.D., Hill, D.A., and Mustoe, N.J. 2000. Bird Census Techniques. 2nd ed. Academic Press, San Diego.

Bondrup-Nielson, S. 1987. Demography of *Clethrionomys gapperi* in different habitats. Can. J. Zool., 65:277–283.

Boonstra, R., and Krebs, C. 2012. Population dynamics of red-backed voles (*Myodes*) in North America. Oecologia, 168:601–620.

Bowman, J., Forbes, G., and Dilworth, T. 2001a. Landscape context and small-mammal abundance in a managed forest. For. Ecol. Manage., 140:249–255.

Bowman, J., Forbes, G., and Dilworth, T. 2001b. Distances moved by small woodland rodents within large trapping grids. Can. Field-Naturalist, 115: 64–67.

Burke, D.M., Elliott, K.A., Holmes, S.B., and Bradley, D. 2008. The effects of partial harvest on the understory vegetation of southern Ontario woodlands. For. Ecol. Manage., 255:2204-2212.

Bütler, R., Anglestam, P., and Schlaepfer, R. 2004. Quantitative snag targets for the three-toed woodpecker *Picoides tridactylus*. In: Angelstam, P., Dönz-Breuss, M., and Roberge, J.-M. (eds.). Targets and Tools for the Maintenance of Forest Biodiversity. Ecological Bulletins, 51:219-232.

Canadian Council of Forest Ministers. 2014. National Forestry Database Program. Can. For. Serv., Ottawa, Ontario, Canada. Available from http://nfdp.ccfm.org/silviculture/quick_facts_e.php

Carey, A., and Wilson, S. 2001. Induced spatial heterogeneity in forest canopies: responses of small mammals. J. Wildl. Manage., 65:1014–1027.

Carlyle, J.C. 1995. Nutrient management in a *Pinus radiata* plantation after thinning: the

effect of thinning and residues on nutrient distribution, mineral nitrogen fluxes, and extractable phosphorus. Can. J. For. Res., 25:1278-1291.

Clarke, K.R., and Gorley, R.N. 2006. PRIMER v6: User Manual/Tutorial. PRIMER-E, Plymouth.

Craig, C., Villard, M.-A., and Taylor, P.D. 2015. Forest management intensity and nesting woodpeckers in an unburned, hemiboreal landscape. J. Wildl. Manage., (Under review).

de Graaf, M.F. 2008. Herbaceous-layer species composition and dynamics in leave patches before and after clearcut harvesting of surrounding forest. MScF Thesis, Faculty of Forestry and Environmental Management, Univ. of New Brunswick, NB, Canada, 208p.

DeGraaf, R.M., and Yamasaki, M. 2001. New England wildlife: habitat, natural history, and distribution. UPNE. Lebanon, New Hampshire, USA. 482 p.

Delaney, S., and Maxwell H. 1981. On using analysis of covariance in repeated measures designs. Multivariate Behav. Res., 16:105–123.

Dollin, P., Majka, C., and Duinker, P. 2008. Saproxylic beetle (Coleoptera) communities and forest management practices in coniferous stands in southwest Nova Scotia, Canada. ZooKeys, 2:291–336.

Dracup, E. 2013. Living in spruce plantations: can commercial thinning revitalize rodent communities in the northern Appalachians? The effect of biomass harvesting, understory vegetation, fine woody debris, and carbohydrate load. MSc Thesis, Dept. of Biology, Univ. of New Brunswick, Fredericton, NB, Canada. 90p.

Efford, M. 2004. Density estimation in live-trapping studies. Oikos, 106:598–610.

Efford, M. 2012. DENSITY 4.4: software for spatially explicit capture–recapture. Dept. Mathematics and Statistics, University of Otago, Dunedin, New Zealand. http://www.otago.ac.nz/density.

Erdle, T.A., and Ward, C. 2008. Management alternatives for New Brunswick's public forest. NB Dept. Nat. Res., Fredericton, NB, 108p. Available from http://www.gnb.ca/0079/ErdleReport-e.asp

Esseen, P.A., Ehnström, B., Ericson, L., and Sjöberg, K. 1992. Boreal forests — the focal habitats of Fennoscandia. Pp. 252-325..*In:* L. Hansson (ed). Ecological Principles of Nature Conservation. Elsevier, Amsterdam, The Netherlands.

Falls, J.B., and Kopachena, J.G. 1994. White-throated sparrow. The Birds of North America, 128:1-30.

Ficken, M.S., McLaren, M.A., and Hailman, J.P. 1996. Boreal Chickadee (*Parus hudsonicus*). In: The Birds of North America, No. 254 (A. Poole and F. Gill, eds.). The Academy of Natural Sciences, Philadelphia, PA, and American Ornithologists' Union, Washington, DC.

Freedman, B., Morash, R., and MacKinnon, D. 1993. Short-term changes in vegetation after the silvicultural spraying of glyphosate herbicide onto regenerating clear-cuts in Nova Scotia, Canada. Can. J. For. Res., 23:2300–2311.

Freedman, B., Zelazny, V., Beaudette, D., Fleming, T., Flemming, S., Forbes, G., Gerrow, J.S., Johnson, G., and Woodley, S. 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. Environ. Rev., 4:238–265.

Freemark, K.E., Dunning, J.B., Hejl, S.J., and Probst, J.R. 1995. A landscape ecology

perspective for research, conservation, and management. Pp. 381-427. In: Ecology and Management of Neotropical Migratory Birds. Oxford University Press, New York, NY.

French, L.J., Smith, G.F., Kelly, D.L., Mitchell, F.J.G., O'Donoghue, S., Iremonger, S.F., and McKee, A.-M. 2008. Ground flora communities in temperate oceanic plantation forests and the influence of silvicultural, geographic and edaphic factors. For. Ecol. Manage., 255:476-494.

Fuller, A., Lachowski, H., and Harrison, D. 2004. Stand scale effects of partial harvesting and clearcutting on small mammals and forest structure. For. Ecol. Manage., 191:373–386.

Gannon, W., and Sikes, R. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal., 88: 809–823.

Grove, S. J. 2002. Saproxylic insect ecology and the sustainable management of forests. Annu. Rev. Ecol. Syst., 33:1–23.

Guénette, J.-S. and Villard, M.-A. 2005. Thresholds in forest bird response to habitat alteration as quantitative targets for conservation. Conserv. Biol., 19: 1168-1180.

Hammond, H.E.J., Langor, D.W., and Spence, J.R. 2001. Early colonization of *Populus* wood by saproxylic beetles (Coleoptera). Can. J. For. Res., 31:1175–1183.

Hammond, H.E.J., Langor, D.W., and Spence, J.R. 2004. Saproxylic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada : spatiotemporal variation and conservation of assemblages. Can. J. For. Res., 19:1–19.

Hartley, M.J. 2002. Rationale and methods for conserving biodiversity in plantation

forests. For. Ecol. Manage., 155:81–95.

Hejl, S.J., Newlon, K.R., McFadzen, M.E., Young, J.S., and Ghalambor. C.K. 2002. Brown creeper (*Certhia americana*). In Poole, A., Gill, F. (eds.), The Birds of North America, No. 669. The Birds of North America, Inc., Cornell Lab of Ornithology, Ithaca, NY.

Jorgensen, E. 2004. Small mammal use of microhabitat reviewed. J. Mammal., 85:531–539.

Juodvalkis, A., Kairiukstis, L., and Vasiliauskas, R. 2005. Effects of thinning on growth of six tree species in north-temperate forests of Lithuania. Eur. J. For. Res., 124:187-192.

Kendeigh, S.C. 1947. Bird population studies in the coniferous forest biome during a spruce budworm outbreak. Biol. Bull. No. 1. Div. of Research, Ont. Dept. Lands and Forests.

Keppie, D., J. Haines, I. Laurion, and M.C. Theriault. 2005. Birds and small mammals use intensely managed conifer plantations in northwestern New Brunswick. Fredericton, New Brunswick; Unpublished.

Klimazewski, J., Bernier-Cardou, M., and Germain, C. 2003. The effects of forestry practices on the abundance of arthropods (Acarina, Araneae, Collembola, Coleoptera and Diptera). Belgian J. Entomol., 5:103-116.

Langor, D.W, Hammond, H.E., Spence, J.R., Jacobs, J., and Cobb, T.P. 2008. Saproxylic insect assemblages in Canadian forests: diversity, ecology, and conservation. Can. Ent., 140:453-474.

Loo, J., and Ives, N. 2003. The Acadian forest: Historical condition and human impacts.

For. Chron., 79:462-474.

Lowther, J.K., and Falls, J.B. 1968. White-throated sparrow. Pp. 1364-1392 *In:* O.L. Austin (Ed.). Life histories of North American cardinals, grosbeaks, buntings, towhees, and allies. U.S. Nat. Mus. Bull., 237, part 3.

MacArthur, R.H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecology, 39:599-619.

MacKay, A., Allard, M., and Villard, M.-A. 2014. Capacity of older plantations to host bird assemblages of naturally-regenerated conifer forests: a test at stand and landscape levels. Biol. Conserv., 170:110-119.

McComb, W.C. and Lindenmayer, D.B. 1999. Dying, dead, and down trees. Pp. 335-372. *In:* Hunter, M.L.Jr. (ed.). Maintaining Biodiversity in Forest Ecosystems. Cambridge University Press, Cambridge, UK.

McCune, B. and Mefford, M.J. 2006. PC-ORD Multivariate analysis of ecological data. Version 5: MjM Software, Gleneden Beach, OR, USA.

McLaren, M.A. 1975. Breeding biology of the Boreal Chickadee. Wilson Bulletin, 87:344-354.

Morris, R. 1955. Population studies on some small forest mammals in eastern Canada. J. Mammal., 36:21–35.

Nadeau, P., Majka, C.G., and Moreau, G. 2015a. Short-term response of Coleopteran assemblages to thinning-induced differences in dead wood volumes. For. Ecol. Manage., 336:44-51.

Nadeau, P., Thibault, M., Horgan, F.G., Michaud, J.-P., Gandiaga, F., Comeau, C., and Moreau, G. 2015b. Decaying matters: Coleoptera involved in heterotrophic

systems. In: Stack, C. (ed.), Beetles: Biodiversity, Ecology and Role in the Environment. Nova Publisher, NY.

Nyland, R.D. 2002. Silviculture: concepts and applications. 2nd ed. McGraw-Hill, New York.

Omari, K., and MacLean, D.A. 2105. Do biomass removal and structure-enhancing treatments influence deadwood characteristics following commercial thinning in spruce plantations in New Brunswick, Canada? Can J. For. Res., 45:1407-1418.

Ovaska, K., and Herman, T. 1988. Life history characteristics and movements of the woodland jumping mouse, *Napaeozapus insignis*, in Nova Scotia. Can. J. Zool., 66:1752–1762.

Paillet, Y., Bergès, L., Hjältén, J., Ódor, P., Avon, C., Bernhardt-Römermann, M., Bijlsma, R.-J., De Bruyn, L., Fuhr, M., Grandin, U., Kanka, R., Lundin, L., Luque, S., Magura, T., Matesanz, S., Meszaros, I., Sebastia, M.-T., Schmidt, W., Standovár, T., Tóthmérész, B., Uotila, A., Valladares, F., Vellak, K., and Virtanen, R. 2010. Biodiversity differences between managed and unmanaged forests: meta-analysis of species richness in Europe. Conserv., Biol. 24:101-112.

Pawson, S.M., Brin, A., Brockerhoff, E.G., Lamb, D, Payn, T.W., Paquette, A., and Parrotta. J.A. 2013. Plantation forests, climate change and biodiversity. Biodiv. Conserv., 22:1203-1227.

Pelletier, G., and Pitt, D.G. 2008. Silvicultural responses of two spruce plantations to midrotation commercial thinning in New Brunswick. Can. J. For. Res., 38:851-867.

Peterson, J.A., Seiler, J.R., Nowak, J., Ginn, S.E., and Kreh. R.E. 1997. Growth and

physiological responses of young loblolly pine stands to thinning. For. Sci., 43:529-534.

Poulin, J.-F., Villard, M.-A., Edman, M., Goulet, P.J., and. Eriksson, A.-M. 2008. Thresholds in nesting habitat requirements of an old forest specialist, the Brown Creeper (*Certhia americana*), as conservation targets. Biol. Conserv., 141:1129–1137.

Poulin, J.-F., D'Astous, E., Villard, M.-A., Hejl, S.J., Newlon, K.R., McFadzen, M.E., Young, J.S., and Ghalambor, C.K. 2013. Brown creeper (*Certhia americana*). *In:* Poole, A. (ed.). The Birds of North America Online. Cornell Lab of Ornithology, Ithaca, NY. Available from http://bna.birds.cornell.edu/bna/species/669doi:10.2173/bna.669

Pyle, C., and Brown, M.M. 2002. The effects of microsite (logs versus ground surface) on the presence of forest floor biota in a second-growth hardwood forest. USDA Forest Service Gen. Tech. Rep. PSW-GTR-181.

R Core Team.2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramovs, B.V., and Roberts, M.R. 2003. Understory vegetation and environment responses to tillage, forest harvesting, and conifer plantation development. Ecol. Applic., 13:1682–1700.

Ramovs, B.V., and Roberts, M.R. 2005. Response of plant functional groups within plantations and naturally regenerated forests in southern New Brunswick, Canada. Can. J. For. Res., 35:1261–1276.

Ranius, T., and Jansson, N. 2000. The influence of forest regrowth, original canopy

cover and tree size on saproxylic beetles associated with old oaks. Access, 3207:85–94.

Ross–Davis, A.L., and Frego, K.A. 2002. Comparison of plantations and naturally regenerated clearcuts in the Acadian Forest: forest floor bryophyte community and habitat features. Can. J. Bot., 80:21–33.

Rudolphi, J., and Gustafsson, L. 2005. Effects of forest–fuel harvesting on the amount of deadwood on clear–cuts. Scand. J. For. Res., 20:235–242.

Sabo, S.R.1980. Niche and habitat relations in subalpine bird communities of the White Mountains of New Hampshire. Ecol. Monogr., 50:241-259.

Simard, M.J., Bergeron, Y., and Sirois, L. 1998. Conifer seedling recruitment in a southeastern Canadian boreal forest: the importance of substrate. J. Veg. Sci., 9:575-582.

Speight, M.C.D. 1989. Saproxylic invertebrates and their conservation. Nature Environ.,42: 1–79.

Stokland, J.N., Siitonen, J., and Jonsson, B.G. 2012. Biodiversity in dead wood. Cambridge University Press, Cambridge, UK.

Sullivan, T., Sullivan, D., Lindgren, P., Ransome, D., Bull, J., and Ristea, C. 2011. Bioenergy or biodiversity? Woody debris structures and maintenance of red-backed voles on clearcuts. Biomass and Bioenergy, 35:4390-4398.

Tremblay, J.A., Ibarzabal, J., Dussault, C., and Savard, J.-P.L. 2009. Habitat requirements of breeding Black-backed Woodpeckers (*Picoides arcticus*) in managed, unburned boreal forest. Avian Conserv. Ecol., 4(1):2. www.ace-eco.org/vol4/iss1/art2

Tremblay, J.A., Ibarzabal, J., and Savard, J.-P.L. 2010. Foraging ecology of black-backed woodpeckers (*Picoides arcticus*) in unburned eastern boreal forest stands. Can. J. For. Res., 40:991–999.

Vanderwel, M.C., Malcolm, J.R., Smith, S.M., and Islam, N. 2006. Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests. For. Ecol. Manage., 225:190–199.

Venier, L.A., Pearce, J.L., Fillman, D.R., McNicol, D.K., and Welsh, D.A. 2009. Effects of spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks on boreal mixed-wood bird communities. Avian Conservation and Ecology, 4(1):3. [Online] http://www.ace-eco.org/vol4/iss1/art3/

Vincent, M., Krause, C., and Zhang, S.Y. 2009. Radial growth response of black spruce roots and stems to commercial thinning in the boreal forest. Forestry, 82:557-571.

Wermelinger, B., Duelli, P., and Obrist, M.K. 2002. Dynamics of saproxylic beetles (Coleoptera) in windthrow areas in alpine spruce forests. Swiss Fed. Inst. Forest Snow Landsc., 148:133–148.

Work, T.T., Brais, S., and Harvey, B.D. 2014. Reductions in downed deadwood from biomass harvesting alter composition of spiders and ground beetle assemblages in jack-pine forests of Western Quebec. For. Ecol. Manage.,321: 19–28.

Zobel, M., Öpik, M., Moora, M., and Pärtel, M. 2006. Biodiversity and ecosystem functioning: it is time for dispersal experiments. J. Veg. Sci., 17:543–547.

Table 1. Summary of pertinent information and predictions for eight focal songbird species, representing four categories of deadwood/forest type use that were assessed in each treatment block in five plantations.

Species	Prediction
Species associated with fine woody material	
1. **White-Throated Sparrow** (*Zonotrichia albicollis*) mainly forages in dense undergrowth or brush piles (Falls and Kopachena, 1994). Territories range from 0.4-1.3 ha (Lowther and Falls, 1968).	Positive response to thinning treatments creating piles of fine woody debris.
Species associated with coarse woody debris	
2. **Winter Wren** (*Troglodytes troglodytes*) may nest in natural cavities, decaying stumps or uprooted trees. Territory size is estimated at 1.2-2.8 ha (Freemark et al., 1995).	May respond positively to treatments that create piles of woody debris.
Species associated with standing dead wood	
3. **Brown Creeper** (*Certhia americana*) is associated with old forests (Hejl et al., 2002;; Poulin et al., 2013) and, in particular, with large-diameter, live trees for foraging (Poulin et al., 2008) and snags for nesting (Poulin et al., 2013). There is a threshold of 66 large stems/ha (>30 cm) in the occurrence of this species, whose breeding territory ranges from 2.3-9.4 ha (Poulin et al., 2013).	No response to enhanced treatment because tree girdling is too recent. Other treatments do not produce preferred nesting/foraging substrates.
4. **Boreal Chickadee** (*Poecile hudsonicus*) nests in well-decayed snags or stumps, or in old woodpecker holes (Ficken et al., 1996) and require at least 5 ha for nesting territories (McLaren, 1975). Tree girdling may provide nesting substrates for this species but this operation was too recent at the time of surveys to allow excavation by this species.	Given large area requirements relative to body size, territories would overlap several different treatments. Tree girdling could increase occurrence, but decomposition of girdled trees would be insufficient at the time of our surveys.
5. **Red-breasted Nuthatch** (*Sitta canadensis*) typically nests in tall, well-decayed snags (DeGraaf and Yamasaki, 2001). It often uses old woodpecker cavities. Territory size in this species is highly variable (from less than 1 ha to ca. 10 ha, Sabo, 1980), and so is its annual density (MacKay et al., 2014).	
6. **Black-backed Woodpecker** (*Picoides arcticus*) is a specialist of old conifer forests requiring recently dead snags for foraging and relatively large snags for nesting (Tremblay et al., 2010; Craig et al., in review). This species is often associated with recently burned stands, but fires are uncommon in New Brunswick. In unburned forests of northern Québec, Black-backed Woodpecker territories contained a density of at least 35 m^3/ha of spruce snags	We predicted that this species would be essentially absent from the 20-25 year old plantations.

(Tremblay et al., 2010). The Black-backed Woodpecker has, by far, the largest home range (~150 ha; Tremblay et al., 2009) of the 8 focal species.	
Species associated with closed spruce-dominated canopy	
7. **Cape May Warbler** (*Dendroica tigrina*) feeds on insects in coniferous foliage (MacArthur, 1958). Cape May Warblers have small territories (0.5 ha; Kendeigh, 1947).	Expected to be negatively affected by thinning treatments but establish territories primarily in unthinned plots.
8. **Bay-breasted Warbler** (*Dendroica castanea*) also forages on insects of coniferous foliage. Bay-breasted Warbler territories are ca. 1.5 ha (Sabo, 1980). Both Cape May and Bay-breasted Warblers are strongly associated with spruce budworm (*Choristoneura fumiferana*) outbreaks and are present at much lower abundance between outbreaks (Kendeigh, 1947, Venier et al., 2009).	Expected to occur more often in unthinned plots.

Table 2. Regression analyses fitted to the longitudinal beetle abundances per year, treatment, and feeding guild (Fig. 5). The degrees of freedom are 4, 9 for 2011 and 4,19 for 2012–2013. A significant effect indicates that at least one of the slope or intercept values differed from the others. Polynomial contrasts by regression, in italics, were carried out to identify the source of differences.

	2011		2012		2013	
	Slope	Intercept	Slope	Intercept	Slope	Intercept
Plant feeder beetles	4.266*	17.059**	1.157	4.551**	0.459	1.865
Old forests vs. Plantations	*0.609*	*0.450*		*0.037*		
Commercial thinned vs. Unthinned	*13.120***	*67.180***		*24.876***		
Status quo vs. Biomass removal	*1.437*	*0.569*		*0.137*		
Status quo vs. Enhanced structure	*0.003*	*1.757*		*0.011*		
Inner bark beetles	0.553	10.651**	5.640**	24.237**	7.004**	14.107**
Old forests vs. Plantations		*0.336*	*11.860***	*41.990***	*6.105**	*12.379***
Commercial thinned vs. Unthinned		*41.728***	*0.432*	*28.818***	*19.640***	*40.029***
Status quo vs. Biomass removal		*0.078*	*1.836*	*1.374*	*0.198*	*0.327*
Status quo vs. Enhanced structure		*0.329*	*0.071*	*1.233*	*0.312*	*0.345*
Outer bark beetles	2.495	13.364**	2.216	7.454**	0.236	8.073**
Old forests vs. Plantations		*2.606*		*1.424*		*0.985*
Commercial thinned vs. Unthinned		*46.082***		*35.108***		*33.217***
Status quo vs. Biomass removal		*1.450*		*0.064*		*1.737*
Status quo vs. Enhanced structure		*2.342*		*1.211*		*1.132*
Predatory beetles	0.654	17.756**	0.615	10.915**	0.431	1.685
Old forests vs. Plantations		*0.817*		*0.105*		

Commercial thinned vs. Unthinned	*30.665***	*46.245***
Status quo vs. Biomass removal	*17.289**	*2.460*
Status quo vs. Enhanced structure	*2.063*	*2.063*

* $0.05 \geq P \geq 0.01$

** $P < 0.01$

Table 3. Mean (n=2) density/ha ± SEM of deer mouse, red-backed vole, woodland jumping mouse, and short-tailed shrew per commercial thinning (CT) treatment per landscape (plantation dominated, hardwood dominated, or mixed) averaged over spring and summer 2011 through 2012 with RM-ANOVA results, in the Black Brook District, northwest New Brunswick.

Species and Landscape	Density/ha (±SEM) per Treatment			RM-ANOVA Landscape			Treatment			Landscape x Treatment		
	Unthinned	Biomass Removal CT	Status Quo CT	df	F	p	df	F	p	df	F	p
Deer mouse												
Hardwood	3.8±1.8	6.7±2.5	5.4±2.2	2	4.07	0.06	2	0.51	0.62	4	1.46	0.29
Mixed	5.8±2.8	3.1±0.9	4.3±1.5									
Plantation	4.1±2.8	0.6±0.5	1.0±0.5									
Woodland jumping mouse												
Hardwood	13.8±4.6	3.6±1.8	2.4±1.2	2	1.09	0.38	2	5.00	0.04	4	0.43	0.79
Mixed	6.1±2.2	2.1±0.9	2.3±1.0									
Plantation	7.4±3.3	1.5±1.0	0.8±0.5									
Red-backed vole												
Hardwood	1.1±0.6	2.6±1.1	7.2±2.3	2	5.18	0.03	2	6.70	0.02	4	0.75	0.58
Mixed	4.2±1.1	3.4±1.6	7.1±1.8									
Plantation	1.2±0.8	0.3±0.2	2.7±1.5									
Short-tailed shrew												
Hardwood	12.3±4.7	5.6±3.4	5.5±3.2	2	0.82	0.47	2	2.77	0.12	4	0.48	0.75
Mixed	12.0±5.3	8.4±4.6	10.1±4.6									
Plantation	9.0±4.2	5.6±3.8	6.3±3.1									

Table 4. Predicted magnitude and speed of response of beetle, plant, small mammal, and bird taxa to three commercial thinning (CT) treatments, relative to the unthinned: status quo thinning, biomass removal thinning, and enhanced structure (unthinned clumps and girdled trees). 'Predict' columns are original predicted response, and 'Results' columns include observed year 3 results. Arrows indicate direction of response (increase or decrease); numbers refer to the three CT treatments.

Taxa	1. Unthinned	2. Status quo CT		3. Biomass removal CT		4. Enhanced structure CT	
		Predict	Results	Predict	Results	Predict	Results
Magnitude of response							
Beetles							
Plant feeder beetles	---	High ↑	High ↑	> 2	= 2	= 2	= 2
Inner bark beetles	---	High ↑	High ↑	< 2	= 2	> 2	= 2
Outer bark beetles	---	High ↑	High ↑	< 2	= 2	> 2	= 2
Predatory beetles	---	High ↑	High ↑	= 2	= 2	≥ 2	= 2
Plants							
Vascular (cover)	---	High ↑	Mod. ↑	High ↑	High ↑	High ↑	Mod. ↑
Vascular (richness)	---	Mod. ↑	Low. ↑	Low. ↑	Low. ↑	Mod. ↑	Low. ↑
Small mammals							
Red Back Voles	---	High ↑	High ↑	Low ↓	High ↓	Unknown	No effect
Deer Mice	---	High ↑	Low	Low ↓	Low	Unknown	No effect
Jumping Mice	---	High ↑	High ↓	Low ↓	High ↓	Unknown	No effect

Birds	---	Mod. ↑	No effect	Low ↓	No effect	High ↑	No effect
Speed of response							
Beetles							
Plant feeder beetles	---	Fast	Fast	Fast	Fast	---	---
Inner bark beetles	---	Fast	Fast	Fast	Fast	Fast	---
Outer bark beetles	---	Moderate	Fast	Moderate	Fast	Moderate	---
Predatory beetles	---	Moderate	Moderate	Moderate	Moderate	---	---
Plants							
Vascular	---	Moderate	Moderate	Fast	Fast	Slow	Moderate
Small mammals							
Red Back Voles	---	Fast	Fast	Moderate	Fast	Slow	Absent
Deer Mice	---	Fast	Unknown	Moderate	Unknown	Slow	Absent
Jumping Mice	---	Fast	Fast	Moderate	Fast	Slow	Absent
Birds	---	Slow	Slow	Slow	Slow	Moderate	Slow

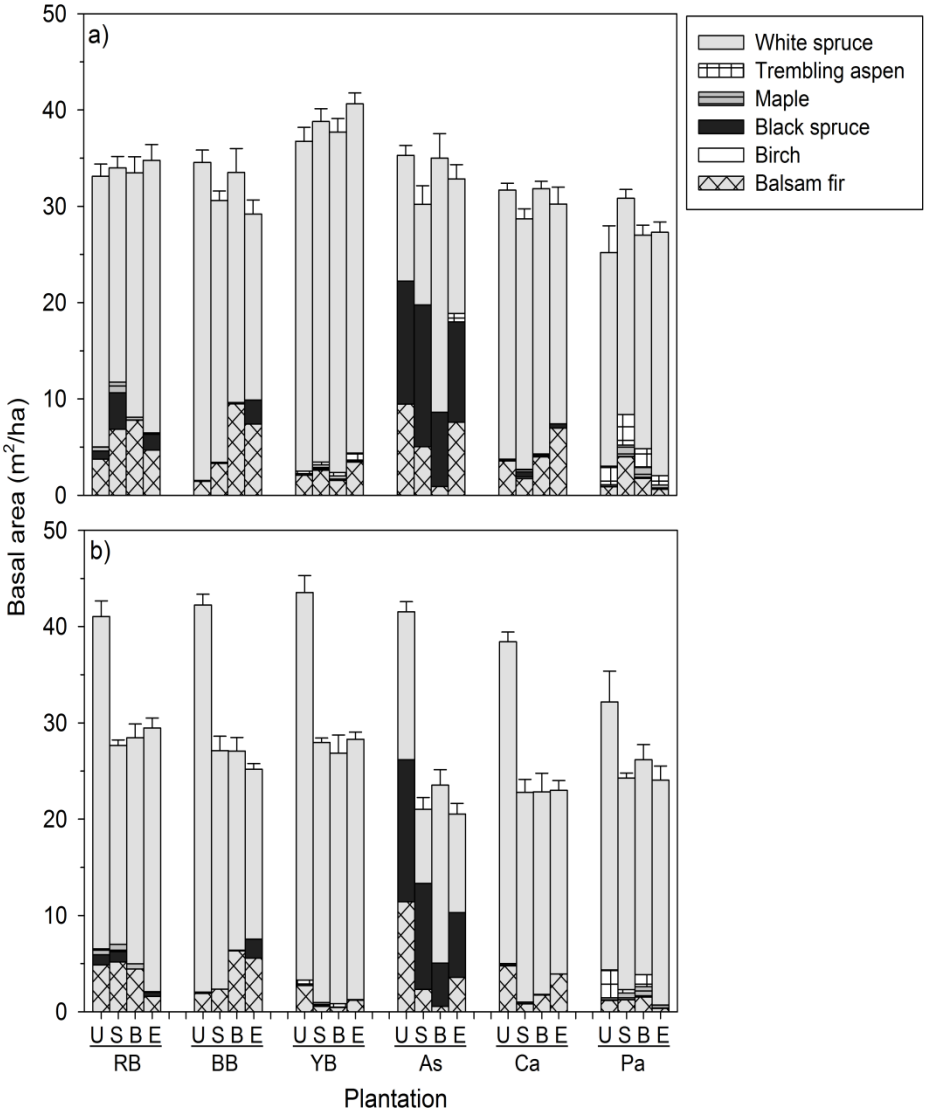

Fig. 1. Basal area by species in each of four treatments in six spruce plantations (a) before and (b) after thinning. Abbreviations: U unthinned, S status quo commercial thinning (CT), B biomass removal CT, and E enhanced structure CT treatments; RB Roussel Brook, BB Brown Brook, YB Yellow Brook, As Airstrip, Ca Canton, and Pa Paget plantations.

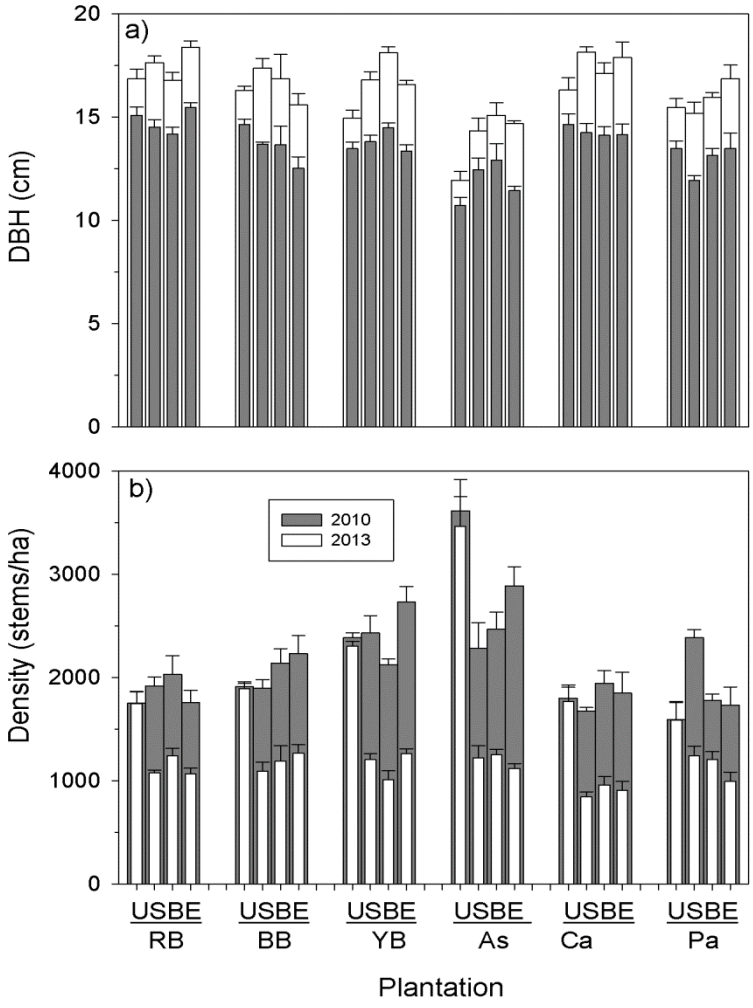

Fig. 2. Mean (a) diameter at breast height (DBH) and (b) tree density in each treatment for six spruce plantations before (2010) and after (2013) thinning. U, S, B, and E represent unthinned, status quo commercial thinning (CT), biomass removal CT, and enhanced structure CT treatments, respectively. RB, BB, YB, As, Ca and Pa represent Roussel Brook, Brown Brook, Yellow Brook, Airstrip, Canton and Paget plantations, respectively.

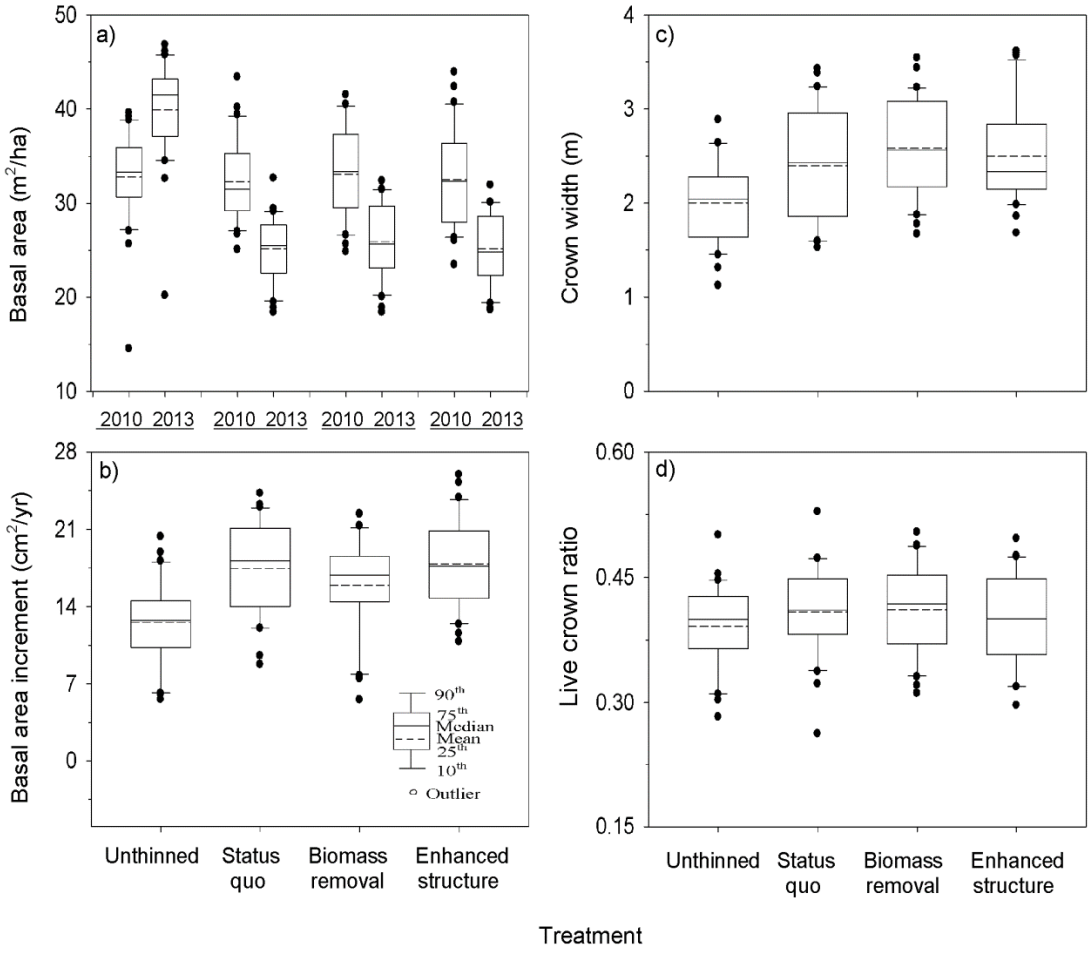

Fig. 3. Basal area (a), (b) basal area increment, (c) crown width, and (d) live crown ratio in 30 plots in each of unthinned and three commercial thinning treatments for six spruce plantations, 3 years after thinning.

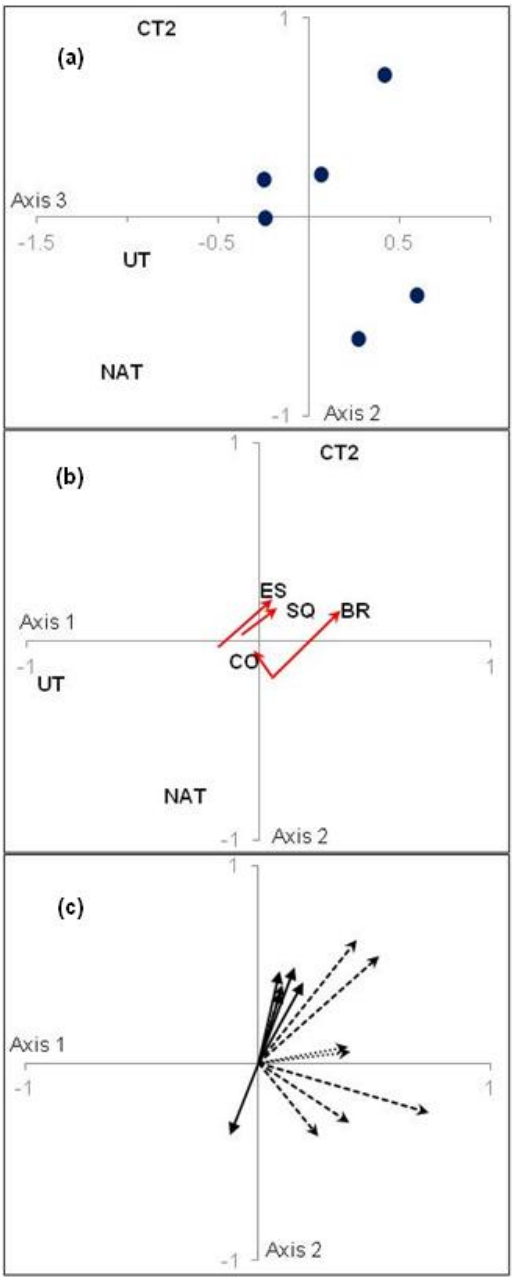

Fig. 4. (a) Reference treatment (codes) and experimental plantation (circles) centroids plotted on Axes 2 and 3 of NMS ordination to show range of compositional variation; (b) Reference treatment (codes) and experimental treatment (vectors from 2001 to 2012 centroid) plotted on Axes 1 and 2 of NMS ordination, and (c) selected species-correlations on Axes 1 and 2 presented as vectors from origin (length of vector =

strength of correlation); solid lines = shrubs and regenerating hardwoods (e.g., *Acer* spp., *Populus tremuloides* Michx.), dashed lines = rhizomatous forest herbs (e.g., *Cornus canadensis* L., *Maianthemum canadense* (Desf.) Greene) and ferns (e.g., *Dryopteris* spp.), and dotted lines = ruderal species (Poaceae, *Chamerion angustifolium* (L.) Holub).

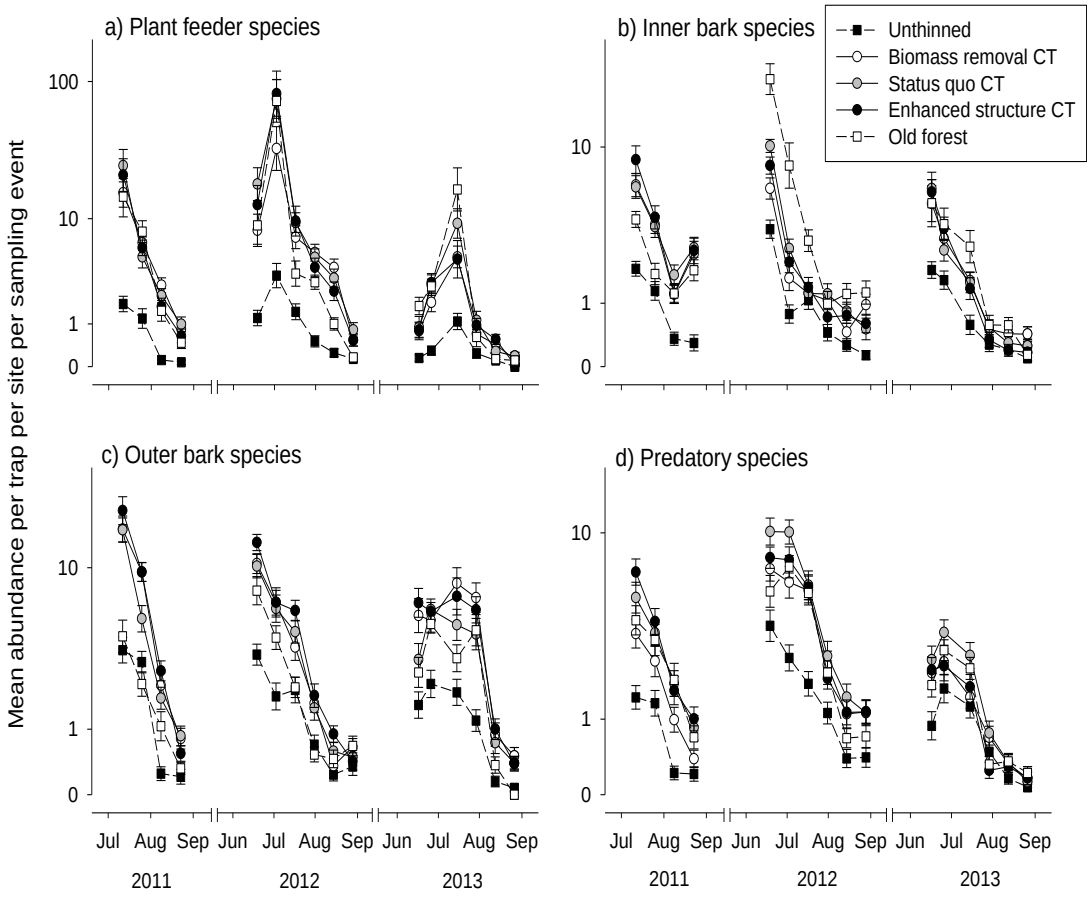

Fig. 5. Mean beetle abundance (± SEM) per trap per two weeks in unthinned and three commercial thinned (CT) treatments as a function of the sampling date for (a) plant feeder beetles (i.e., species consuming leafy vegetation, pollen, nectar, roots and/or decomposing plant material), (b) inner bark beetles (i.e., species feeding on xylem, phloem and/or sap), (c) outer bark beetles (i.e., species grazing on fungal fruiting bodies, fungal hyphae and/or slime molds), and (d) predatory beetles (i.e., species consuming invertebrates and/or decomposing animal material).

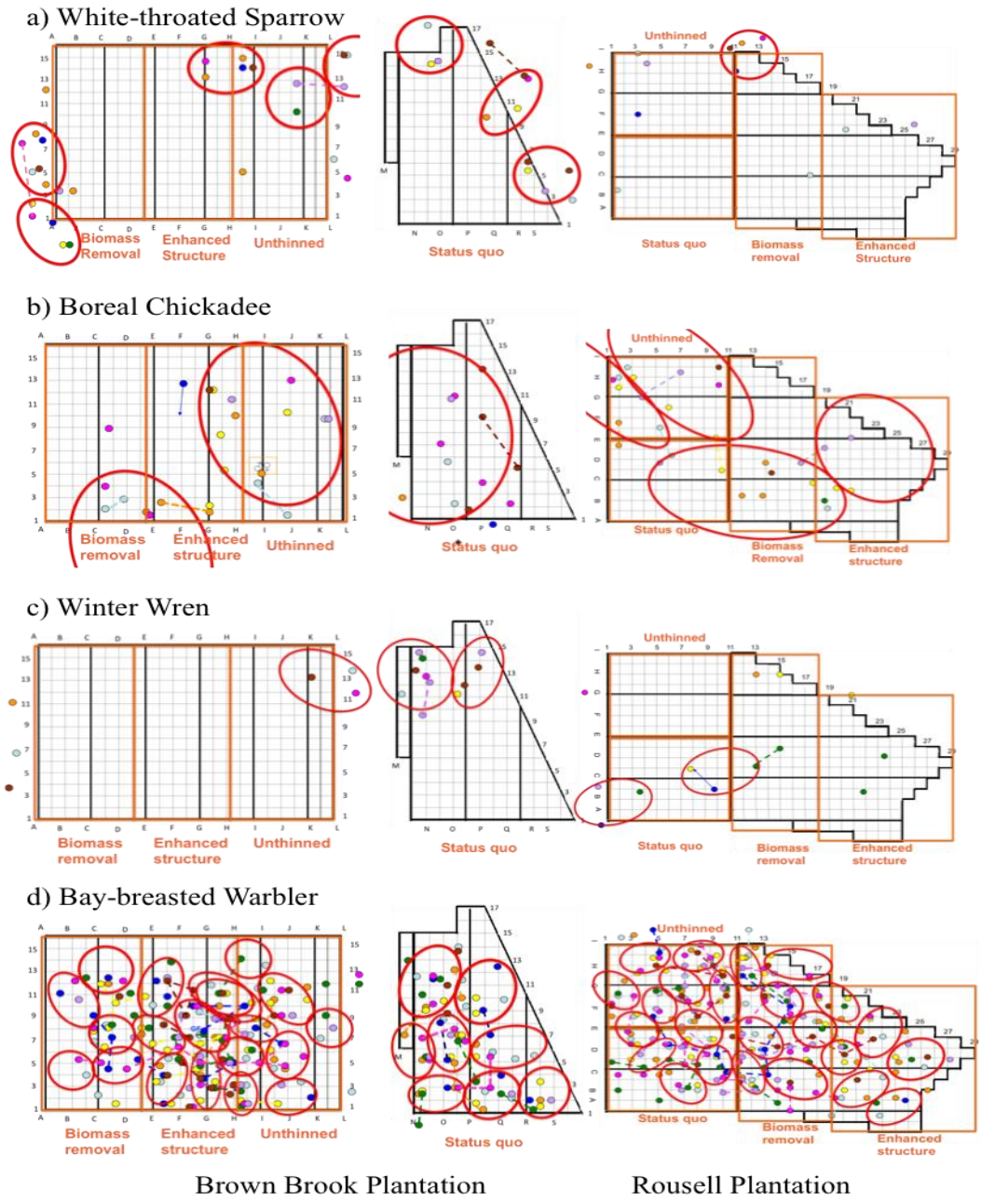

Fig. 6. Detections of White-throated Sparrow, Boreal Chickadee, Winter Wren, and Bay-breasted Warbler (coloured dots, with colours representing eight survey dates from May-June 2011), and estimated territories (red ellipses) in two 25 year-old spruce plantations. Treatment blocks that are not separated by roads are delineated by orange rectangles.

APPENDIX 2 ARTICLE COPYRIGHT PERMISSION

Chapter 2: NRC Research Press

Please review: http://www.nrcresearchpress.com/page/authors/information/rights

As one of the authors of this paper, you may reuse your published material. Permission is granted.

Thank you for checking.

Regards,
Thera Pritchard
Customer Service and Sales Coordinator
Canadian Science Publishing
65 Auriga Drive, Suite 203, Ottawa, ON K2E 7W6
T: 613-656-9846 ext. 231 F: 613-656-9838

Chapter 3: Elsevier License Terms and Conditions

Apr 13, 2016

This is a License Agreement between Kwadwo Omari ("You") and Elsevier ("Elsevier") provided by Copyright Clearance Center ("CCC"). The license consists of your order details, the terms and conditions provided by Elsevier, and the payment terms and conditions. All payments must be made in full to CCC. For payment instructions, please see information listed at the bottom of this form.

Supplier	Elsevier Limited The Boulevard, Langford Lane Kidlington, Oxford, OX5 1GB, UK
Registered Company Number	1982084
Customer name	Kwadwo Omari
Customer address	758 Regent Street Fredericton, NB E3B 3Y4
License number	3847411474417
License date	Apr 13, 2016
Licensed content publisher	Elsevier
Licensed content publication	Forest Ecology and Management
Licensed content title	Effect of local stand structure on leaf area, growth, and growth efficiency following thinning of white spruce

Licensed content author	Kwadwo Omari, David A. MacLean, Michael B. Lavigne, John A. Kershaw, Greg W. Adams
Licensed content date	15 May 2016
Licensed content volume number	368
Licensed content issue number	n/a
Number of pages	8
Start Page	55
End Page	62
Type of Use	reuse in a thesis/dissertation
Portion	full article
Format	both print and electronic
Are you the author of this Elsevier article?	Yes
Will you be translating?	No
Title of your thesis/dissertation	STAND STRUCTURAL CHANGES FOLLOWING COMMERCIAL THINNING FO WHITE SPRUCE
Expected completion date	May 2016
Estimated size (number of pages)	204
Elsevier VAT number	GB 494 6272 12
Permissions price	0.00 CAD
VAT/Local Sales Tax	0.00 CAD / 0.00 GBP
Total	0.00 CAD

Terms and Conditions

INTRODUCTION

1. The publisher for this copyrighted material is Elsevier. By clicking "accept" in connection with completing this licensing transaction, you agree that the following terms and conditions apply to this transaction (along with the Billing and Payment terms and conditions established by Copyright Clearance Center, Inc. ("CCC"), at the time that you opened your Rightslink account and that are available at any time at http://myaccount.copyright.com).

GENERAL TERMS

2. Elsevier hereby grants you permission to reproduce the aforementioned material subject to the terms and conditions indicated.

3. Acknowledgement: If any part of the material to be used (for example, figures) has appeared in our publication with credit or acknowledgement to another source, permission must also be sought from that source. If such permission is not obtained then that material may not be included in your publication/copies. Suitable acknowledgement to the source must be made, either as a footnote or in a reference list at the end of your publication, as follows:

"Reprinted from Publication title, Vol /edition number, Author(s), Title of article / title of chapter, Pages No., Copyright (Year), with permission from Elsevier [OR APPLICABLE SOCIETY COPYRIGHT OWNER]." Also Lancet special credit "Reprinted from The Lancet, Vol. number, Author(s), Title of article, Pages No., Copyright (Year), with permission from Elsevier."
4. Reproduction of this material is confined to the purpose and/or media for which permission is hereby given.
5. Altering/Modifying Material: Not Permitted. However figures and illustrations may be altered/adapted minimally to serve your work. Any other abbreviations, additions, deletions and/or any other alterations shall be made only with prior written authorization of Elsevier Ltd. (Please contact Elsevier at permissions@elsevier.com)
6. If the permission fee for the requested use of our material is waived in this instance, please be advised that your future requests for Elsevier materials may attract a fee.
7. Reservation of Rights: Publisher reserves all rights not specifically granted in the combination of (i) the license details provided by you and accepted in the course of this licensing transaction, (ii) these terms and conditions and (iii) CCC's Billing and Payment terms and conditions.
8. License Contingent Upon Payment: While you may exercise the rights licensed immediately upon issuance of the license at the end of the licensing process for the transaction, provided that you have disclosed complete and accurate details of your proposed use, no license is finally effective unless and until full payment is received from you (either by publisher or by CCC) as provided in CCC's Billing and Payment terms and conditions. If full payment is not received on a timely basis, then any license preliminarily granted shall be deemed automatically revoked and shall be void as if never granted. Further, in the event that you breach any of these terms and conditions or any of CCC's Billing and Payment terms and conditions, the license is automatically revoked and shall be void as if never granted. Use of materials as described in a revoked license, as well as any use of the materials beyond the scope of an unrevoked license, may constitute copyright infringement and publisher reserves the right to take any and all action to protect its copyright in the materials.
9. Warranties: Publisher makes no representations or warranties with respect to the licensed material.
10. Indemnity: You hereby indemnify and agree to hold harmless publisher and CCC, and their respective officers, directors, employees and agents, from and against any and all claims arising out of your use of the licensed material other than as specifically authorized pursuant to this license.
11. No Transfer of License: This license is personal to you and may not be sublicensed, assigned, or transferred by you to any other person without publisher's written permission.
12. No Amendment Except in Writing: This license may not be amended except in a writing signed by both parties (or, in the case of publisher, by CCC on publisher's behalf).
13. Objection to Contrary Terms: Publisher hereby objects to any terms contained in any purchase order, acknowledgment, check endorsement or other writing prepared by you,

which terms are inconsistent with these terms and conditions or CCC's Billing and Payment terms and conditions. These terms and conditions, together with CCC's Billing and Payment terms and conditions (which are incorporated herein), comprise the entire agreement between you and publisher (and CCC) concerning this licensing transaction. In the event of any conflict between your obligations established by these terms and conditions and those established by CCC's Billing and Payment terms and conditions, these terms and conditions shall control.

14. Revocation: Elsevier or Copyright Clearance Center may deny the permissions described in this License at their sole discretion, for any reason or no reason, with a full refund payable to you. Notice of such denial will be made using the contact information provided by you. Failure to receive such notice will not alter or invalidate the denial. In no event will Elsevier or Copyright Clearance Center be responsible or liable for any costs, expenses or damage incurred by you as a result of a denial of your permission request, other than a refund of the amount(s) paid by you to Elsevier and/or Copyright Clearance Center for denied permissions.

LIMITED LICENSE

The following terms and conditions apply only to specific license types:

15. Translation: This permission is granted for nonexclusive world English rights only unless your license was granted for translation rights. If you licensed translation rights you may only translate this content into the languages you requested. A professional translator must perform all translations and reproduce the content word for word preserving the integrity of the article.

16. Posting licensed content on any Website: The following terms and conditions apply as follows: Licensing material from an Elsevier journal: All content posted to the web site must maintain the copyright information line on the bottom of each image; A hypertext must be included to the Homepage of the journal from which you are licensing at http://www.sciencedirect.com/science/journal/xxxxx or the Elsevier homepage for books at http://www.elsevier.com; Central Storage: This license does not include permission for a scanned version of the material to be stored in a central repository such as that provided by Heron/XanEdu.

Licensing material from an Elsevier book: A hypertext link must be included to the Elsevier homepage at http://www.elsevier.com. All content posted to the web site must maintain the copyright information line on the bottom of each image.

Posting licensed content on Electronic reserve: In addition to the above the following clauses are applicable: The web site must be password-protected and made available only to bona fide students registered on a relevant course. This permission is granted for 1 year only. You may obtain a new license for future website posting.

17. For journal authors: the following clauses are applicable in addition to the above: Preprints: A preprint is an author's own write-up of research results and analysis, it has not been peer-reviewed, nor has it had any other value added to it by a publisher (such as formatting, copyright, technical enhancement etc.). Authors can share their preprints anywhere at any time. Preprints should not be added to or enhanced in any way in order to appear more like, or to substitute for, the final versions of articles however authors can update their preprints on arXiv or RePEc with their Accepted Author Manuscript (see below). If accepted for publication, we encourage authors to link from the preprint

to their formal publication via its DOI. Millions of researchers have access to the formal publications on ScienceDirect, and so links will help users to find, access, cite and use the best available version. Please note that Cell Press, The Lancet and some society-owned have different preprint policies. Information on these policies is available on the journal homepage.
Accepted Author Manuscripts: An accepted author manuscript is the manuscript of an article that has been accepted for publication and which typically includes author-incorporated changes suggested during submission, peer review and editor-author communications.
Authors can share their accepted author manuscript:
- immediately
    - o via their non-commercial person homepage or blog
    - o by updating a preprint in arXiv or RePEc with the accepted manuscript
    - o via their research institute or institutional repository for internal institutional uses or as part of an invitation-only research collaboration work-group
    - o directly by providing copies to their students or to research collaborators for their personal use
    - o for private scholarly sharing as part of an invitation-only work group on commercial sites with which Elsevier has an agreement
- after the embargo period
    - o via non-commercial hosting platforms such as their institutional repository
    - o via commercial sites with which Elsevier has an agreement

In all cases accepted manuscripts should:
- link to the formal publication via its DOI
- bear a CCBYNCND license - this is easy to do
- if aggregated with other manuscripts, for example in a repository or other site, be shared in alignment with our hosting policy not be added to or enhanced in any way to appear more like, or to substitute for, the published journal article.

Published journal article (JPA): A published journal article (PJA) is the definitive final record of published research that appears or will appear in the journal and embodies all value-adding publishing activities including peer review coordination, copyediting, formatting, (if relevant) pagination and online enrichment.
Policies for sharing publishing journal articles differ for subscription and gold open access articles:
Subscription Articles: If you are an author, please share a link to your article rather than the full-text. Millions of researchers have access to the formal publications on ScienceDirect, and so links will help your users to find, access, cite, and use the best available version. Theses and dissertations which contain embedded PJAs as part of the formal submission can be posted publicly by the awarding institution with DOI links back to the formal publications on ScienceDirect. If you are affiliated with a library that subscribes to ScienceDirect you have additional private sharing rights for others' research accessed under that agreement. This includes use for classroom teaching and internal training at the institution (including use in course packs and courseware programs), and inclusion of the article for grant funding purposes.
Gold Open Access Articles: May be shared according to the author-selected

end-user license and should contain a CrossMark logo, the end user license, and a DOI link to the formal publication on ScienceDirect. Please refer to Elsevier's posting policy for further information.
18. For book authors the following clauses are applicable in addition to the above: Authors are permitted to place a brief summary of their work online only. You are not allowed to download and post the published electronic version of your chapter, nor may you scan the printed edition to create an electronic version. Posting to a repository: Authors are permitted to post a summary of their chapter only in their institution's repository.
19. Thesis/Dissertation: If your license is for use in a thesis/dissertation your thesis may be submitted to your institution in either print or electronic form. Should your thesis be published commercially, please reapply for permission. These requirements include permission for the Library and Archives of Canada to supply single copies, on demand, of the complete thesis and include permission for Proquest/UMI to supply single copies, on demand, of the complete thesis. Should your thesis be published commercially, please reapply for permission. Theses and dissertations which contain embedded PJAs as part of the formal submission can be posted publicly by the awarding institution with DOI links back to the formal publications on ScienceDirect.
Elsevier Open Access Terms and Conditions
You can publish open access with Elsevier in hundreds of open access journals or in nearly 2000 established subscription journals that support open access publishing. Permitted third party reuse of these open access articles is defined by the author's choice of Creative Commons user license. See our open access license policy for more information.
Terms & Conditions applicable to all Open Access articles published with Elsevier:
Any reuse of the article must not represent the author as endorsing the adaptation of the article nor should the article be modified in such a way as to damage the author's honour or reputation. If any changes have been made, such changes must be clearly indicated. The author(s) must be appropriately credited and we ask that you include the end user license and a DOI link to the formal publication on ScienceDirect.
If any part of the material to be used (for example, figures) has appeared in our publication with credit or acknowledgement to another source it is the responsibility of the user to ensure their reuse complies with the terms and conditions determined by the rights holder.
Additional Terms & Conditions applicable to each Creative Commons user license:
CC BY: The CCBY license allows users to copy, to create extracts, abstracts and new works from the Article, to alter and revise the Article and to make commercial use of the Article (including reuse and/or resale of the Article by commercial entities), provided the user gives appropriate credit (with a link to the formal publication through the relevant DOI), provides a link to the license, indicates if changes were made and the licensor is not represented as endorsing the use made of the work. The full details of the license are available at http://creativecommons.org/licenses/by/4.0.
CC BY NC SA: The CC BYNCSA license allows users to copy, to create extracts, abstracts and new works from the Article, to alter and revise the Article, provided this is not done for commercial purposes, and that the user gives appropriate credit (with a link

CURRICULUM VITAE

Candidate's full name: Kwadwo Omari

Universities attended:
University of New Brunswick, Fredericton, Canada
Diploma in University Teaching (2011)

University of Freiburg, Freiburg, Germany (2009-2010)
Master of Science in Forest Ecology and Management (European Forestry program)

University of Eastern Finland, Joensuu, Finland (2008-2010)
Master of Science in Agriculture and Forestry (European Forestry program)

Kwame Nkrumah University of Science and Technology, Kumasi, Ghana (2003-2007)
Bachelor of Science in Natural Resources Management

Articles published in refereed journals:

Omari, K., MacLean, D.A., Lavigne, M.B., Kershaw, J.A. Jr., and Adams, G.W. 2016. Effect of local stand structure on leaf area, growth, and growth efficiency following thinning of white spruce. For. Ecol. Manage., 368:55-62. (This thesis, Ch. 3).

Omari, K., and MacLean D.A. 2015. Do biomass removal and structure-enhancing treatments influence deadwood characteristics following commercial thinning in spruce plantations in New Brunswick, Canada? Can J. For. Res., 45:1407-1418. (This thesis, Ch. 2).

MacLean, D.A., Dracup, E., Gandiaga, F., Haughian, S.R., MacKay, A., Nadeau, P**.,** Omari, K., Adams, G., Frego, K.A., Keppie, D., Moreau, G., and Villard, M-A. 2015. Experimental manipulation of habitat structures in intensively managed spruce plantations to increase their value for biodiversity conservation. For. Chron., 91:161-175. (This thesis, Appendix 1).

Selected non-refereed contributions (posters, presentations):

Omari, K., and MacLean, D.A. 2015. Effect of local stand structure on leaf area, growth, and growth efficiency following thinning of white spruce. Oral presentation at JDI Forest Research and Advisory Committee meeting, Jun. 16, St. Leonard, NB., Canada.

Omari, K., and MacLean, D.A. 2014. Stand structure and deadwood dynamics in white

spruce (*Picea glauca* (Moench) Voss) plantations following alternative commercial thinning. Oral presentation at Eastern CANUSA Forest Science Conference, Oct. 16-18, Rimouski, QC, Canada.

Omari, K., and MacLean, D.A. 2014. Effect of alternative commercial thinning on deadwood dynamics in white spruce (*Picea glauca* (Moench) Voss) plantations. Oral presentation at Science Atlantic Environment Conference, Mar. 14-15, Antigonish, NS, Canada.

Omari, K., and MacLean D.A. 2013. Deadwood dynamics in white spruce (*Picea glauca* (Moench) Voss) plantations following alternative commercial thinning treatments. Poster presentation at Ecological Society of America Annual Meeting, Aug. 4-9, Minneapolis, MN, USA.

Omari, K., and MacLean, D.A. 2012. Stand structure and light changes in white spruce plantations in response to commercial thinning and nutrient enrichment (thinning effects on coarse woody debris, snags and stand structure). Oral presentation at JDI Forest Research and Advisory Committee meeting, Jun. 20, St. Leonard, NB., Canada.

Omari, K., and MacLean, D.A. 2011. Stand structure and light changes in white spruce plantations in response to commercial thinning and nutrient enrichment (effect of thinning on stand structure). Oral presentation at JDI Forest Research and Advisory Committee Meeting, Nov. 29, Fredericton, NB., Canada.