UNIVERSITÉ DU QUÉBEC À MONTRÉAL

DYNAMIQUE DE LA RÉGÉNÉRATION DE L'ÉPINETTE NOIRE ET DU PIN GRIS APRÈS FEU, COUPE DE RÉCUPÉRATION, ET ÉCLAIRCIE PRÉCOMMERCIALE

THÈSE

PRÉSENTÉE

COMME EXIGENCE PARTIELLE

DU DOCTORAT EN SCIENCES DE L'ENVIRONNEMENT

PAR

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DEDICATION

To my beautiful wife Amanda Savoie, my wonderful children (Hunter, Olivia, and Angus), my parents (Andrzej and Zofia Splawinski), and everyone else who participated in helping make this project successful. My deepest thank you for your dedication, support, encouragement, and contribution.

FOREWORD

This thesis is composed of a global introduction, four chapters that represent the work of my doctoral research, a global conclusion, and an annex. The four chapters are presented in scientific article format, and are either published in peer-reviewed journals or submitted for review. With collaboration from co-authors, I was responsible for developing and writing each of the four chapters. Each chapter includes an introduction, literature review, objectives, methodology, results, discussion, and brief conclusion.

The first chapter, titled *A stand-level tool for predicting the natural regeneration density of black spruce and jack pine following fire and salvage*, has been accepted for publication (in press) in the journal *The Forestry Chronicle*. The co-authors are my project supervisors, Sylvie Gauthier, David F. Greene, and Yves Bergeron. I was responsible for developing the methodology, conducting a review of the literature, obtaining field data, running simulations, presenting results, and writing of the first and final draft of the manuscript. Each co-author contributed to the objectives, general structure, and the revision of this manuscript.

The second chapter, titled *A landscape-level tool for assessing natural regeneration density of black spruce and jack pine following fire and salvage*, will be submitted in the near future. The co-authors are my project supervisors, Sylvie Gauthier, David F. Greene, and Yves Bergeron, as well as Osvaldo Valeria. I was responsible for developing the objectives, conducting a review of the literature, obtaining field data, conducting the statistical analysis, running simulations, presenting results, and writing of the first and final draft of the manuscript. Each co-author contributed to the methodology, the general structure, and the revision of this manuscript.

The third chapter, titled *Pre-commercial thinning of black spruce and jack pine stands following fire: impact of treatment timing and stand composition on growth*, will be submitted in the near future. The co-authors are my project supervisors, Sylvie Gauthier, David F. Greene, and Yves Bergeron, as well as Igor Drobyshev. I was responsible for developing the objectives, conducting a review of the literature, obtaining field data, preparing tree disks for analysis, dating trees, measuring annual and obtaining average growth rates, presenting results, and writing of the first draft of the manuscript. Each co-author contributed to the methodology, statistical analysis, and the revision of this manuscript.

The fourth chapter, titled *The impact of early pre-commercial thinning of dense jack pine (Pinus banksiana Lamb.) stands on the mortality of thinned stems*, was published in 2014 in the journal *The Forestry Chronicle, 90, 371-377*. The co-authors are my project supervisors, Sylvie Gauthier, David F. Greene, and Yves Bergeron. I developed the idea to study this topic, and was responsible for creating the research design (objectives, methodology), conducting a review of the literature, obtaining field data, performing statistical analysis, presenting results, and writing of the first and final draft of the manuscript. Each co-author contributed to the revision of this manuscript.

Two manuscripts that were used to develop the first two chapters in this thesis are included in annex A and B following the references. These manuscripts represent work from my MSc thesis at Concordia University (Post-fire and post-salvage regeneration dynamics of *Picea mariana* and *Pinus banksiana*), however a significant portion of my PhD research time was devoted to ameliorating their content and making them suitable for publication.

The first manuscript (annex A) (Greene et al. 2013) outlines the abscission schedules of black spruce and jack pine following fire, taking into account the full temporal window of seed rain. Originally this process was modeled as a negative exponential function, however following my MSc studies, it was changed to a two-parameter Weibull distribution. Additionally, abscission data for both species was added from additional fires and significant revisions were made as suggested by reviewers.

The second manuscript (annex B) (Splawinski et al. 2014a) presents a post-fire and post-salvage natural regeneration model, parameterized using empirical data and ecological principles taken from existing literature, including the abscission schedule from Greene et al. (2013). Additional work during my doctoral program included significant de-bugging of the model, modification of parameters based on newly available literature, re-running of all simulations, a change in statistical approach, the addition of a sensitivity analysis, and a change in the presentation of figures in the prescriptive simulations section.

Prior to beginning work on the stand and landscape-level natural regeneration assessment tools presented in the first two chapters, these two manuscripts first had to be subjected to the scrutiny of peer-review. This was necessary in order to avoid having the underlying approach of these tools called into question.

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LIST OF ABBREVIATIONS AND ACRONYMS

A	Aspen
Al	Alder spp.
B	Birch
BAI	Basal area increment
BI	Burned intact
BS	Black spruce
C	Cherry
CPRS	Cutting with protection of regeneration and soils
DBH	Diameter at breast height
Dpi	Dots per inch
DSH	Diameter at stump height
JP	Jack pine
N/A	Not available
UQAM	Université du Québec à Montréal
UQAT	Université du Québec en Abitibi-Témiscamingue
CFS	Canadian Forest Service
EE	Pure black spruce
FQRNT	Fonds de recherche du Québec – Nature et technologies
GIS	Geographic Information Systems
JIN	Young uneven-age
NSERC	Natural Sciences and Engineering Research Council of Canada
PGPG	Pure jack pine
S	Salvaged
SFM	Sustainable Forest Management
VIN	Old uneven-aged
W	Willow spp.

LIST OF SYMBOLS AND UNITS OF MEASUREMENT

CI	Confidence interval
CL	Confidence limit
cm	Centimeter
°C	Degrees Celsius
ha	Hectare
km	Kilometer
m	Meter
mm	Millimeter
N	North
n	Sample size
Prob.	Probability
W	West
α	Alpha
$\sum$	Sum
°	Degrees

RÉSUMÉ

Le feu est la perturbation dominante dans la forêt boréale de l'Amérique du Nord et il influence de manière significative la structure et la composition des communautés forestières en réinitialisant la succession des peuplements. Dans les peuplements brulés, l’épinette noire et le pin gris vont généralement se régénérer avec des densités similaires qui existaient avant feu, maintenant ainsi leur prédominance en raison de leurs nombreux caractères adaptatifs. Toutefois, la coupe de récupération est souvent employée, réduisant ainsi la régénération naturelle et nécessitant donc des investissements couteux en termes d’efforts de reboisement. En outre, l'éclaircie précommerciale est souvent nécessaire dans les peuplements denses, afin de contrôler la compétition et l'espacement dans le but d'augmenter la croissance radiale des conifères résiduels et de diminuer l'âge de révolution du peuplement.

L'objectif principal de cette thèse est d'améliorer l’aménagement durable des peuplements d’épinette noire et du pin gris. Avec une meilleure compréhension des facteurs responsables de la régénération après feu et coupe de récupération, on pourra fournir aux gestionnaires forestiers des outils et des recommandations sylvicoles qui pourront réduire le besoin d’interventions après feu tout en augmentant leur succès lorsqu'elles sont utilisées; minimisant ainsi les couts d’investissements.

Ce projet de doctorat porte sur l'amélioration de la gestion durable des peuplements d'épinette noire et du pin gris, les deux espèces de conifères les plus abondantes et commercialement importantes dans la forêt boréale du nord-ouest du Québec. Plus précisément, il examine deux étapes importantes de la régénération après feu et coupe de récupération : (1) la phase d’établissement initial, et (2) la réponse de croissance suite à des opérations d’éclaircie précommerciale dans le stade juvénile du développement.

Les deux premiers chapitres se concentrent sur la phase d'établissement. Un modèle de régénération après feu est utilisé pour créer un outil à l'échelle du peuplement et du paysage pour évaluer rapidement la densité de la régénération naturelle de l'épinette noire et du pin gris après feu et coupe de récupération. Les troisième et quatrième chapitres se concentrent sur l'amélioration de la réussite et la réduction des couts d’opérations d'éclaircie précommerciale appliquées durant le stade juvénile. Ces deux derniers chapitres s’appuient principalement sur des données de terrain et de dendrochronologie.

L'outil à l'échelle du peuplement présenté dans le premier chapitre identifie le pourcentage de lits de germination optimal nécessaire qui donnerait une densité de semis concordante avec le plein boisement selon les écarts de surfaces terrières généralement observées sur le terrain. Cet outil peut être utilisé pour guider les décisions de gestion sur la planification de la construction routière et la séquence de

la récolte. Par opposition aux inventaires de semis classiques, l’outil tient compte de la phase d’établissement en entier. De plus, cet outil peut être utilisé pour ajuster le calendrier de récolte, pour minimiser le besoin de reboisement et pour estimer le coût final probable de plantation pour un feu donné.

L'outil à l'échelle du paysage présenté dans le deuxième chapitre combine l'utilisation de SIG, de données terrain, de données des placettes temporaires et de données d'inventaire forestier. Il permet aux gestionnaires forestiers d'évaluer rapidement les besoins de reboisement au niveau du paysage et peut être utilisé pour mieux planifier les opérations de récupération et l'application de traitements sylvicoles ultérieurs. L’estimation des couts potentiels de futures interventions telles que la plantation, l'ensemencement aérien et l'éclaircie précommerciale peuvent être calculées. Les forestiers peuvent également évaluer la vulnérabilité actuelle des unités de gestion au feu et identifier les régions particulièrement à risque.

Le troisième chapitre examine l'impact du moment où sont réalisées les opérations d'éclaircie précommerciale et de la composition des peuplements sur la réponse de la croissance radiale de l'épinette noire et du pin gris. Il examine aussi la nouvelle production de pousses et la mortalité des feuillus éclaircis. Les résultats peuvent guider les gestionnaires de la forêt pour l'amélioration de la sélection des sites pour l’éclaircie précommerciale, ainsi que la période et l'intensité des opérations afin d'accroître la croissance radiale des arbres résiduels et de minimiser les couts.

Le quatrième chapitre se concentre sur l'impact de la hauteur de l’éclaircie précommerciale et du calendrier des opérations sur la régénération des tiges de pin gris éclaircies. Des recommandations sont faites sur la hauteur de l’éclaircie et le calendrier des opérations afin de minimiser la repousse des tiges éclaircies, améliorant ainsi la réussite du traitement et minimisant les chances de devoir faire d'autres interventions. Aussi, divers indicateurs sont présentés afin de mieux planifier les opérations d'éclaircies.

Les résultats présentés dans cette thèse augmentent la compréhension des dynamiques de régénération et de croissance après feu et récupération de l'épinette noire et de pin gris. En plus d’ajouter à nos connaissances fondamentales, ils fournissent aux forestiers de nouveaux outils pour l'évaluation de la régénération naturelle et des recommandations sur où et comment employer des traitements sylvicoles tels que la plantation et l'éclaircie précommerciale. Minimiser la planification opérationnelle et le temps de réponse après feu et récupération, augmenter l’utilisation de la régénération naturelle, augmenter la réponse de croissance radiale des tiges résiduelles dans les peuplements éclaircis et minimiser les couts d’interventions conduiront à une meilleure gestion durable de cette ressource naturelle importante.

Mots-clefs: Feu de forêt, coupe de récupération, épinette noire, pin gris, régénération, éclaircie précommerciale, plantation, croissance, mortalité, évaluation, paysage, peuplement.

ABSTRACT

Fire is the dominant disturbance in the boreal forest of North America, and significantly influences forest community structure and composition by resetting stand succession. Due to numerous adaptive traits, both black spruce and jack pine typically regenerate burned stands to similar densities that existed prior to fire thereby maintaining dominance. Salvage logging however is now often employed, reducing natural regeneration and requiring costly investments in reforestation efforts. In addition, pre-commercial thinning is often required in dense stands following fire and salvage logging to control competition and spacing in order to increase the radial growth of target conifers and decrease stand rotation age.

The principal objective of this thesis is to improve the understanding of factors responsible for post-fire and post-salvage regeneration and then provide forest managers with tools and silvicultural recommendations that would increase the sustainable management of black spruce and jack pine stands, and decrease the need for post-fire interventions but increase their success when employed. It also seeks to minimize the cost of investments.

This doctoral project focuses on improving the sustainable management of stands of black spruce and jack pine, the two most abundant and commercially important conifer species in the boreal forest of northwestern Quebec. Specifically it examines two important stages of regeneration following forest fire and salvage logging: (1) The initial establishment phase, and (2) subsequent growth response following pre-commercial thinning operations in the juvenile stage of development.

The first two chapters focus on the establishment phase. A post-fire regeneration model is used to create a stand and landscape-level tool for quickly assessing natural regeneration density of black spruce and jack pine following fire and salvage. The third and fourth chapters focus on improving the success and minimizing the cost of pre-commercial thinning operations applied in the juvenile stage. They rely primarily on field data and dendrochronology.

The stand-level tool presented in the first chapter identifies the percentage of optimal seedbeds that would yield a seedling density concordant with full stocking for a range of basal areas typically expected in the field. This tool can be used to guide management decisions about the planning of road construction and the harvest sequence, and as opposed to conventional seedling surveys, takes into account the entire establishment phase. Additionally, this tool can be used to adjust the harvesting schedule to minimize the need for planting, and to estimate the likely final cost of reforestation for an entire burn.

The landscape-level tool presented in the second chapter combines the use of GIS, field and temporary plot data, and forest inventory data. It allows managers and foresters to quickly assess reforestation needs at the landscape level, and can be used to better plan salvage operations and subsequent silvicultural treatment application. Potential cost estimates of future interventions such as planting, aerial seeding, and pre-commercial thinning could be made. Foresters can also assess the current vulnerability of management units to fire and can identify regions at particular risk.

The third chapter examines the impact of the timing of pre-commercial thinning operations and competition on the radial growth response of black spruce and jack pine. It also examines new shoot production and mortality of thinned hardwoods. Results can guide forest managers in improving site selection for pre-commercial thinning, as well as the timing and intensity of operations in order to increase the radial growth of residual trees and minimize costs.

The fourth chapter focuses on the impact of pre-commercial thinning height and timing on the re-growth of thinned jack pine stems. Recommendations are made on optimal cut height and timing of operations in order to minimize regrowth of thinned stems, thereby improving treatment success and minimizing odds of further interventions. In addition, various on-site indicators are presented to better plan thinning operations.

The results presented in this thesis increase the understanding of post-fire and post-salvage regeneration and growth dynamics of black spruce and jack pine. In addition to increasing fundamental knowledge, the results provide foresters with new natural regeneration assessment tools and recommendations on where and how to employ silvicultural treatments such as planting and pre-commercial thinning. Minimizing operational planning and response time following fire and salvage, increasing reliance on natural regeneration, improving radial growth response of residual stems in thinned stands, and minimizing costs of interventions, will lead to better management and sustainability of this important natural resource.

Keywords: Forest fire, salvage logging, black spruce, jack pine, recruitment, regeneration, pre-commercial thinning, planting, growth, regrowth, mortality, assessment, landscape, stand.

GLOBAL INTRODUCTION

As the primary disturbance in the boreal forest of North America, fire plays a significant role in driving forest community composition and structure by resetting stand succession (Payette 1992; Webber and Flannigan 1997; Stocks et al. 2002; Brassard and Chen 2006; Madoui et al. 2010). At the landscape level this results in a heterogeneous distribution of age classes and species assemblages, as well as surviving residual habitat (Morissette et al. 2002; Schmiegelow et al. 2006; Madoui et al. 2010). Across the boreal forest, the fire return time ranges from 50 to 500+ years (McRae et al. 2001; Johnstone et al. 2004; Gauthier et al. 2009), burning approximately 2.8 million ha annually (Stocks et al. 2002). Since 1995 Canada has committed itself to maintaining sustainable forest management practices (CCFM 1995); this includes sustained timber production over time, maintaining forest ecosystem health, and conservation of biological diversity. Since fire is a common and important disturbance in the Canadian boreal forest it is essential to insure proper re-establishment of the forest following this disturbance. However, the effects of both fire and post-fire salvage logging on recruitment and long-term forest recovery is not yet fully understood; indeed, a good understanding of regeneration, growth, stand productivity, and succession in young forest stands is still lacking (Van Bogaert et al. 2015).

Salvage logging is defined as the harvesting of burnt trees following wildfire. It is frequently practiced due to provincial limits in annual allowable cut, and in order to minimize economic losses (i.e. recuperate burnt timber that would otherwise be lost) (Greene et al. 2006; Lindenmayer and Noss 2006). Since fire frequency is expected to increase in the future (Bergeron et al. 2010), it will likely lead to an increase in salvage logging (Nappi et al. 2004; Lindenmayer and Noss 2006). A good understanding of the ecological effects of salvage logging, forest recovery, preparations for land reclamation, and tree growth are still lacking. Indeed foresters currently lack the tools needed to quickly assess natural regeneration densities following fire. In consequence, there are few ecologically oriented guidelines aimed at preserving biodiversity and reducing ecosystem damage (Morissette et al. 2002; Schmiegelow et al. 2006) following fire; industry guidelines merely attempt to reduce net cost. But knowledge is lacking on what type of intervention would engender maximum regeneration and growth at minimal cost. Presently, adequate regeneration of burned sites is achieved via natural regeneration (inexpensive) or treatments such as planting, aerial seeding, scarification and pre-commercial thinning (all of which are quite costly).

It is important to increase our knowledge on salvage logging and subsequent silvicultural treatments that affect the establishment and growth of trees in post-fire environments. This knowledge could potentially greatly reduce the need for, or cost of, post harvest interventions such as planting and pre-commercial thinning. Between 1998-2003, nearly 141 500 hectares of forest have burned in the regions of Abitibi and Nord-du-Québec. If one considers that interventions in the restoration of burnt areas represent more than $ 35 million annually (Portrait forestier des regions de l'Abitibi-Témiscamingue et du nord du Québec 2004), decisions relating to treatment type and timing are a key issue.

Black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) are the most common conifers in the North American boreal forest (Greene et al. 1999, 2006; Charron and Greene 2002; De Groot et al. 2004). Their widespread distribution is due mainly to their ability to quickly re-establish following fire using aerial seedbanks (Greene et al.

2013), thereby effectively out-competing other vegetation. However even with this evolutionary adaptation poor natural conifer regeneration following both fire and salvage can be observed (Greene et al. 2006). This is especially evident in stands that burn before reaching reproductive maturity (Viglas et al. 2013).

Salvage logging aims at removing timber from a burnt area (Lindenmayer and Noss 2006) and typically occurs by the first winter following fire to prevent damage to lumber by wood-boring beetles, splitting and checking, and other degradation agents (Saint-Germain and Greene 2009). It often has a negative effect on conifer recruitment and regeneration, especially for the commercially valuable species black spruce (Donato et al. 2006; Greene et al. 2006, 2013). This is attributed to the removal of the aerial seedbank, which effectively removes the seed-source crucial to the re-establishment of both these species (Greene et al. 2006, 2013; Schmiegelow et al. 2006), and the mortality of advanced regeneration as a result of the passing of salvage machinery (Greene et al. 2006). Furthermore it can lead to more dry, open conditions, resulting in faster rates of evaporation thus reducing the receptivity of seedbeds (Calogeropoulos et al. 2004; Greene et al. 2006; Schmiegelow et al. 2006). Much like traditional harvest (clearcutting) (McRae et al. 2001), changes in species composition from conifer to hardwood dominated are often observed following salvage (Greene et al. 2006; Ilisson and Chen 2009) as trees like aspen and paper birch favor these conditions.

Presently, adequate regeneration of burned and salvaged sites is achieved either via natural regeneration or through treatments such as planting. Moreover, a number of years after recruitment has ceased, pre-commercial thinning is often required as stand density is high enough that competition can decrease the growth rate of desired species. All of these treatments are quite costly, and the reasons for success/ failure are poorly understood. When natural regeneration is inadequate, as is often the case with salvage, forest companies are required to plant trees at an average cost of CAD 1000/ha (Saint-Germain and Greene 2009) to attain adequate stand stocking. Planting, as compared to natural regeneration, has the advantage of providing control for spacing and density (Science and Information Resources Division 1998), which can preclude the need to thin the stand in the future.

In order to sustainably manage pure and mixed black spruce and jack pine stands, it is essential to maintain forest composition following fire, salvage logging, and pre-commercial thinning (Vaillancourt and Leduc 2009; Nappi et al. 2011). Ideally, this would be accomplished through the reliance on natural conifer regeneration, and through the implementation of thinning strategies that minimize the presence of undesirable species but maximize growth of crop trees. Such an approach would generate numerous environmental and economic benefits, including the preservation of biodiversity, maintaining forest resilience to disturbance, sustained timber production over time of desired conifer species, decreased cost of post-fire interventions, and reduced stand rotation age. This approach could reduce the negative effects of salvage logging (Greene et al. 2006; Nappi et al. 2011; Lindenmayer et al. 2012; Splawinski et al. 2014), thereby improving sustainable forest management and bringing operations more in-line with an ecosystem management approach, which aims to mimic natural disturbance (Vaillancourt and Leduc 2009); in this case, reducing the effect of what has been identified as a double disturbance (Greene et al. 2006; Lindenmayer and Noss 2006).

1 Objectives and thesis structure

The four chapters in this thesis examine the juvenile-stage regeneration dynamics of *Picea mariana* (black spruce) and *Pinus banksiana* (jack pine) following fire, salvage, planting and pre-commercial thinning. They seek to answer questions posed directly by forest industry (here Resolute Forest Products), and thus address practical and applied rather than fundamental aspects in ecology and resource management. Specifically, our industrial partner was interested in determining where and when post-fire and post-salvage interventions (planting) would be necessary in order to assure adequate regeneration of black spruce and jack pine, and how to improve the application of pre-commercial thinning operations in order to maximize growth of residual trees.

We will therefore address current gaps in knowledge concerning post-fire and post-salvage regeneration and tree growth dynamics, as well as provide forest managers with tools and silvicultural recommendations that would increase the sustainable management of black spruce and jack pine stands. These include increasing the reliance on natural regeneration, decreasing the need for post-fire interventions such as planting and pre-commercial thinning but increase their success when employed, and reducing operational planning and response time. We focus on two important stages of regeneration following forest fire and salvage logging: (1) The initial establishment phase (Chapters 1 and 2), and (2) the subsequent juvenile stage of development (Chapters 3 and 4).

The first chapter presents a stand-level tool for assessing natural regeneration potential of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana* Lamb.) following fire and salvage; a post-fire regeneration model is used to identify the proportion of good seedbeds necessary to yield adequate natural regeneration densities across a range of basal areas expected in the field. The second links a post-fire regeneration model with forest inventory maps to create a landscape-level tool for assessing natural regeneration density of black spruce (*Picea mariana*) and jack pine

(*Pinus banksiana* Lamb.) following fire and salvage, thereby allowing for the prescription of post-fire interventions such as planting and pre-commercial thinning, and identification of regions susceptible to fire.

In order to develop the stand and landscape-level tools presented in chapters 1 and 2 of this thesis, two main pieces (chapters) from my MSc thesis had to first be completed. The first task was directed at improving the abscission schedule for black spruce and jack pine. New information was added from other studies, and a new model for both schedules was derived. This work resulted in a publication (Greene et al. 2013) (annex A) within which I updated the literature, and made significant revisions as suggested by reviewers.

The second publication (Splawinski et al. 2014a) presents a post-fire and post-salvage natural regeneration model of black spruce and jack pine (annex B). The abscission schedule from Greene et al. (2013) was one of the primary model parameters. It therefore had to be published before we could submit the model manuscript for peer-review. Once this was achieved, I was responsible for de-bugging the model, modifying parameters based on newly available literature, re-running all simulations and updating results, changing the statistical approach, adding a sensitivity analysis, and changing the presentation of figures in the prescriptive simulations section. Following submission for peer-review, I was then responsible for making revisions suggested by the reviewers. Once this manuscript was published I was able to begin developing the tools presented in chapters 1 and 2.

The third chapter examines the impact of the timing of pre-commercial thinning operations and competition on the radial growth response of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana* Lamb.), and the effect of pre-commercial thinning on the mortality and re-growth density of hardwoods. The fourth examines the early pre-commercial thinning of dense jack pine (*Pinus banksiana* Lamb.) stands following fire and salvage, and the impact of treatment height on the mortality and re-growth of thinned stems.

Finally, the global conclusion summarizes the objectives, the new knowledge obtained, and the results and recommendations of this study. Additionally, the link between the two separate stages of development examined in this thesis is established (establishment and juvenile stage of development), and potential consequences of current forest management practices are outlined. The section concludes with a review of future research needs.

CHAPTER I

A STAND-LEVEL TOOL FOR PREDICTING THE NATURAL REGENERATION DENSITY OF BLACK SPRUCE AND JACK PINE FOLLOWING FIRE AND SALVAGE LOGGING

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1.1 Résumé

Un outil a été développé afin de permettre aux gestionnaires et forestiers d'évaluer rapidement les besoins de reboisement après feu et après coupe de récupération à l’échelle du peuplement, aussi bien dans les peuplements purs que mélangés d’épinette noire et de pin gris. Cet outil d'évaluation opérationnelle sur site a été créé en utilisant un modèle de régénération de la forêt qui simule les densités de régénération naturelle de l'épinette noire et de pin gris après feu et après coupe de récupération. Les surfaces terrières utilisées pour les simulations représentent l'intervalle naturel attendu sur le terrain. Pour chaque accroissement de la surface terrière, le pourcentage des lits de germination optimaux qui donneraient au moins un semis/m^2, soit la densité attendue selon un plein boisement, a été enregistré. L'outil permet également la planification rapide des opérations de récupération et de plantation. Il possède de nombreux avantages importants par rapport aux relevés de semis classiques : il peut être utilisé immédiatement après un feu, il peut guider les décisions de gestion sur la planification de la construction des routes et la séquence de la récolte, et il peut prendre en compte toute la phase d'établissement. Grâce à cet outil qui permet d'ajuster le calendrier de récolte afin de minimiser la plantation, le coût final probable de reboisement peut être estimé pour un brûlis au complet. L'outil montre qu'un pourcentage plus élevé de lits de germination optimaux sont nécessaires : (1) pour permettre à l'épinette noire de se régénérer adéquatement après feu dans les peuplements récupérés par rapport au pin gris (donc, le recours à la plantation sera presque toujours nécessaire pour régénérer adéquatement l’épinette noire après récupération); (2) étant donné que la surface terrière des espèces d'intérêt diminue; et (3) pour se régénérer adéquatement dans les peuplements brulés non-récupérés et récupérés après incendie, dans les feux de fin de saison par rapport à ceux de début de saison.

Mots-clefs: Feu de forêt, coupe de récupération, épinette noire, pin gris, régénération naturelle, modèle de régénération naturelle, plantation, besoins de reboisement à l'échelle du peuplement.

Abstract

A tool was developed to allow managers and foresters to quickly assess reforestation needs following forest fire and salvage logging at the stand level in both pure and mixed black spruce and jack pine stands. This on-site operational assessment tool was created using a forest regeneration model that simulates the natural regeneration densities of black spruce and jack pine following fire and salvage. Tree species basal areas used for simulations represent the natural range expected in the field. For each increment of basal area, the percentage of optimal seedbeds that would yield at least 1 seedling/m^2, the expected density concordant with full stocking, was recorded. The tool also allows for rapid planning of both salvage operations and planting. It has important advantages over conventional seedling surveys in that it can be employed immediately following fire, can guide management decisions about the planning of road construction and the harvest sequence, and takes into account the entire establishment phase. Using the tool to adjust the harvesting schedule to minimize replanting, the likely final cost of reforestation can be estimated for an entire burn. The tool shows that a higher percentage of optimal seedbeds are necessary (1) for black spruce to regenerate adequately in burned, salvaged stands when compared to jack pine (i.e. planting of black spruce will almost always be necessary), (2) as basal area of the species of interest decreases, and (3) to adequately regenerate burned intact and salvaged stands in late-season fires compared with those from early-season fires.

Keywords: Forest fire, salvage logging, black spruce, jack pine, natural regeneration, natural regeneration model, planting, stand-level assessment.

1.1 Introduction

The North American species black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) are the two most common conifers in Canada (Rudolph and Laidly 1990; Viereck and Johnstone 1990), and are well adapted to the wildfires common to the circumboreal forest via aerial seedbanks, i.e. canopy seed storage (Enright et al. 1998; Greene et al. 1999; Stocks et al. 2002; De Groot et al. 2004). The passage of the flaming front results in the opening of scales on the cones, thus allowing seeds to abscise (Lamont et al. 1991; Enright et al. 1998; Johnstone et al. 2009; Greene et al. 2013). These seeds are then dispersed onto organic layers that have been reduced by smoldering combustion following medium to high severity fires, with about 40% of the substrate on average rendered into optimal seedbeds of a few cm organic thickness or less (Miyanishi 2001; Miyanishi and Johnson 2002; Greene et al. 2007). At times, conifer recruitment can be low following low severity fire due to fewer suitable seedbeds as less organic matter is removed (Veilleux-Nolin and Payette 2012), and by lower availability of seeds (Lecomte et al. 2006).

The abscission period for black spruce seeds is more protracted than for jack pine, requiring roughly 5 years to abscise 90% of seeds compared to just 1 year for jack pine (Greene et al. 2013). Salvage operations are typically scheduled within the first few months following fire to minimize degradation of fire-killed boles by saprophagous beetle larvae and by checking (Saint-Germain and Greene 2009). The removal of these boles effectively removes the non-abscised portion of the aerial seedbank (Greene et al. 2006, 2013; Splawinski et al. 2014a), and the operation also leads to dramatic mortality among the first cohort of germinants. This has a profoundly negative effect on black spruce, and to a far lesser extent jack pine, regeneration potential (Greene et al. 2006, 2013; Splawinski et al. 2014a). Stands that exhibit poor stocking following salvage must be planted at a cost of about CAD 1000$/ha (Saint-Germain and Greene 2009).

With the exception of seedling surveys, managers and foresters currently do not possess stand-level tools to assess reforestation needs following fire and salvage in both pure and mixed black spruce and jack pine stands. The conventional seedling survey is often carried out in the first year or two following fire, and therefore cannot take into account subsequent recruitment. Thus it is not possible to rapidly make decisions about which areas within a recent burn will likely need to be planted. An on-site assessment tool capable of identifying reforestation needs immediately after the fire should reduce the planning time of both salvage operations and subsequent planting, and can save money on replanting. Further, it can show the manager which stands would have acceptable stocking levels if only the salvage was delayed for a specified period.

The objective of this paper therefore is to develop an operational tool using the Splawinski et al. (2014a) regeneration model that will permit estimation of natural regeneration densities of black spruce and jack pine following moderate to severe fire, either early or late in the growing season, followed by salvage logging. This will be accomplished by identifying what proportion of good seedbeds are required to obtain adequate stand stocking under a range of expected pre-fire basal areas. In particular, we produce four figures, two of which illustrate simulation results, and two (the assessment tool itself) that can be used in the field by foresters in a fresh burn, perhaps as laminated cards that fit in a shirt pocket for easy use, or on a smartphone.

Planted conifers are typically spaced approximately 2 meters apart to minimize competition, thereby increasing growth and volume (Zhang et al. 2002), however due to the variable spatial distribution of seedbeds and their effect on the survivorship of naturally regenerated stems, clumping would be observed on good seedbeds (which make up a relatively low proportion of total seedbeds), whereas poor seedbeds would exhibit lower densities (Greene et al. 2006; Splawinski et al. 2014a). Therefore a seedling density of ~$1/m^2$ (10,000 seedlings/ha) or greater is considered adequate to fully re-stock a naturally regenerated stand (Greene et al. 2002). In addition to the work of Splawinski et al. (2014a), here we examine the minimal proportion of good seedbeds required to yield 1 seedling/m^2 across a range of basal areas under an early and late season fire date.

1.3 Methods

Splawinski et al. (2014a) developed a regeneration model capable of predicting the natural regeneration densities (seedlings/m^2) of black spruce and jack pine following fire and salvage at the stand level during the establishment phase (the first 6 years post-fire). The main parameters are: (1) initial seed availability, computed as a function of source tree basal area, seed survival through the passage of the flaming front, and salvage proportion; (2) seed abscission as a function of time since fire; (3) seedling survivorship as a function of seed mass (germinant size), seedbed proportion, and granivory; and (4) seedling and seed mortality as a function of salvage operations.

Detailed information on the parameterization, and limits of the model are available in Splawinski et al. (2014a). Briefly, the model uses three types of seedbed classes in simulations: good, poor, and lethal. Each class is characterized by a single survivorship value. The good-seedbed category is subdivided into exposed mineral soil and living mosses (feathermoss and *Sphagnum*), while the poor-substrate category includes lichens, burnt or residual duff, and thick layers of unburnt leaves or dead mosses. Finally, the lethal-seedbed category includes firm but non-burned logs, charred logs, rocks, and standing puddles. An average lethal-seedbed proportion of 10% ground cover was obtained from 4 fires, the 3 wildfires used for model validation in Splawinski et al. (2014a), and from unpublished fieldwork conducted in the 2010 La Tuque wildfire (northwestern Quebec), following the same field-sampling methodology as used by Splawinski et al. (2014a) at the Lebel-sur-Quevillon wildfire. Therefore for this approach, if the good-seedbed proportion is increased, the poor-seedbed proportion is decreased accordingly; however the lethal proportion always remains constant at 10%.

The post-fire regeneration model was validated using field data obtained from three fires, two in Quebec and one in Saskatchewan. Log-transformed regressions were performed on observed versus simulated seedling densities of black spruce and jack pine, for all fires and treatments, to determine if the intercept was significantly different from 0 and slope significantly different from 1. Results of the analysis can be found in table 1.1.

Table 1.1. Power law regression results for observed versus simulated seedling densities (seedlings/m^2) from Splawinski et al. (2014a). Note: For intercept or slope values, * represents a significant difference from 0 and 1 respectively.

Fire	Species	Treatment	Intercept	Slope	r^2	*n*
Lebel-sur-Quevillion (Quebec)	*P. mariana*	Lumped	0.225	1.308	0.920	6
Val Paradis (Quebec)	*P. mariana*	Intact	-0.477	0.639	0.325	16
		Salvaged	-2.541*	0.018*	0.000	19
	P. banksiana	Intact	0.06	0.062	0.003	10
		Salvaged	0.053	1.271	0.423	17
Muskeg	*P. mariana*	Intact	0.841*	0.978	0.567	18
(Saskatchewan)	*P. banksiana*	Intact	0.553	0.735	0.498	19

A sensitivity analysis was also performed indicating that the model is most sensitive to seed mortality resulting from the passage of the flaming front and the post-fire granivory rate. It assumes a 53% seed survival rate following the passage of the flaming front for black spruce and a 100% survival rate for jack pine (Greene and Johnson 1999; De Groot et al. 2004). Extreme fire severity, however, may greatly reduce seed viability, even in the well-protected cones of jack pine (Pinno et al. 2013); therefore our approach applies only to stands exhibiting 100% tree mortality and subjected to moderate – high severity fires. There is a relative lack of empirical data on post-fire granivory rates. Based on two studies (Greene and Johnson 1998; Charron and Greene 2002), the survivorship through the granivory stage is estimated at 95% for the summer of the fire itself, and is subsequently reduced to 43% for the reminder of the simulation (Splawinski et al. 2014a); of course if fire-wide values differ greatly from these expected values (including the fixed lethal proportion) then the user should make use of the original model available from the author to adjust the predation parameters.

Prescriptive simulations

Two scenarios are simulated (1) regeneration density of black spruce and jack pine in burned intact stands, and (2) in 100% salvaged stands. Moreover, an early and late season fire are examined. First, a June fire date is used, since late spring/early summer represents the period of most frequent fire occurrence in the Canadian boreal forest (Stocks et al. 2002). Second, an August fire date is used, as this month represents the late fire season (Stocks et al. 2002).

These fire dates were mostly selected to illustrate the potential differences in seed predation following early and late-season fires. Based on the limited granivory data currently available for the boreal forest, the Splawinski et al. (2014) regeneration model assumes that 5% of seeds will be consumed during the summer of the fire, after which the rate will rise to 57% for the remainder of the simulation. This is based on the argument that medium to high severity fires will greatly reduce granivore populations, with a significant amount of time necessary (at least 4 months) before they are able to re-establish (Splawinski et al. 2014). Thus the earlier the fire, the more time the first cohort has to establish under a lower granivory rate; conversely the later the fire, the more seeds will end up germinating in the second cohort under a higher granivory rate. It should be noted however that these dates are not used to contrast different levels of fire severity on the soil organic matter, and does not reflect any possible differences in the generation of good seedbeds between a spring and summer fire.

A December salvage date is used for both fire dates as this month represents the median salvage month observed in the Lebel-sur-Quevillon wildfire (Splawinski et al. 2014a). Simulations are carried out for pre-fire basal areas ranging from 5 to 50 m^2/ha, in increments of 2.5 m^2/ha. This represents the range of basal areas expected in the field as observed in the temporary plot data of the Quebec Ministry of Forests, Wildlife and Parks in the boreal forest of northwestern Quebec (Lake Matagami lowland ecological region 6a). This ecological region is delimited using a hierarchical ecological classification system, with territories sub-divided based on ecological factors (Blouin et Berger 2005). For every increment of basal area, the percentage of good-seedbeds that will yield $\geq$ 1 seedling/m^2 is identified. Although the model simulates seedlings/m^2, and the basal area parameter is in m^2/m^2, both are converted to seedlings/ha and m^2/ha respectively, as this represents the standard used by foresters in the field.

1.4 Results and Discussion

Following fire in burned intact stands, a black spruce-dominated stand with ~20 m^2/ha basal area for spruce will exhibit adequate stand stocking (1 seedling/m^2) for this species as long as the good-seedbed category has at least 9% coverage following a June fire (Figure 1.1a), and 10% coverage following an August fire (Figure 1.1b). A jack pine-dominated stand with that same basal area (20 m^2/ha) should always achieve adequate stand stocking if the substrates in the good-seedbed category are ≥ 4% of the total following a June fire (Figure 1.2a). However, following an August fire in jack pine, good seedbeds must comprise ≥ 6% of the total (Figure 1.2b). This difference is due to the shorter abscission schedule of jack pine (Greene et al. 2013; Splawinski et al. 2014a). Since granivory rates increase substantially following the summer of the fire (Splawinski et al. 2014a), more jack pine seeds will be consumed as the schedule has been shifted forward by 2 months.

Fires occurring later in the fire season have the potential to produce greater proportions of favorable seedbeds than those occurring in the spring by removing more organic matter through smoldering combustion; this is primarily due to lower duff moisture content (Kasischke et al. 2000a, 2000b; Miyanishi 2001). This may offset to some degree the increased seed losses to granivores. However such an analysis is beyond the scope of this chapter; we are merely trying to identify what proportion of good seedbeds is necessary to obtain adequate stand stocking based on pre-fire basal area. Of course, for either species, as the percentage of good seedbeds rises, the required basal area (directly proportional to local seed supply) for adequate regeneration declines.

As argued by Splawinski et al. (2014a) and supported by the empirical literature, with respect to establishment potential the larger-seeded pine outperforms black spruce on intact (un-salvaged) burnt sites. Further, jack pine tends to occupy sites that have a thinner organic layer depth prior to the burn and a much higher proportion of good seedbeds after the fire (Greene et al. 2007). Generally, while Greene et al. (2007) found an average of 40% post-fire coverage of good seedbeds in the boreal forest, that value was much greater for pine (drier sites) than black spruce (wetter sites), and much higher in western Canada than the more humid east. This was further supported by observations made by Greene et al. (2006) and Splawinski et al. (2014a) in northwestern Quebec. Based on this, an estimated good-seedbed proportion of 27% was calculated and subsequently used by Splawinski et al. (2014a) in the exploratory simulations. In short, in the absence of salvage, we expect pure pine stands to reliably replace themselves and mixed stands to increase their proportion of pine (*cf* Greene and Johnson 1999). For black spruce, however, regeneration adequacy will depend very much on post-fire seedbed quality and can be problematic even if the pre-fire basal area is high. This constraint ultimately is due to the fact that spruce has more demanding seedbed requirements, due to its smaller seeds, and to it typically occupying sites with thick pre-fire organic layers that smoldering combustion can often not adequately reduce. Importantly, although sphagnum, which is typically found in wetter sites and is considered a good seedbed for germination, it is actually a poor growth medium due to its relatively low nutrient supply (Lavoie et al. 2007). Therefore, sites that exhibit high post-fire proportions of sphagnum may require planting (Lavoie et al. 2007).

If 100% salvage is employed in the first winter following a June fire, black spruce will need to be planted if basal area is ≤ 40 m^2/ha with good seedbeds comprising 27% of the total (Figure 1.1c). Following 100% salvage in the first winter after an

August fire, black spruce will need to be planted no matter what the seed source strength (Figure 1.1d). For example, even with 35 m^2/ha of basal area for spruce, good-seedbed coverage of ≥ 65%, which is a very unrealistic value for sites dominated by this species, would be required for adequate stocking. By contrast, following a June fire, jack pine should exhibit adequate stand stocking with all but the lowest (5 m^2/ha) pre-fire basal area given a good-seedbed proportion of 27% (Figure 1.2c). Conversely, following an August fire the minimum required basal area increases to 15 m^2/ha (Figure 1.2d). Since jack pine releases seeds quickly following fire, a late-season fire results in significantly more non-abscised seeds in the aerial seedbank, which will be removed by operations as compared to that from an early season fire with a similar salvage date (Greene et al. 2013; Splawinski et al. 2014a). In addition, the first summer cohort for both species will have significantly less time to establish following a late season fire; 1 month for an August fire compared to 3 months for a June fire (Splawinski et al. 2014a). Once again, as mentioned earlier for burned intact stands, this may be offset by the possibility of greater proportions of favorable seedbeds created by late-season fires.

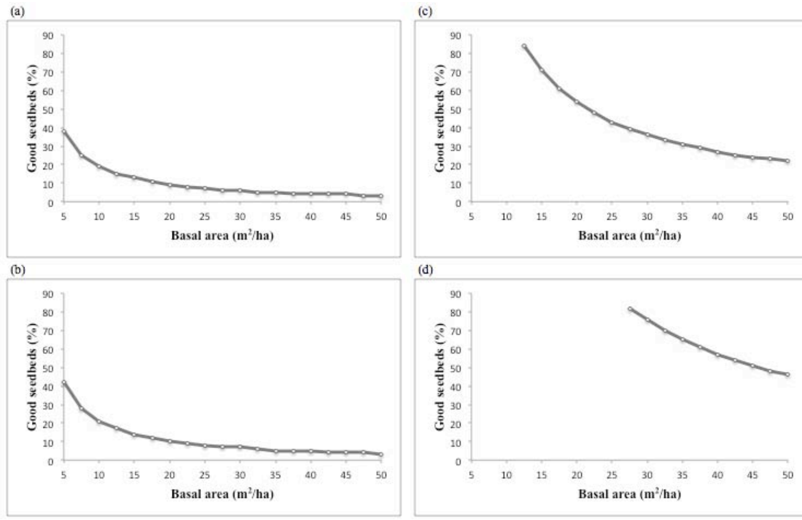

Figure 1.1. Simulated percentage of good seedbeds needed for sufficient stocking according to different pre-fire basal area for black spruce in a burned intact stand following a June (a) and August (b) fire, and a 100% salvaged stand following a June (c) and August (d) fire. Line represents the minimum stand-stocking threshold of 1 seedling/m^2.

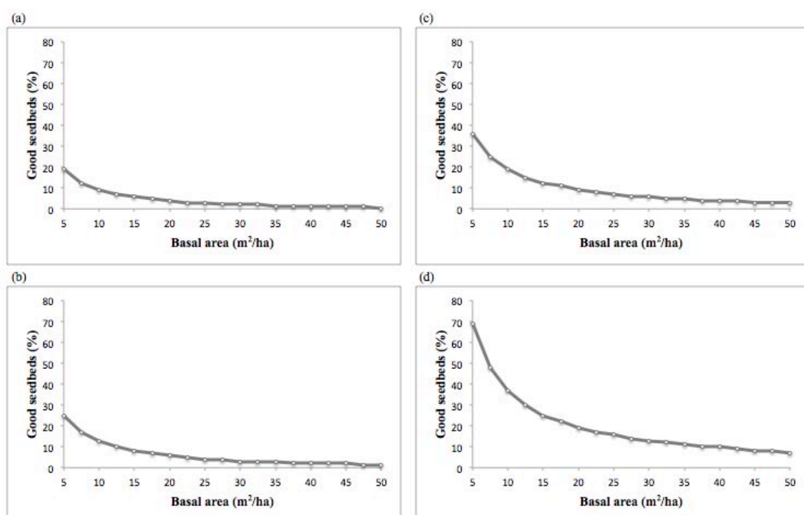

Figure 1.2. Simulated percentage of good seedbeds needed for sufficient stocking according to different pre-fire basal area for jack pine in a burned intact stand following a June (a) and August (b) fire, and a 100% salvaged stand following a June (c) and August (d) fire. Line represents the minimum stand-stocking threshold of 1 seedling/m^2.

The good seedbed proportion needed to obtain adequate stand stocking for burned intact black spruce following a June fire is similar to that of 100% salvaged jack pine with the same fire date under the full range of basal areas. This illustrates the advantage of possessing a rapid post-fire abscission schedule, as is this case for jack pine; more seeds are abscised prior to salvage and fewer are subjected to predation by granivores.

Salvaged stands (Figures 1.1c,d and 1.2c,d) show more constrained regeneration than burned intact stands (Figures 1.1a,b and 1.2a,b) for two reasons. First, the removal of the aerial seedbank limits establishment potential. Black spruce is much more deleteriously affected by salvage than is pine because a far higher proportion of its seeds have not yet abscised by the time salvage occurs (Splawinski et al. 2014a). While there are a large number of reasons that forest companies prefer to begin salvaging as quickly as tertiary roads can be constructed, nonetheless early salvage necessarily curtails the regeneration of species that abscise their seeds slowly over many years (Saint-Germain and Greene 2009). Secondly, the harvesting equipment will trample about 30% of already established germinants from the first summer cohort (Greene et al. 2006).

The natural regeneration assessment tool presented in Figure 1.3 and 1.4 can be used by foresters in the North American boreal forest as laminated guides for post-fire evaluation of the percentage of the burned area that will require planting. Basal area can be taken from inventories. While seed source strength (i.e. basal area) also could be measured via a prism, the field survey is primarily intended to provide a quantification of the seedbeds; this can easily be accomplished through the employment of a line transect following a simplified approach of Splawinski et al. (2014a) (i.e. 1 randomly oriented transect, 25 meters in length, with seedbed type identified every 50 cm). A proxy for seedbed quality, perhaps obtained from remotely sensed data, would obviate the need for fieldwork, but this has not yet been attempted by any researchers. Estimates of fire severity based on the percentage of trees immediately killed by the burn are not well correlated with measures of seedbed quality (e.g. residual organic layer depth); indeed, most partially-killed trees die within two years following fire (Angers et al. 2011).

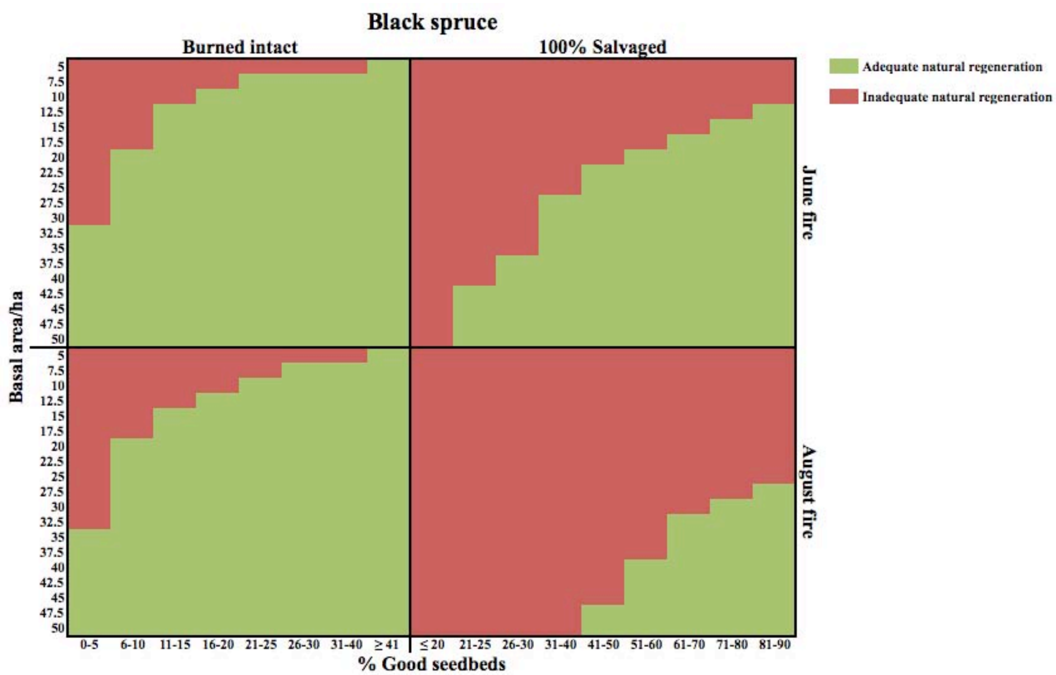

Figure 1.3. Simulated black spruce natural regeneration assessment tool illustrating percent of good seedbeds needed to obtain the adequate stand stocking threshold of 1 seedling/m^2 for every increment of basal area, under both scenarios and fire dates.

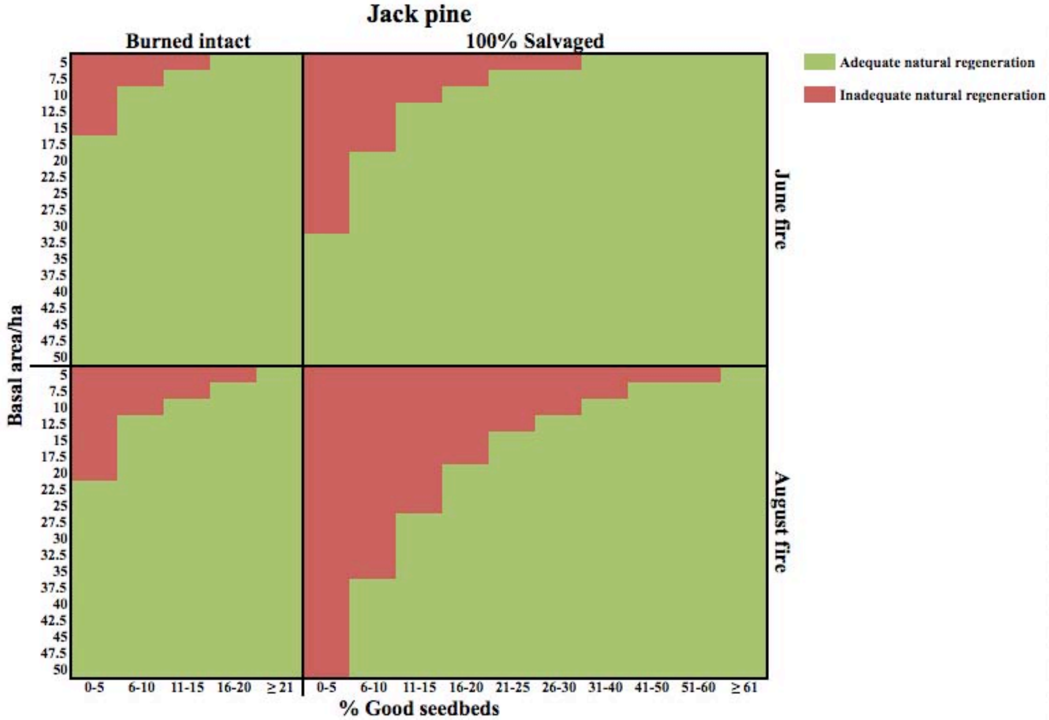

Figure 1.4. Simulated jack pine natural regeneration assessment tool illustrating percent of good seedbeds needed to obtain the adequate stand stocking threshold of 1 seedling/m^2 for every increment of basal area, under both scenarios and fire dates.

The potential error associated with predictions made in the tools (figures 1.3 and 1.4) is moderate, based on the r^2 values (non-adjusted) obtained from power law regressions for observed versus simulated seedling densities from Splawinski et al. (2014a) (Table 1.1). Their results indicated a variable chance of error ($1-r^2$) depending on the fire that was examined; the Lebel-sur-Quevillion fire exhibited little chance of error ($r^2 = 0.920$), the Val Paradis fire exhibited a large chance of error ($r^2 = 0.000$ to 0.423), and the Muskeg fire exhibited a moderate chance of error ($r^2 = 0.498$ to 0.567).

Unexplained variation in seedling densities observed by Splawinski et al. (2014a) was described by five factors: seed mortality resulting from the passage of the flaming front, the post-fire granivory rate, the estimation of seed production based on pre-fire basal area, first-summer age-specific survivorship of seedlings due to variation in precipitation, and estimation of seedling survivorship based on the grouping of seedbed types and on-site factors (Splawinski et al. 2014a). Although a moderate prediction error exists in the tools themselves, we believe that they provide foresters with a novel and important method for assessing post-fire and post-salvage natural regeneration densities, planning operations and estimating cost of future interventions. We do not suggest that they replace conventional seedling surveys at this time, but be employed together in order to assess their validity and avoid potential consequences of erroneous decisions.

Future research should therefore focus on evaluating the applicability and success of this tool in estimating post-fire and post-salvage regeneration potential. Additionally further data can be gathered on poorly understood parameters (i.e., post-fire granivory rates, effect of fire severity on seed mortality, and post-fire seedbed proportions). This knowledge can then be used to improve the current assessment tools, as well as the main model.

While the modelling approach adopted in Splawinski et al. (2014a) can be applied to any species with an aerial seedbank, we hesitate to suggest applying the results presented here to any other species except perhaps serotinous populations of lodgepole pine (*Pinus contorta)* in the western mountains of North America. That species is closely related to jack pine and has a similar seed mass (and thus expected juvenile survivorship).

1.5 Conclusion

This operational tool provides a novel approach for managers and foresters to quickly assess reforestation needs following fire and salvage at the stand level. Rapid planning of both salvage operations and planting application will improve both efficiency and response time, thereby increasing the sustainability of this resource while minimizing operational costs. Evaluation can also be used to suggest which sites should be given ameliorative prescriptions such as partial cutting of burned black spruce or direct seeding (Greene et al. 2006; Splawinski et al. 2014a).

CHAPTER II

A LANDSCAPE-LEVEL TOOL FOR ASSESSING NATURAL REGENERATION DENSITY OF BLACK SPRUCE AND JACK PINE FOLLOWING FIRE AND SALVAGE LOGGING

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2.1 Résumé

Nous présentons un outil d'évaluation opérationnelle de régénération naturel à l'échelle du paysage créé en lien avec un modèle de régénération de la forêt validé avec des cartes d'inventaires forestiers. A l'aide des surfaces terrières obtenues à partir de placettes temporaires et des distributions des lits de germination provenant de données de terrain, les densités de semis sont simulées pour des peuplements purs d'épinette noire et de pin gris selon des scénarios brulés non-récupérés et 100 % récupérés. Ces peuplements sont regroupés selon la classe d'âge, le couvert forestier avant feu, le dépôt de surface et le drainage. Suivant ce système de classification, les densités de semis simulées sont transférées sur des cartes d'inventaire forestier de la région écologique du lac Matagami (6a) dans la forêt boréale du Québec. La sortie finale du modèle est une estimation de semis/m^2 suivant un feu modéré à sévère et suivi de 100 % de récupération dans les peuplements purs d'épinette noire et de pin gris.le modèle permet aussi de simuler la récupération partielle. Les résultats sont exprimés en semis/ha et montrent que dans notre zone d'étude, seulement 36 % des peuplements intacts d'épinette noire et 28 % des peuplements intacts de pin gris nécessiteraient un reboisement après feu. Toutefois, selon le scénario de 100 % de récupération, 100 % des peuplements d'épinette noire et 74 % des peuplements de pin gris nécessiteraient la plantation. Notre outil permet aux gestionnaires et aux forestiers d'évaluer rapidement les besoins de reboisement et de récupération après feu à l'échelle du paysage et peut être utilisé pour une meilleure planification des opérations de récupération et de l'application de traitements sylvicoles ultérieurs. En plus d'être capable de planifier les opérations plus rapidement, les forestiers seront également en mesure d'identifier rapidement les régions où la régénération naturelle pourrait être insuffisante ou excessive. Les coûts potentiels de futures interventions telles que la plantation, l'ensemencement aérien et l'éclaircie pré-commerciale

pourraient être estimés. Les forestiers pourraient également évaluer la vulnérabilité actuelle des unités d’aménagement face au feu et ainsi identifier les régions à risque.

Mots-clefs: Régénération naturelle, modèle de régénération naturelle, plantation, éclaircie pré-commerciale, cartes d'inventaire forestier, besoins de reboisement.

Abstract

We present a landscape-level operational natural regeneration assessment tool, created by linking a validated forest regeneration model with forest inventory maps. Using basal areas obtained from temporary plots and seedbed distributions from field data, seedling densities are simulated for pure black spruce and jack pine stands under burned intact and 100% salvaged scenarios. These stands are grouped by age class, pre-fire stand cover, surficial deposit, and drainage. Following this classification scheme, simulated seedling densities are transferred onto forest inventory maps for the Lake Matagami lowland ecological region (6a) in the boreal forest of Quebec. The final output of the model is an estimate of seedlings/m^2 following moderate to severe fire and fire followed by 100 % salvage in pure black spruce and jack pine stands, however it is also capable of simulating partial salvage. Results are expressed as seedlings/ha, and illustrate that in our study area, only 36% of intact black spruce and 28% of intact jack pine stands need to be planted following fire; however under the 100% salvage scenario 100% of black spruce and 74% of jack pine stands necessitate planting. This tool allows managers and foresters to quickly assess reforestation needs following fire and salvage at the landscape level, and can be used to better plan salvage operations and subsequent silvicultural treatment application. In addition to being able to schedule operations faster, foresters will also be able to quickly identify regions where natural regeneration could be inadequate or excessive. Potential cost estimates of future interventions such as planting, aerial seeding, and pre-commercial thinning could be made. Foresters can also assess the current vulnerability of management units to fire and can identify regions at particular risk.

Keywords: Natural regeneration, natural regeneration model, planting, pre-commercial thinning, forest inventory maps, regeneration assessment.

2.2 Introduction

Fire is the dominant disturbance in the boreal forest of North America, burning approximately ~2 million ha of forest in Canada annually between 1959 and 1997 (Stocks et al. 2002). 97% of total area burned is caused by large (>200 ha), high intensity, stand-replacing fires (Amiro et al. 2001; Flannigan et al. 2001; Stocks et al. 2002). The regional and continental-scale fire regime in the boreal forest is predominantly controlled by climate (Carcaillet et al. 2001). Fire frequency (Amiro et al. 2001; Flannigan et al. 2001, 2009; Bergeron et al. 2004, 2010; Soja et al. 2007; Wotton et al. 2010), fire season length (Wotton and Flannigan 1993; Boulanger et al. 2013), and area burned (Flannigan et al. 2005) are expected to increase throughout the boreal forest as the climate warms in the future (IPCC 2013).

Black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) are two common conifer tree species in the boreal forest of North America (Charron and Greene 2002; De Groot et al. 2004), and also the significant target species of the forest industry. These two species are well adapted to fire; jack pine is serotinous and black spruce is semi-serotinous. Both possess aerial seedbanks that effectively distribute seeds following this disturbance (Gauthier et al. 1993; Enright et al. 1998; Greene et al. 1999). Jack pine releases approximately 90% of its seeds in the first year following fire whereas black spruce takes up to five years to release the same amount (Greene et al. 2013). Furthermore, smoldering combustion of the organic layer creates seedbeds that are more receptive (Miyanishi 2001; Miyanishi and Johnson 2002) to these two species.

Stand stocking can sometimes be inadequate following fire. Stands can be young when burned and therefore the trees are not mature enough to produce adequate seed (Viglas et al. 2013; Zasada 1971; Viereck and Johnston 1990; Gauthier et al. 1993), or pre-fire densities of mature trees can be low; conversely some fires can be so severe that they kill the seeds in the aerial seedbank (Pinno et al. 2013) regardless of pre-fire stand density or age. However, in terms of species composition there are usually no dramatic post-fire changes (Greene and Johnson 1999; Ilisson and Chen 2009; Boucher et al. 2014). Natural regeneration density, and by extension stand stocking, can be reduced even further by salvage operations due to the removal of the aerial seedbank (Greene et al. 2006, 2013; Splawinski et al. 2014a). It has an especially deleterious effect on black spruce due to its extended abscission (seed release) schedule (Splawinski et al. 2014a). Salvage is typically applied within the first winter following fire to minimize degradation of burnt boles due to wood-boring insects, stain fungi, wood-decay fungi, and checking (cracking/splitting of wood due to wind, freezing, irregular drying, etc.) (St. Germain and Greene, 2009), due to easier accessibility to stands that are located far from an established road network, and less damage to the ground due to freezing and snow accumulation (O'Mahony et al. 2000). These stands can be regenerated artificially through planting (Saint-Germain and Greene 2009) or, if access is restricted, through aerial seeding, however treatment application is costly. Conversely, when regeneration densities are excessive, pre-commercial thinning can be employed to control stand density, thereby maximizing growth and yield of residual trees and minimizing rotation period (Vassov and Baker 1988).

Due to limited understanding of post-fire and post-salvage regeneration processes, managers and foresters currently lack the tools needed to quickly assess reforestation needs following fire and salvage at the landscape level. An operational assessment tool that projects regeneration density following fire and salvage can be used to better plan salvage operations and subsequent silvicultural treatment application through the identification of regions and stands where natural regeneration density will be inadequate or excessive. They can then estimate the potential cost of future interventions such as mechanical site preparation, planting, aerial seeding, and pre-commercial thinning. Foresters can also assess the vulnerability of management units to the current fire regime, and can identify regions at particular risk.

The objectives of this study are threefold: (1) to use a regeneration model (Splawinski et al. 2014a) along with Quebec forest inventory maps and temporary plots to simulate natural regeneration densities in pure black spruce and jack pine stands following moderate to severe fire and salvage across the Lake Matagami lowland ecological region (6a) in the boreal forest of Quebec; (2) transfer simulated results onto GIS forest inventory maps; and (3) provide recommendations on silvicultural practices based on simulated seedling densities.

2.3 Methods

Study area

The Quebec Ministry of Forests, Wildlife and Parks (formerly the Ministry of Natural Resources) employs a hierarchical ecological classification system that sub-divides territories based on ecological factors from the continental to local scale. The Lake Matagami lowland ecological region (6a) is located in the western part of the managed continuous boreal forest of Quebec, and represents part of the western portion of the spruce-moss bioclimatic domain (Figure 2.1) (Blouin et Berger 2005; Bergeron et al. 1998). It covers an area of 48,231 km^2, and is dominated by black spruce, jack pine, and balsam fir (Abies balsamea (L.) Mill.) forest, interlaced with bogs, rivers, and lakes (Blouin et Berger 2005; Bergeron et al. 1998). The regional climate of the western portion of the spruce-moss bioclimatic domain is sub-polar sub-humid continental, with approximately 825 mm of total precipitation per year; the growing season lasts four to five months and average annual temperature ranges from 0° to -2.5° C (Blouin et Berger 2005; Bergeron et al. 1998). The landscape of ecological region 6a is dominated by glaciolacustrine clays and sands, Cochrane tills, glacial tills, and organic surficial deposits; underlain by crystalline rock of granitic and volcanic origin (Blouin et Berger 2005; Bergeron et al. 1998). Our study area makes up 43,572 km^2 or 90% of ecological region 6a. Forest inventory data in the remaining area was not available for simulation.

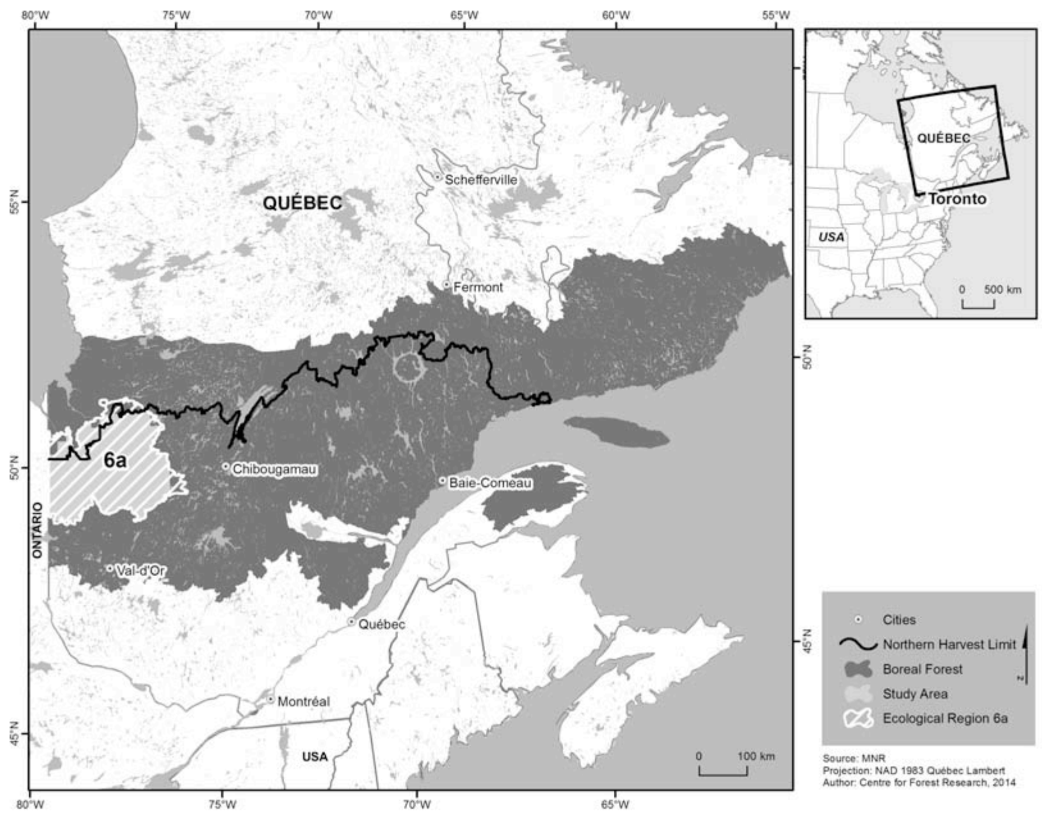

Figure 2.1. Map of Quebec illustrating Lake Matagami lowland ecological region (6a) with study area, the boreal forest, and the northern harvest limit.

The model

The regeneration model developed by Splawinski et al. (2014a) simulates natural regeneration densities (seedlings/m^2) of black spruce and jack pine, following fire and salvage at the stand level in the first 6 years following fire, here defined as the establishment phase. The model has been parameterized based on: (1) initial seed availability as a function of pre-fire tree basal area (m^2/m^2), survival of seeds through the passing of the flaming front, and salvage proportion in terms of basal area removed; (2) seed abscission as a function of time; (3) seedling survivorship as a function of seed mass, the proportion of good, poor, and lethal seedbeds, and granivory; and (4) seedling and seed mortality as a function of salvage operations. It is most sensitive to the parameters of seeds survival through the passing of the flaming front, and granivory. The regeneration model was successfully validated in Splawinski et al. (2014a) by comparing simulated vs. observed seedling densities obtained from 3 wildfires under burned intact and 100% salvaged scenarios. For the purpose of this study both the simulated seedling density and the tree basal area parameter will be converted to seedlings/ha and m^2/ha respectively, as this represents the standard used by foresters in the field.

We know of only one other spatial model (Valeria et al. 2011) that examines regeneration following fire in the boreal forest, however it is conceptual in nature, does not include salvage, and model projections are expressed as: good, average, low natural regeneration or not predicted. It qualitatively estimates the capacity of the expected regeneration in boreal forests following fires based on the scientific literature and research conducted by the Natural Sciences and Engineering Research Council of Canada (NSERC) - Université du Québec en Abitibi-Témiscamingue (UQAT) - Université du Québec à Montréal (UQAM) Industrial Chair in Sustainable Forest Management (SFM Chair) and the Canadian Forest Service (CFS) over fifteen years.

Simulations

For model simulations two parameters were required: 1) pre-fire basal area to calculate initial seed availability, and 2) seedbed proportions to calculate seedling germination and survival (see Chapter 1). The remaining parameter values (seed abscission schedules, seed mass, granivory rate, seedling and seed mortality and seed removal as a function of salvage operations, and seasonal availability of seeds for germination) were taken from Splawinski et al. (2014a). Currently in the province of Quebec data are available on stand and landscape-level attributes. It can be obtained from both forest inventory maps and temporary and permanent plots (Lord and Faucher 2003; Ministère des Ressources naturelles 2007, 2009; Pelletier et al. 2007). These data were used to estimate the two parameters, thus allowing simulation of the natural regeneration density following both fire and salvage, and the creation of a landscape tool for Lake Matagami lowland ecological region (6a) (Figure 2.2).

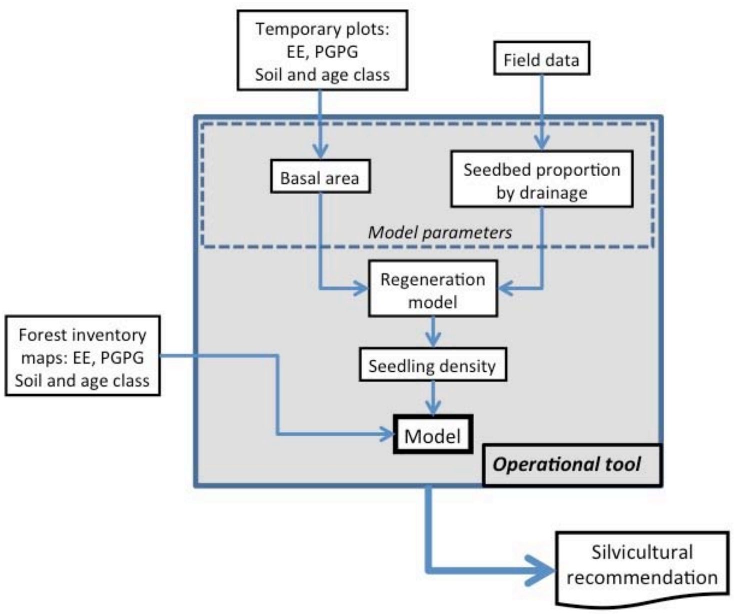

Figure 2.2. Conceptual diagram illustrating the steps and data sources used in the modeling, and the subsequent creation of the landscape-level assessment tool for both pure black spruce (EE) and jack pine (PGPG) stands.

Temporary plots are sampled on-site across the boreal forest of Quebec during each inventory period, which is carried out roughly every decade. Each plot is 400m^2 (circular, sampled using an 11.28m radius). It provides stand-level details on species composition, diameter at breast-height (DBH), age, stem density, height, surficial deposit, and drainage (Ministère des Ressources naturelles 2007). The 3rd inventory period was completed in 2002 (Ministère des Ressources naturelles 2008). The 4th inventory is currently underway, however it has not yet been completed, thus the data are as yet unavailable.

In order to obtain estimates of the basal area for stands of a given composition, we used the 3rd inventory temporary plot data (pure jack pine (PGPG) (n = 191) and pure black spruce (EE) (n = 2,423) stands); we subsequently refer to these species with these codes. In order to be classified as a pure stand, each species must make up at least 75% of the stand basal area. The surficial deposits and drainage observed in these 2,623 temporary plots were grouped into soil classes (Table 2.1). This was done as surficial deposit and drainage will have an effect on both forest composition (Gauthier et al. 1996), stand productivity, and tree growth (Bonan and Shugart 1989; Rudolph and Laidly 1990; Beland and Bergeron 1996; Harper et al. 2002). Deposit and drainage codes were developed by the Quebec Ministry of Forests, Wildlife and Parks. Surficial deposits are classed based on texture, composition, origin, and morphology; drainage is classed based on both the horizontal and lateral drainage potential, ranging from excessive to very poor (Ministère des Ressources naturelles 2009).

Table 2.1. Grouping of deposits and drainage into soil class, and age class for black spruce and jack pine, Lake Matagami lowland ecological region (6a).

Species	Soil class	Sample size (n)	Age class	Deposit code	Drainage code
Black spruce	Sand	225	≥ 50 years	2A, 2AE, 2AK, 2B, 2BD, 2BE, 3AC, 3AE, 3AN, 4GS, 4GSM, 4GSY, 4P, 5S, 5SM, 5SY, 6S, 6SM, 6SY, 9, 9S, 9A	ALL
	Shallow rock	36	≥ 50 years	R, R1, R1A, R4A, R4GA, R4GS, R5S, R6S, R7T, R1AA, M1AA, M1A, 1AR, 8A	ALL
	Till	1,575	≥ 50 years	1A, 1AD, 1AM, 1AY, 1AB, 1BD, 1BF, 1BG, 1BI, 1BIM, 1BIY, 1BP, 1BT, 1Y	ALL
	Cochrane till	92	≥ 50 years	1AA, 1AAM, 1AAY, 1AAR	ALL
	Mesic clay	28	≥ 50 years	4A, 4GA, 4GAM, 4GAR, 4GAY, 5A, 5AM, 5AY	00,10,13,16,20,21, 30,31,33
	Hydric clay	209	≥ 50 years	4A, 4GA, 4GAM, 4GAR, 4GAY	40,41,43,50,51,53, 54,60,61,62,63
	Organic	266	≥ 50 years	7, 7E, 7T, 7TM, 7TY	N/A
Jack pine	Sand	118	≥ 30 years	2A, 2AE, 2AK, 2B, 2BD, 2BE, 3AC, 3AE, 3AN, 4GS, 4GSM, 4GSY, 4P, 5S, 5SM, 5SY, 6S, 6SM, 6SY, 9, 9S, 9A	ALL
	Till	74	≥ 30 years	1A, 1AD, 1AM, 1AY, 1AB, 1BD, 1BF, 1BG, 1BI, 1BIM, 1BIY, 1BP, 1BT, 1Y	ALL

The mean and upper and lower 95% confidence limit for observed basal areas was obtained for each soil class, further subdivided by stand cover class (Table 2.2). These cover classes were developed by the Quebec Ministry of Forests, Wildlife and Parks, and represent the % of forest crown cover in a stand (Ministère des Ressources naturelles 2009). Cover class A represents > 80%, B represents 60-80%, C represents 40-60%, and D represents 25-40%. Certain cover classes were labeled N/A (not available) as their sample size in the temporary plot number was too small to determine basal area. A total of 2,623 temporary plots were used to determine basal area, 2,431 for black spruce and 192 for jack pine. All stems of black spruce and jack pine sampled within these plots were included in the analysis. Details on temporary plot sample size can also be found in Table 2.2.

Table 2.2. Sample size, basal area m^2/ha (mean, lower and upper 95% confidence limit -CL) for black spruce (EE) and jack pine (PGPG) by soil and cover class. Levels of significant factors were compared using Tukey HSD.

Species	Soil class	Cover class	Sample size (n)	% by cover class	Basal area/ha Mean	Upper 95% CL	Lower 95% CL	Significance Tukey HSD
EE	Sand	A	6	2.7	38.6	41.5	35.7	a
		B	27	12.0	29.9	31.7	28.1	b
		C	96	42.7	21.3	22.7	20.0	c
		D	96	42.7	14.7	15.7	13.7	d
EE	Shallow rock	A	1	2.8	N/A	N/A	N/A	N/A
		B	3	8.3	N/A	N/A	N/A	N/A
		C	11	30.6	17.7	21.9	13.4	a
		D	21	58.3	12.3	14.5	10.0	a
EE	Till	A	25	1.6	37.5	39.9	35.2	a
		B	238	15.1	30.2	31.1	29.3	b
		C	655	41.6	21.2	21.6	20.7	c
		D	657	41.7	14.2	14.6	13.8	d
EE	Cochrane till	A	1	1.1	N/A	N/A	N/A	N/A
		B	16	17.4	32.2	35.4	29.1	a
		C	52	56.5	21.8	23.2	20.4	b
		D	23	25.0	14.7	17.4	11.9	c
EE	Mesic clay	A	0	0	N/A	N/A	N/A	N/A
		B	13	46.4	32.8	35.7	29.8	a
		C	11	39.3	24.5	29.5	19.5	b
		D	4	14.3	19.2	27.5	10.9	b
EE	Hydric clay	A	2	1.0	N/A	N/A	N/A	N/A
		B	30	14.4	30.8	33.1	28.5	a
		C	90	43.1	22.1	23.3	20.8	b
		D	87	41.6	15.8	17.0	14.6	c
EE	Organic	A	1	0.4	N/A	N/A	N/A	N/A
		B	15	5.6	28.8	33.1	24.6	a
		C	109	41.0	20.8	21.9	19.6	b
		D	141	53.0	13.7	14.5	12.8	c
PGPG	Sand	A	0	0	N/A	N/A	N/A	N/A
		B	11	9.3	18.5	21.3	15.6	a
		C	62	52.5	13.5	14.6	12.4	b
		D	45	38.1	8.9	10.0	7.7	c
PGPG	Till	A	1	1.4	N/A	N/A	N/A	N/A
		B	10	13.5	18.0	20.6	15.5	a
		C	37	50.0	14.4	16.0	12.8	a
		D	26	35.1	8.2	9.5	6.9	b

Stand age classes were grouped as follows: For black spruce all stands with an age class of ≥50 years were grouped into the mature category, whereas for jack pine we used ≥30 years (Table 2.1). This follows the argument of (Zasada 1971; Viereck and Johnston 1990; Gauthier et al. 1993; Viglas et al. 2013) which indicates that below these respective ages adequate seed production will not be achieved by either species regardless of the stand basal area. Stands identified as young uneven-age (JIN) or old-growth (> 120 year age class) (VIN) were excluded from the analysis, as the former does not achieve adequate growth/volume to warrant harvesting or salvage (Ministère des Ressources naturelles 2003), whereas seed production is expected to decline in the latter due to old age, senescence, and gap formation. ANOVA was used to compare the mean basal area/ha by soil class for both black spruce and jack pine to make sure the grouping scheme was done correctly and would prove useful; levels of significant factors were compared using Tukey's HSD post-hoc method (Table 2.2). A α value of 0.05 was used for all statistical analyses.

Expected seedbed proportions following fire were determined for 3 drainage types: xeric, mesic, and hydric (Table 2.3) by combining available data from 2 sources: The first being the seedbed proportions used in the original model; details on methodology can be found in Splawinski et al. (2014a). This included (1) the 2005 Lebel-sur-Quevillon (Quebec) wildfire, and (2) the 1997 Val Paradis (Quebec) wildfire. The second source comes from unpublished fieldwork conducted in the 2010 La Tuque wildfire (Quebec), following the same methodology used at the Lebel-sur-Quevillon wildfire. Seedbeds were divided into classes: good (mineral soil, living mosses); poor i.e., high porosity (residual duff, thick layer of leaves, dead mosses, lichens); and lethal (exposed rocks, firm logs, charred logs, and standing puddles) Splawinski et al. (2014a).

Table 2.3. Seedbed proportions by drainage types.

Drainage	**Seedbed proportion (%)**			
	Mineral soil	**Moss**	**High porosity**	**Lethal**
Xeric	9	1	85	5
Mesic	1	2	87	10
Hydric	0	9	81	10

The drainage types were then associated with each soil class (Table 2.4) thereby providing an expected seedbed proportion. Sand and shallow rock were considered xeric; till, Cochrane till, and mesic clay were considered mesic; and lastly, hydric clay and organic were considered hydric. Since seedbed data were unavailable for the organic soil class, for the purpose of the simulations we used the hydric seedbed proportions.

Table 2.4. Species and the seedbed proportions associated with each soil class.

Species	**Soil class**	**Associated seedbed proportions**
Black spruce	Sand	Xeric
	Shallow rock	Xeric
	Till	Mesic
	Cochrane till	Mesic
	Mesic clay	Mesic
	Hydric clay	Hydric
	Organic	Hydric
Jack pine	Sand	Xeric
	Till	Mesic

Two scenarios of natural regeneration density of black spruce and jack pine were simulated: (1) in burned intact stands; and (2) in 100% salvaged stands following moderate to severe fire. Here we define moderate and high severity fire as resulting in 100% stand mortality, not necessarily a function of intensity. We simulate a June fire date, since the majority of fires in the boreal forest burn in late spring (Stocks et al. 2002).

Salvage operations are typically carried out during the first winter following fire; for the purpose of the simulations, we employ a December salvage date, representing the median month as seen in the Lebel-sur-Quevillon fire from Splawinski et al. (2014a). Simulations were carried out using the mean basal area, and for the upper and lower 95% confidence interval value (Table 2.2) thereby providing seedlings/ha for each combination.

Transfer of results onto forest inventory maps

Quebec forest inventory maps provide details on forest classes subdivided by: species composition, stand cover, age class, height, forest layers stand origin (i.e., fire, partial burn, clearcut, insect outbreak, plantation), slope class, surficial deposit, and drainage at the landscape level (Lord and Faucher 2003). Maps are generated through the interpretation of aerial photos at a scale of 1:15,000 (Lord and Faucher 2003).

Resulting seedling densities obtained for both species under both scenarios were transferred onto existing forest inventory maps of the 3rd decadal inventory using GIS (here ESRI® Arc GIS 10.1). First, forest types (EE or PGPG), cover, age, and soil class were identified for the Lake Matagami lowland ecological region (6a) of the boreal forest of western Quebec following the classification scheme found in Tables 2.1 and 2.2. The Splawinski et al. (2014a) regeneration model was then used to simulate seedling densities based on each basal area found in Table 2.2, including the mean basal area, as well as the upper and lower 95% confidence limit. The resulting seedling densities were then classed under a silvicultural prescription (color coded) and attributed to each representative forest polygon. The following 3 silvicultural prescriptions (based on the resulting seedling density) were used: (1) Planting required: fully re-stocked stands are generally obtained with a seedling density ≥ 10,000/ha (≥ 1 seedling/m^2) (Greene et al. 2002), therefore any stands that exhibit seedling densities below this threshold need to be planted in the future. This silvicultural recommendation was further broken down into 2 categories: a) planting required regardless of salvage, representing stands that did not achieve adequate stand stocking due either to inadequate pre-fire basal area or stand cover; and b) planting required due to salvage, representing stands that exhibited adequate stand stocking under the burned intact scenario but subsequently needed to be planted under the 100% salvage scenario. (2) Adequate natural regeneration and potential pre-commercial thinning: Any stands that exhibit seedling densities at or above this threshold will not require planting as stand stocking should be considered as sufficient; conversely, since these stands exhibit a seedling density ≥ 10,000/ha, they may need to be thinned at some point in time in order to increase growth rates in residual trees (Morris et al. 1994). (3) Planting required due to stand immaturity: black spruce stands younger than 50 years and jack pine stands younger than 30 years were not simulated (Table 2.1), as they will not produce adequate seed stock given their young age (Zasada 1971; Viereck and Johnston 1990; Gauthier et al. 1993; Viglas et al. 2013). These stands were automatically considered as having inadequate natural regeneration and thus will require planting in order to achieve adequate stand stocking.

2.4 Results

Simulations

Simulated natural seedling regeneration densities for burned intact and 100% salvaged forest (Table 2.5) varied by soil and cover class. As expected, the higher the cover class, the higher the seedling density for both species. For both burned intact and 100% salvage scenarios, black spruce exhibited the greatest seedling densities on the hydric clay soil class, followed by organic, sand, shallow rock, mesic clay, and cochrane till, with lowest seedling densities on till. For jack pine (under both scenarios) the greatest seedling densities were observed on the sand soil class, followed by till.

For black spruce under the burned intact scenario, adequate natural regeneration densities (full stand stocking) on the sand soil class are obtained for cover classes A through C, with planting necessary in cover class D. For shallow rock, data are unavailable for cover class A and B, however based on the simulated densities in the subsequent classes it is safe to assume that adequate natural regeneration densities will be obtained. For cover class C planting may be necessary as the upper CL density exceeds the minimum threshold for planting whereas the lower CL does not; planting will be necessary for cover class D. On the till soil class, adequate natural regeneration densities are obtained for cover class A, with a potential need for planting in cover class B (the upper CL density exceeds the minimum threshold for planting however the lower CL does not); planting will be necessary in cover class C and D. For both Cochrane till and mesic clay, data are unavailable for cover class A, however we can assume that adequate natural regeneration densities will be achieved; as for cover class B, adequate densities are obtained. Conversely, for cover class C and D planting will be necessary on both soil classes. For both hydric clay and organic soil classes, adequate natural regeneration densities are obtained under all cover classes.

For jack pine under the burned intact scenario, adequate natural regeneration densities on the sand soil class are obtained for cover class A through C, with a potential need for planting in cover class D as the upper CL density exceeds the minimum threshold for planting whereas the lower CL does not. On the till soil class adequate natural regeneration densities are obtained for cover class A and B, with a potential need for planting in cover class C (the upper CL density exceeds the minimum threshold for planting however the lower CL does not), and a definite need for planting in cover class D.

Turning to the 100% salvaged scenario, planting will be necessary for black spruce on all soil and cover classes. For jack pine, adequate natural regeneration densities on sand are obtained for cover class A, with a potential need for planting in cover class B (the upper CL density exceeds the minimum threshold for planting however the lower CL does not). Planting will be necessary on both the C and D cover classes. On the till soil class planting will be necessary in all cover classes. Although data on cover class A are unavailable for both deposits, we can safely assume expected densities based on simulated densities in the subsequent classes i.e., on sand, adequate natural regeneration should be obtained in cover class A, given how high the densities are in cover class B; conversely on till given the low density in cover class B, planting will most likely be necessary in cover class A.

Table 2.5. Simulated seedlings/ha (mean, upper and lower 95% confidence limit -CL) for burned intact (BI) and 100% salvaged (S) forest for pure black spruce (EE) and jack pine (PGPG) stands by soil and cover class.

Species	**Soil class**	**Cover class**	**Seedling density/ha**					
			Mean		**Upper 95% CL**		**Lower 95% CL**	
			BI	**S**	**BI**	**S**	**BI**	**S**
EE	Sand	A	19,500	3,700	20,900	4,000	18,100	3,500
		B	15,300	2,900	16,200	3,100	14,400	2,800
		C	11,100	2,100	11,800	2,300	10,400	2,000
		D	7,800	1,500	8,300	1,600	7,300	1,400
EE	Shallow rock	A	N/A	N/A	N/A	N/A	N/A	N/A
		B	N/A	N/A	N/A	N/A	N/A	N/A
		C	9,300	1,800	11,400	2,200	7,100	1,400
		D	6,600	1,300	7,700	1,500	5,400	1,000
EE	Till	A	11,900	2,300	12,600	2,400	11,200	2,100
		B	9,700	1,900	9,900	1,900	9,400	1,800
		C	6,900	1,300	7,000	1,300	6,700	1,300
		D	4,700	900	4,800	900	4,600	900
EE	Cochrane till	A	N/A	N/A	N/A	N/A	N/A	N/A
		B	10,300	2,000	11,200	2,200	9,300	1,800
		C	7,100	1,400	7,500	1,400	6,600	1,300
		D	4,900	900	5,700	1,100	4,000	800
EE	Mesic clay	A	N/A	N/A	N/A	N/A	N/A	N/A
		B	10,400	2,000	11,300	2,200	9,500	1,800
		C	7,900	1,500	9,400	1,800	6,400	1,200
		D	6,300	1,200	8,800	1,700	3,700	700
EE	Hydric clay	A	N/A	N/A	N/A	N/A	N/A	N/A
		B	22,800	4,400	24,400	4,700	21,100	4,100
		C	16,600	3,200	17,500	3,400	15,700	3,000
		D	12,100	2,300	12,900	2,500	11,200	2,100
EE	Organic	A	N/A	N/A	N/A	N/A	N/A	N/A
		B	21,400	4,100	24,400	4,700	18,400	3,500
		C	15,700	3,000	16,500	3,200	14,800	2,800
		D	10,500	2,000	11,100	2,100	9,900	1,900
PGPG	Sand	A	N/A	N/A	N/A	N/A	N/A	N/A
		B	17,900	9,800	20,300	11,100	15,500	8,500
		C	13,700	7,500	14,600	8,000	12,700	7,000
		D	9,600	5,200	10,600	5,800	8,400	4,600
PGPG	Till	A	N/A	N/A	N/A	N/A	N/A	N/A
		B	11,500	6,300	12,900	7,100	10,100	5,500
		C	9,500	5,200	10,400	5,700	8,600	4,700
		D	5,900	3,200	6,600	3,600	5,000	2,800

*EE = > 75% black spruce; PGPG = >75% jack pine

Transfer of results onto forest inventory maps

The simulated pure black spruce and jack pine stands make up 26% of the study area in the Lake Matagami ecological region (6a). Non-simulated areas represent other forest types, including both pure and mixed coniferous stands (8%), mixed coniferous-deciduous stands (7%), and deciduous stands (3%). Recent (≤30 year age class) clear-cuts and CPRS without an associated forest type (due to their young age) represent 10% of other forest area, with other disturbances (including recent fires) representing 5%. Water represents 8%, and non-forest (mostly bogs) 33%.

Results were applied to 81,543 pure black spruce and 1,234 jack pine stands, representing an area of 11,010 km^2 and 155 km^2, respectively, in our study area, for a total of 82,777 stands (Figure 2.3). For black spruce under the burned intact scenario (excluding immature stands which make up 2% of the total), planting is only required in 36% of stands whereas adequate natural regeneration densities are obtained in 64% of stands. For jack pine (also excluding immature stands which make up 0.2% of the total), planting is only required in 28% of stands whereas adequate natural regeneration densities are obtained in 72% of stands (Table 2.6).

For black spruce under the 100% salvaged scenario (excluding immature stands), planting is required in 100% of stands. For jack pine (also excluding immature stands), planting is required in 74% of stands whereas adequate natural regeneration densities are obtained in 26% of stands (Table 2.6).

Figure 2.3 illustrates that three areas within ecological region (6a) are vulnerable to fire (i.e. less likely to regenerate naturally): middle-west, middle-east, and north-east, as they contain the greatest density of stands requiring planting. Virtually all stands are vulnerable to fire under the 100% salvaged scenario except for the densest pre-fire jack pine stands found on sand (Table 2.5), and will require planting (Figure 2.3, 100% salvaged scenario, yellow, orange, and red).

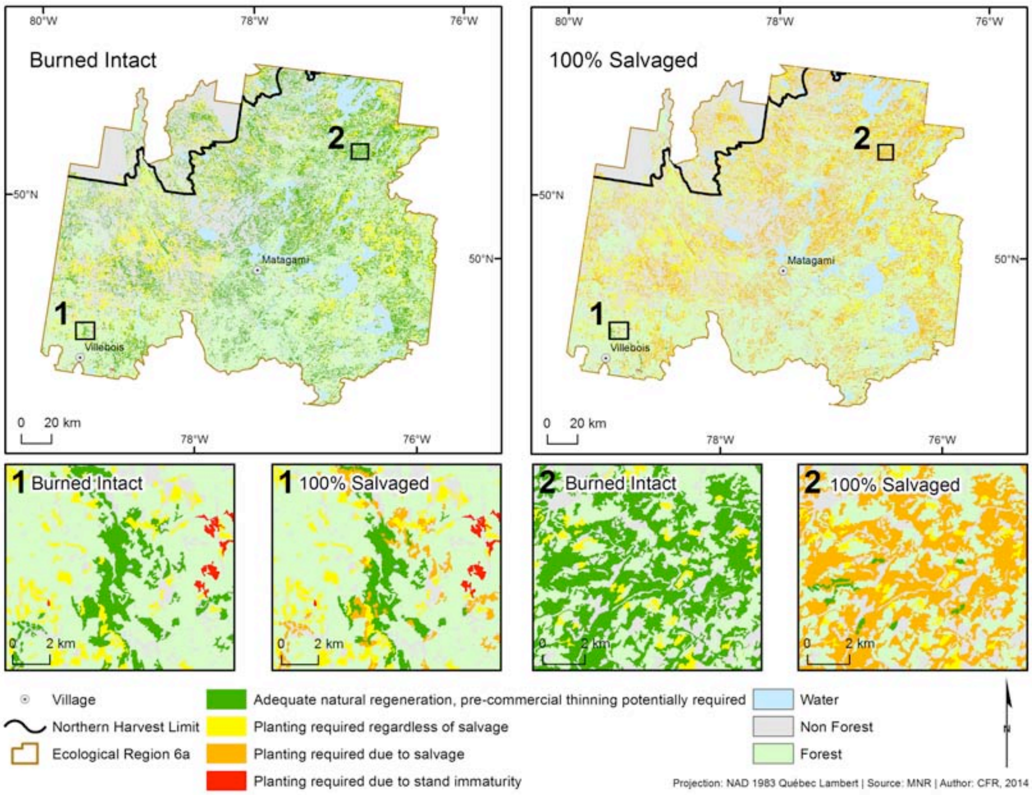

Figure 2.3. Spatial assessment tool with silvicultural prescriptions for all pure black spruce and jack pine stands used in the burned intact and 100% salvaged scenarios for ecological region (6a), including greater detail for 2 regions. Light green represents all other forest types not simulated; these include pure coniferous stands excluding black spruce and jack pine, as well as mixed coniferous and deciduous stands, and pure deciduous stands.

Table 2.6. Forest stand sample size (n) and percent of stands (%) by scenario for each silvicultural recommendation by species.

Species	**Silvicultural recommendation**	**Sample size (n) and percent (%) by scenario**			
		Burned intact		**100% Salvaged**	
		n	**%**	**n**	**%**
EE	Adequate natural regeneration	50,882	63.83	0	0
	Planting required	28,830	36.17	79,712	100
	Planting required due to stand immaturity (excluded)	1,831	2.25	1,831	2.25
PGPG	Adequate natural regeneration	884	71.64	323	26.22
	Planting required	348	28.25	909	73.78
	Planting required due to stand immaturity (excluded)	2	0.16	2	0.16

2.5 Discussion

The results illustrate that both black spruce and jack pine are well adapted to fire (Figure 2.3, burned intact scenario). As expected, post-fire regeneration densities are greatest in stands that exhibit higher pre-fire tree densities; conversely, it illustrates how salvage operations have a negative impact on the regeneration potential of black spruce, and to a lesser extent, jack pine, due to the removal of the aerial seedbank (Table 2.5; Figure 2.3 100% salvaged scenario). Salvage operations that de-limb boles and leave the cone-bearing branches near the stump (cut-to-length system) rather than in slash piles by skidding to landings (tree-length system) typically still create piles of branches. While the cones on these branches will eventually open, there will be little lateral movement of the winged seeds so close to the ground due to very low wind speeds (Greene and Johnson 1996), and even lower among the branches; i.e., the dispersal potential is essentially eliminated. Further, many of the seeds will fall on fresh wood (a lethal substrate) or germinate on an otherwise unsuitable microsite in the dense shade created by the tangle of branches. Thus, the seeds in these cones can add little to stand stocking.

Here we prescribe planting when densities are < 10,000 seedlings/ha, under both burned intact and 100% salvaged scenarios. This does not mean that stands under the burned intact scenario are not regenerating properly following fire; indeed in terms of species composition and final stem density there are no dramatic post-fire changes (Greene and Johnson 1999; Ilisson and Chen 2009; Boucher et al. 2014), therefore we would not expect a stand with low density prior to fire to regenerate at high density following fire. The planting prescription is based on suitable density for future harvesting; that is, producing the maximum volume/ha that can be harvested under the next rotation period.

Using GIS software, the maps generated under both scenarios can be used as an operational assessment tool (Figure 2.3) to better plan salvage operations and subsequent silvicultural treatment application by identifying stands and regions where natural regeneration density will be expected inadequate or potentially excessive. Foresters and managers could use this tool to estimate potential costs of mechanical site preparation, planting, and aerial seeding in stands that are inaccessible for summer planting, as well as pre-commercial thinning in their management units. Additionally assessment of the vulnerability of management units to fire and the identification of regions at particular risk is also possible, especially if the goal is to maintain or create productive stands that yield maximum potential volume for future harvesting. From an economic perspective, stands that require planting due to either low pre-fire stand density or immaturity are most vulnerable to fire under the burned intact scenario (Figure 2.3, burned intact scenario, yellow and red).

Black spruce and jack pine stands that have not yet reached reproductive maturity (i.e. optimal seed production potential), are most susceptible to fire, as they do not possess adequate seed stock to successfully regenerate following this type of disturbance (Greene et al. 1999). Current boreal forest management practices attempt to mimic stand-replacing wildfires by employing even-aged management (Bergeron et al. 2002; 2001); indeed it is the dominant management method in Canada (CCFM 2009). Clearcutting is most widely used under this management scheme (Keenan and Kimmins 1993; Masek et al. 2011), representing approximately 90% of forest harvested (CCFM 2009; Masek et al. 2011). Like fire, even-aged management reduces the proportion of older stands as it re-sets succession (Weber and Flannigan 1997; Bergeron et al. 2001; 2002, Flannigan et al. 2001; McRae et al. 2001). With a typical rotation period of ~100 years, and a fire return interval of ~150 years in eastern Canada (Bergeron et al. 2002), the proportion of younger age-classes will undoubtedly increase in the future. This may be accelerated by the expected increases in fire frequency and area burned (Amiro et al. 2001; Flannigan et al. 2001, 2005, 2009; Bergeron et al. 2004, 2010; Soja et al. 2007; Wotton et al. 2010). With an increase in younger age classes, the susceptibility of management units to poor natural regeneration following fire may increase, requiring more widespread and costly reforestation interventions at the landscape level.

In Quebec, pre-commercial thinning is generally applied to stands with a density of at least 4,000 stems/ha (Ministère des Ressources naturelles 1999). Here we use a density ≥ 10,000 seedlings/ha (≥ 1 seedling/m^2) as a threshold for this silvicultural prescription. As these stands are regenerated naturally, seedlings will establish in greater density on more favorable seedbeds, which occupy a relatively smaller proportion of total available seedbeds in a stand. This means that stem density will not be homogenously distributed across the stand. Since 10,000 seedling/ha should yield full stand stocking (Greene et al. 2002), it would not make sense to prescribe thinning in stands with 4,000 seedlings/ha (0.4 seedlings/m^2).

Natural regeneration densities are constrained by the availability of suitable seedbeds, which are generally lower in eastern Canada than the west following fire (Greene et al. 2006, 2007; Splawinski et al. 2014a). In xeric stands, the thin organic layer is reduced significantly by smoldering combustion to expose mineral soil, however few mosses survive; in mesic stands, the thicker organic layers yield far less mineral soil but slightly more mosses; in hydric stands mineral soil is not exposed however many more mosses survive (Table 2.3). If the good seedbeds (mineral soil and moss) are grouped, xeric and hydric stands exhibit similar proportions, whereas in mesic stands the proportion is significantly lower (Table 2.3). Sphagnum, which is typically found in hydric and organic sites, is considered a very good seedbed for germination due to its water holding capacity; conversely, it is considered a poor growing medium as it has a poor nutrient status (Lavoie et al. 2007). Our approach examines establishment density and not subsequent growth. We point out however, that paludified mesic and hydric stands containing large amounts of sphagnum may need to be mechanically scarified and planted even when natural regeneration densities are adequate in order to expose the underlying surficial deposit, thereby improving growth rates (Lafleur et al. 2011). Conversely in sphagnum bogs where the organic layer is deeper than the effective range of the scarifier, scarification and subsequent planting may not improve growth rates, therefore a reliance on the natural regeneration, if adequate, may be considered. In our opinion, such sites should be avoided altogether due to their unproductive nature; they will maybe never achieve volume that would warrant harvesting in the future.

The Splawinski et al. (2014a) regeneration model is parameterized to examine moderate to high intensity fires, i.e., where 100% stand mortality occurs. Potential future research could focus on updating the model to simulate low severity fire. Such fires have been shown to negatively affect conifer recruitment due to less removal of the organic layer, thereby creating fewer suitable substrates for germination (Veilleux-Nolin and Payette 2012); and also may have the potential to reduce the availability of seeds as fewer serotinous cones would be opened by the passage of the flaming front (Lecomte et al. 2006).

Model limitations

Model limitations are discussed in detail in Splawinski et al. (2014a). The following limitations are related to the approach taken in this study.

Aerial photos used to determine forest type, structure, and age are interpreted at a scale of 1:15,000, with a minimum polygon size of 4 to 8 ha (Ministère des Ressources naturelles 2009). Given this relatively coarse resolution, discrepancies between stands identified through this method and data collected on-site through temporary plots was sometimes observed (e.g., a forest type identified through aerial photography as pure black spruce with a cover class A was actually labeled black spruce mixed with some jack pine, with a cover class B using the temporary plot observation). This is an issue of scale, since temporary plots are 400m^2 in size.

The surficial deposits obtained from forest inventory maps are interpreted at the landscape level. Local variations in topography, slope, aspect, and organic layer depth may result in differing drainage patterns. For example even though the regional surficial deposit may be classified as sand, organic matter accumulation at the base of a slope may result in sphagnum bog development, yielding poor drainage at the stand level. This problem illustrates the challenges associated with linking top-down and bottom-up controls on, in this case, forest type, stand cover class, and drainage patterns.

The classification scheme used for grouping deposits, drainage, as well as other attributes such as age (Tables 2.1 and 2.2) was necessary given the limited sample size of temporary plots for each forest type (Table 4.2). Perhaps a better grouping scheme would be possible if a substantially greater sample size for each forest type was available. Indeed, although the model can also be applied to mixed coniferous or coniferous-deciduous stands containing black spruce or jack pine, the lack of a sufficient temporary plot sample size prevented the pursuit of this objective.

We also associated a particular drainage (in this case for seedbed distribution) to a particular surficial deposit. In Table 2.4 for example, we associated xeric seedbeds to a deposit of sand, whereas we associated mesic seedbeds to a deposit of till. In reality a deposit of sand can also be mesic whereas a deposit of till can be xeric. In addition, we had to associate the hydric seedbed proportions to the organic deposits due to a lack of seedbed data. In reality we expect organic deposits to have a greater proportion of living sphagnum following fire, therefore we are most likely under-representing simulated results for this deposit.

We suggest pre-commercial thinning when black spruce or jack pine densities ≥ 10,000 seedlings/ha, thus we only examine conifer density. We simulate pure coniferous stands, and the model is incapable of including a hardwood component; thus species such as aspen or birch were not included. The species classification scheme used in the 3rd inventory considers a stand as being pure black spruce or jack pine if these species make up at least 75% of the basal area (Pelletier et al. 2007). This means that hardwoods (< 25%) can in fact be present even in stands that are considered “pure” coniferous. This has important implications, as aspen and birch also readily regenerate following fire, albeit by basal sprouting and root suckering as opposed to seed from aerial seedbanks (Greene et al. 1999). Indeed, their relative densities can increase in salvaged stands due to more favorable growing conditions (Greene et al. 2006; Boucher et al. 2014).

2.6 Conclusion

This novel spatial operational tool allows foresters and managers to not only determine reforestation needs for both black spruce and jack pine following fire and salvage at the landscape level, but to also identify which management units are most susceptible to fire due to a lack of suitable natural regeneration following these disturbances. Costs of reforestation and the application of pre-commercial thinning could also be estimated across a large region, thereby aiding in determining future budget allocations. In ecological region (6a), according to our model, only 36% of black spruce and 28% of jack pine stands need to be planted following fire; however under the 100% salvage scenario, 100% of black spruce and 74% of jack pine stands necessitate planting. More widespread reforestation interventions may be required in the future due to an increase in younger age classes at the landscape level resulting from even-aged management practices and increases in fire frequency and area burned. Importantly, this project illustrates how the Splawinski et al. (2014a) regeneration model can be linked with government and industry forest inventory maps to provide a unique spatial assessment tool. It also indicates that more accurate inventory classification is required. Although we only present results from Lake Matagami lowland ecological region (6a) in Quebec’s boreal forest, this tool can be created for other jurisdictions that possesses the necessary data on stand attributes.

CHAPTER III

PRE-COMMERCIAL THINNING OF BLACK SPRUCE AND JACK PINE STANDS FOLLOWING FIRE: IMPACT OF TREATMENT TIMING AND COMPETITION ON GROWTH RESPONSE

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3.1 Résumé

La compétition de début succession entre les espèces arborescentes et arbustives en forêt boréale et son effet sur la croissance des arbres a été une source majeure d'incertitude dans l'établissement efficace de recommandations pour les éclaircies pré-commerciales et le débroussaillage. Nous examinons l'effet de la densité pré-éclaircie des compétiteurs, l'effet de la densité post-éclaircie des rejets des espèces compétitrices, les diamètres des tiges et le moment de l'éclaircie sur la réponse de croissance des gaules d'épinette noire et de pin gris suivant une éclaircie pré-commerciale dans des peuplements issus du feu. En outre, nous examinons le taux de mortalité des espèces feuillues après éclaircie et le nombre de rejets de feuillus qui ont survécus à l'éclaircie. La réponse de croissance a été plus grande lorsque les opérations d'éclaircie ont été utilisées entre 4 et 9 ans après un feu dans les peuplements de pin gris alors qu'aucune relation significative n'a été identifiée entre l'âge et le traitement pour l'épinette noire. Une analyse de régression multiple a indiqué que la réponse de croissance du pin gris a été significativement influencée par la densité de compétiteurs avant traitement, par la densité des rejets des espèces compétitrices post-traitement, et le diamètre des tiges avant traitement. Aucune relation significative n'a été observée entre la réponse de croissance et toutes les variables testées pour l'épinette noire, probablement en raison de la faible variation de la densité de compétiteurs et d'une plus grande tolérance à l'ombre. Les taux de mortalité et la production de nouvelles pousses de feuillus ont varié considérablement entre les espèces. Compte tenu du potentiel de croissance élevé du saule et de l'aulne, nous recommandons que les peuplements présentant de faibles densités de ces espèces doivent être laissés sans éclaircie. Nos résultats peuvent aider les forestiers dans l'identification des peuplements qui nécessitent l'éclaircie pré-commerciale et ainsi possiblement modifier les stratégies d'éclaircie actuellement utilisées.

Mots-clefs: Éclaircie précommerciale, moment de l'éclaircie, densité de compétiteurs, réponse de croissance, régénération des espèces feuillues.

Abstract

Early successional competition among boreal forest tree and shrub species and its effect on commercial tree growth has been a major source of uncertainty in establishing efficient pre-commercial thinning and brushing prescriptions. We examine the effect of pre-thinning competitor density, post-thinning competitor regrowth density, stem diameter, and the timing of thinning on the growth response of black spruce and jack pine saplings following pre-commercial thinning in fire-initiated stands. Additionally we examine the mortality rate of hardwoods following thinning and the number of new shoots produced per surviving thinned hardwood stem. Growth response was greatest when thinning operations were employed between 4 and 9 years following fire in jack pine stands whereas no significant relationship with the age at treatment was identified for black spruce. A multiple regression analysis indicated that in jack pine, growth response was significantly affected by pre-treatment competitor density, post-treatment competitor regrowth density, and pre-treatment stem diameter. No significant relationship was observed between growth response and any variables for black spruce, likely due to low variation in competitor density, and greater shade tolerance. Mortality rates and production of new shoots in hardwoods varied significantly between species. Considering the high regrowth potential of willow and alder we recommend that stands exhibiting low densities of these species should be left un-thinned. Our results could aid foresters in the identification of stands that require pre-commercial thinning and call for modification of currently used thinning strategies.

Keywords: Pre-commercial thinning; timing; competition density; growth response; hardwood regrowth

3.1 Introduction

Early successional competition among boreal forest tree and shrub species and its effect on commercial tree growth and yield has been a major source of uncertainty in establishing efficient intensive management strategies, including pre-commercial thinning programs (OMNR 1998b; Thompson and Pitt 2003). Pre-commercial thinning and brushing reduces tree and shrub density, and is typically applied during the first 30 years of stand's lifespan (Smith 1986, Cole et al. 2010). By increasing the growing space, the amount of light and nutrients available for residual trees, competitor removal improves both radial and vertical growth rates (Smith 1986), thereby reducing rotation age (Fleming 1994). Thinning is less costly and labor intensive in young than in mature stands due to relatively smaller diameters of stems (Riley 1973; Smith et al. 1986), and it generates greater growth response in residual trees (Vassov and Baker 1988). Indeed, in thinning trials of jack pine, treatment costs were lowest in the youngest age class tested (9 years) (Riley 1973; Smith 1984; Smith et al. 1986).

Cleaning and brushing may result in the regrowth of cut trees and shrubs that can potentially offset any short-term gains in growth of residual trees by increasing competition density in the long term beyond what was observed pre-treatment. These stands may then require additional thinning treatments (Smith 1986; OMNR 1998b; Thompson and Pitt 2003). For example willow (*Salix* spp.) and speckled alder (*Alnus rugosa* (DuRoi) Sprengel.) are able to quickly regenerate following cutting to a greater density than existed pre-treatment (Richardson 1979; Habgood 1983; Haeussler and Coates 1986; Bell 1991). This can be further exacerbated if cutting occurs during the dormant period for these two taxa (Bell 1991; Thompson and Pitt 2003). Conversely, regrowth of young birch (*Betula papyrifera* Marsh.) may be greater following cutting during the growing season (Bell 1991). Additionally, heavy thinning can lead to over-thinning of the stand, which could make residual trees susceptible to wind, ice, snow, temperature stress, sun scalding, and photoinhibition, thereby decreasing their growth rates (Janas and Brand 1988; Krishka and Towill 1989; Bell 1991; Aussenac 2000).

A good understanding of the optimal time to employ pre-commercial thinning and brushing operations, growth response to removal of competition at various densities, and the regeneration potential of hardwood trees and shrubs following pre-commercial thinning can aid foresters in the identification of stands in need this type of intervention and can also be used to modify current techniques in order to maximize growth response of residual trees, minimize treatment costs, and limit subsequent interventions.

This study examined seven tree and shrub species commonly found in the boreal forest of North America. These species have been earlier shown to influence regeneration and growth of conifers (Bell 1991). Black spruce (*Picea mariana* (Mill.) BSP) and jack pine (*Pinus banksiana* Lamb.) are both the two most common and harvested conifers in the boreal forest (Greene et al. 1999). They are well adapted to fire and regenerate through the use of aerial seedbanks following this disturbance (Greene et al. 1999). Trembling aspen (*Populus tremuloides* Michx.) and paper birch (*Betula papyrifera* Marsh.) are two common hardwood tree species that regenerate following disturbance by basal sprouting, and in the case of the former, through root suckering as well (Bell 1991; Greene et al. 1999; Thompson and Pitt 2003), but are not considered commercial tree species. Pin cherry (*Prunus pensylvanica* L.), willows (*Salix* spp.), and alders (*Alnus* spp.) are common small hardwood trees and shrubs, and generally reproduce by suckering and basal sprouting when cut (Brown and Hansen 1954; Fulton 1974; Haeussler and Coates 1986; Rudolph and Laidly 1990;

Viereck and Johnston 1990; Wendel 1990; Thompson and Pitt 2003). As these major competitors can all obtain substantial stature and their stems are similar (or greater) in size as the preferred conifer stems, the term “thinning” is hereafter used to denote the reduction in density of all competing species.

Objectives

The objective of this study was to examine the response of both conifers (black spruce and jack pine) and competing hardwoods to early pre-commercial thinning. We specifically aimed to evaluate: (1) the effect of pre-commercial thinning timing on the growth response of black spruce and jack pine; (2) the effect of competitor density (both deciduous and coniferous) on the growth response of these two species; (3) the average number of new shoots produced per cut stem across competing hardwood species; and (4) the mortality rates of thinned hardwood species.

3.2 Methods

Study Area:

Our study area was located in the western part of the managed continuous boreal forest of Quebec. A sub-polar sub-humid continental climate dominates the western portion of the spruce-moss bioclimatic domain, with total annual precipitation between 800-1000 mm, and an average annual temperature of 0° at the southern limit. The length of the growing season is approximately five months (Bergeron et al. 1998). The landscape is dominated by glaciolacustrine clays and sands, Cochrane tills, glacial tills, glacio-fluvial complexes, and organic surficial deposits (Bergeron et al. 1998; Blouin et Berger 2005).

Sites that were thinned and easily accessible were sampled in stands regenerating after three forest fires, situated along the boundary between the southern limit of the western spruce-moss and northern limit of the western balsam fir-white birch bioclimatic domains (Bergeron et al. 1998; Blouin et Berger 2005). We examined sites affected by three forest fires occurring between 1995 and 1998 (Figure 3.1).

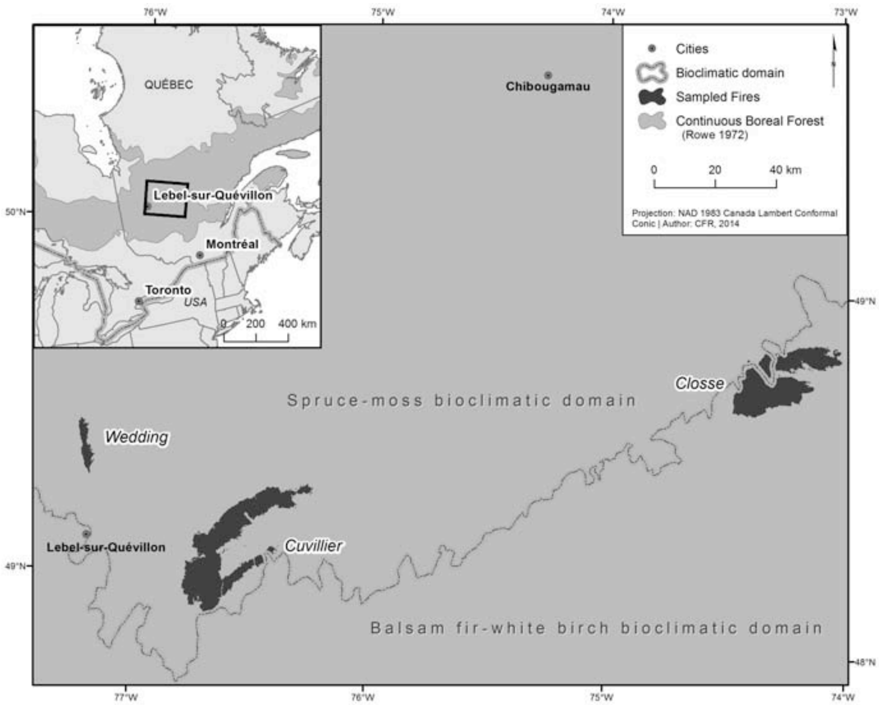

Figure 3.1. Location of the 3 fires sampled in this study.

The Wedding fire was located in northwestern Quebec 37 km north of the town of Lebel-sur-Quevillon (49° 17.789’ N, 76° 52.446’ W). Ignited accidentally on May 16 1998, it burned 4,130 ha of forest before it was extinguished by rain on June 16. The Cuvillier fire was located in northwestern Quebec 40 km south-east of the town of Lebel-sur-Quevillon (48° 49.513’ N, 76° 37.224’ W). Ignited accidentally on August 16 1995, it burned 47,709 ha of forest before it was extinguished by rain on October 20. The Closse fire was located in northwestern Quebec 100 km south-east of the town of Lebel-sur-Quevillon (48° 41.242’ N, 75° 58.793’ W). Ignited accidentally on August 20 1995, it burned 6,925 ha of forest before it was extinguished by rain on October 20.

Within these three fires, we sampled (in the summers of 2011 and 2012) a total of 21 thinned mesic and xeric stands that established following fire severity that caused 100% tree mortality. All stands were salvage logged; in addition all black spruce stands were planted, whereas only four jack pine stands were planted. Planting occurred within three year following fire, at a density of approximately 2750 stems/ha. We limited our sampling to stands dominated by black spruce (n = 8), jack pine (n = 12) or a combination of both (n = 1). Thinning dates were identified using data provided by the forestry companies responsible for treatment application and the Quebec Ministry of Forests, Wildlife and Parks. All stands were thinned manually by brush saw.

In each of these sites 10 circular plots of 4 m^2 spaced 10 m apart along a single transect were sampled in order to calculate natural and planted (where applicable) tree density. These plots were centered on the dominant black spruce or jack pine tree (depending on site). Within each plot all stems of black spruce, jack pine, aspen, birch, pin cherry, willow, and alder were counted, and the state of each tree (alive, dead, and/or thinned) was recorded. The height, diameter at breast-height (DBH), and diameter at stump-height (DSH) of the dominant tree was also recorded. Stems that were cut but re-grew were measured to a radius of 2 m (12.56 m^2) from the dominant tree; for each individual, we measured the number of cut stumps and the density of re-grown stems. Surficial deposit was identified by digging a total of five pits (every second plot) per site. The surficial deposit and indicator plant species were used to determine site drainage, which was grouped into 2 categories: xeric and mesic.

We dated trees and estimated growth rates using stem disks from five dominant trees sampled in every second plot. Only trees without evidence of top injury were chosen for dendrochronological analyses. Trees were cut at ground level with disks taken just above the root collar. We sanded disks with up to a 400 grit sandpaper and dated them under a binocular microscope. Stem diameter at the end of the last dormant period preceding thinning operations was measured using a caliper.

Disks were scanned at 2400 dpi and tree rings were measured in CooRecorder (Larsson 2010) along three radii at 0, 120 and 240 degrees from the North direction. If problems were encountered with the disk (branch whorls, cracks) the lines were moved by 30 degrees in the clockwise fashion from their original position. In case the problem persisted, the radii were once again moved by 30 degrees in the opposite direction. If the problem persisted further, the process was repeated in increasing angular increments by 10 degrees. Tree-ring data for each tree were averaged in CDendro. We obtained a tree-level estimate of growth response to thinning by averaging three radii in CDendro (Larsson 2010).

Statistical analyses

To provide a proxy of tree response to thinning we developed an index based on a ratio describing the cumulative basal area increment (BAI) prior to and following the thinning. Since the sampled trees were young (< 17 years), they exhibited a positive relationship between their age and BAI i.e. BAI increases with age. Therefore, a simple ratio of pre- and post-thinning increments would underestimate growth response by assuming no age-related difference in growth rate between periods. To address the age trend (in this case an increase of BAI with time), we first defined and estimated a linear function relating age and BAI, parameterized using the pre-thinning period for each tree analysed. Such a linear function explained, on average, 89% (R^2min = 43%, R^2max = 99%) of variability in tree-specific regression equations. Each tree's growth rate was then projected for the post-treatment period using its own growth equation. The projections were extended to 2011, the most recent year for which we had the growth chronologies from all sampled trees. This allowed us to project BAI as if the trees were growing at the same rate both before and after the treatment. The ratio between the observed and the projected cumulative growth (expressed as a percentage), which we refer to as "growth response" later in the text, was then used as dependent variables in subsequent analyses. The period length used with that ratio varied between sites as thinning operations took place in different years over 2002-2009.

We used R package *nlme* (Pinheiro et al. 2014) to run a non-linear mixed effect model with growth response of jack pine or black spruce as the dependent variable, and age of thinning and site drainage index as independent factors. We then used R package *AICcmodavg* (Mazerolle 2014) to select the most parsimonious model from the initial pool of candidate models including both interactive and non-interactive effects. Due to low variability in the competitor density, we could not use ANOVA to test for their effects on growth response for either of the coniferous species. Instead, we considered the coniferous and deciduous competitors together.

In order to evaluate the extent to which other factors (other than age at treatment) could affect the growth response, we then performed a multiple regression independently for both the black spruce and jack pine datasets. Growth response was the dependent variable, and total competitor density removed by thinning, total regrowth density, age of thinning, stem diameter at the end of the last dormant period preceding thinning operations, and site drainage were independent variables. The model that accounted for the most variance and the greatest number of significant independent variables was then selected.

To examine the mean number of new shoots produced by hardwoods based on the number of cut stems (per individual) following thinning, we used a mixed effects ANOVA with site variation assigned as a random factor; Tukey's HSD post-hoc method was used to determine where the differences occurred. The response variable was the ratio of new shoots produced following cutting to the number of stems prior to cutting. Variables were log-transformed to comply with assumptions of normality and homoscedasticity.

To compare the mortality rates among hardwood species following thinning we used a Chi^2 test. A α value of 0.05 was used for all statistical analyses.

3.3 Results

Black spruce and jack pine growth response following thinning

Thinning resulted in a positive growth response in the majority of sampled trees, 95.56% for black spruce and 75% for jack pine. A positive growth response is defined as any growth response value greater than 100%. Details on the distribution of growth response data by species can be found in table 3.1.

Table 3.1. Distribution of growth response data (%) for all sampled black spruce and jack pine trees

Species	Mean	Std Dev	Min.	Max.	n
Black spruce	240.47	123.16	95.85	570.53	45
Jack pine	211.36	132.94	56.15	649.50	64

Growth response versus timing of thinning operations

No significant relationship was identified between the growth response (%) and age of thinning (years since fire) for black spruce (Figure 3.2A); however trees thinned at 6 years showed the lowest growth response. Although also not significant, site drainage was a better predictor of growth than age at thinning. For jack pine, sites thinned between 4 and 9 years following disturbance had a significantly greater growth response than those thinned 10+ years following disturbance (Figure 3.2B). Detailed results of the analyses can be found in table 3.2.

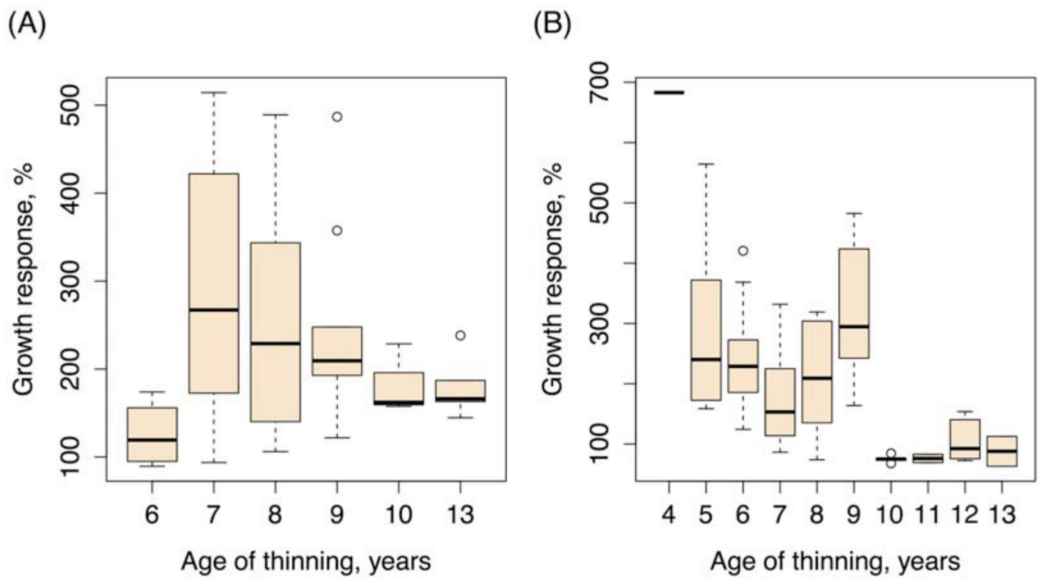

Figure 3.2. Boxplot of growth response versus thinning age for black spruce (A) and jack pine (B). Sample size for individual age classes (from youngest to oldest) are as follows: for black spruce: 4, 8, 14, 4, 5 for jack pine: 1, 6, 15, 16, 6, 5, 5, 2, 6, 2.

Table 3.2. Best non-linear mixed effect models for release of black spruce and jack pine after thinning. Only the best predictive model is presented for each species.

Species	Model	Coefficient	Std. Error	DF	t-value	p-value	Correlation
Black spruce	Drainage	39.52	57.31	7	0.69	0.51	-0.67
	Intercept	210.86	38.21	31	5.52	0.00	
Jack pine	Thinning age	-24.57	10.30	37	-2.39	0.02*	-0.95
	Intercept	398.60	84.30	37	4.73	0.00	

Growth response versus stem diameter, competitor density removed, competitor regrowth density, and thinning timing

For black spruce, multiple regressions showed no significant relationship (R^2 = 0.12, p-value = 0.268) between growth response and competitor density removed, competitor regrowth density, age of thinning, or stem diameter at the end of the last dormant period preceding thinning operations although this last variable was close to being significant (Table 3.3). For jack pine, significant effects were observed for all independent variables except treatment age (R^2 = 0.36, p-value = 0.0001) (Table 3.3); stem diameter at the time of thinning exhibited the highest significance, followed by competitor density removed, and competitor regrowth density.

Table 3.3. Multiple regression results for black spruce and jack pine growth responses.

Species	Model	Estimate	t-value	p-value
Black spruce	Competitor density	1.68	0.25	0.8049
	Regrowth density	3.14	0.38	0.7084
	Stem diameter	-30.86	-1.78	0.0828
	Treatment age	-1.53	-0.12	0.9070
Jack pine	Competitor density	2.70	2.24	0.0285*
	Regrowth density	-6.53	-2.10	0.0399*
	Stem diameter	-25.82	-3.26	0.0019*
	Treatment age	-9.06	-1.10	0.2769

In order to determine whether stem diameter was related to treatment age, we then performed multiple regressions examining the effect of treatment age and competition density removed on stem diameter of dominant trees. For black spruce, stem diameter was significantly affected by treatment age but not competitor density (R^2 = 0.23, p-value = 0.0046); for jack pine, stem diameter was significantly affected by both independent variables, with treatment age exhibiting the highest significance, followed by competitor density removed (R^2 = 0.46, p-value = <0.0001) (Table 3.4).

Table 3.4. Multiple regression results for black spruce and jack pine examining stem diameter.

Species	Model	Estimate	t-value	p-value
Black spruce	Treatment age	0.35	3.32	0.0019*
	Competitor density	-0.02	-0.57	0.5686
Jack pine	Treatment age	0.65	6.29	<0.0001*
	Competitor density	-0.04	-3.36	0.0014*

Mortality frequency and mean number of new shoots per thinned stem by hardwood species

The abundance of hardwood species varied across the study sites, with aspen and pin cherry being the most frequently observed, followed by willow spp., paper birch, and alder spp. (Table 3.5).

Table 3.5. Presence of hardwood species out of total sites sampled (n = 21), sample size (number of saplings) by species for both the mortality and regrowth study.

Species	Sites present	n for mortality	n for stem regrowth
Trembling aspen	16	497	526
Pin cherry	16	222	204
Paper birch	8	75	88
Willow spp.	13	143	193
Alder spp.	7	53	87

We observed that the mortality of competitors following thinning varied significantly among species. Figure 3.3 illustrates the results of the Chi^2 test. Trembling aspen exhibited the highest mortality (40%) among the five hardwoods compared, followed by pin cherry (35%) and paper birch (29%), with willow spp. (3%) and alder spp. (2%) exhibiting the lowest mortality rate.

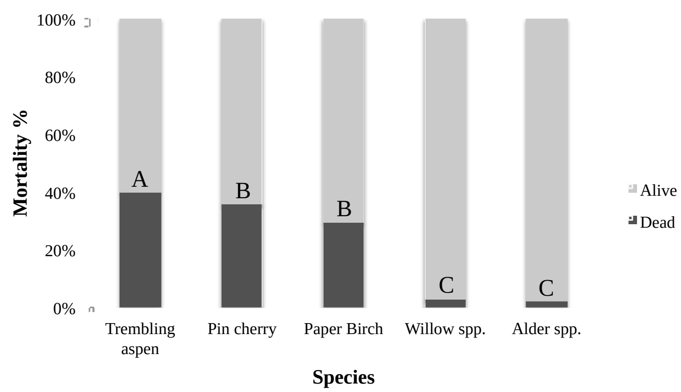

Figure 3.3. Percent stem mortality by species (Prob. > Chi^2 <0.0001). Letters illustrate significant differences in mortality between species.

Mixed model ANOVA indicates that the after/before ratio of shoots produced by cutting varied significantly among hardwood species (Prob. <0.0001) (Figure 3.4). Alder spp. produced significantly more shoots per stump than willow spp., paper birch, pin cherry, and trembling aspen (Tukey HSD). Details on adjusted and observed mean shoot production, upper and lower 95% confidence limits, and minimum and maximum values by species can be found in table 3.6).

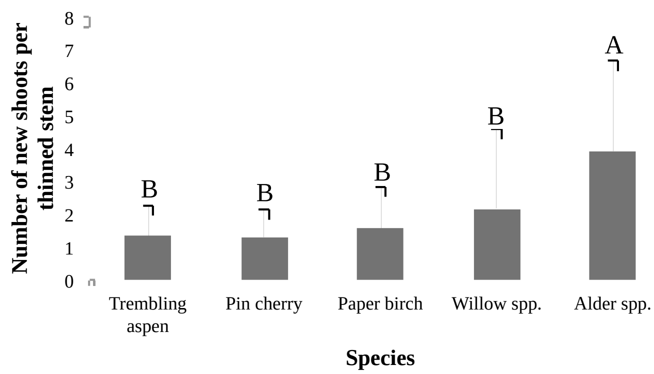

Figure 3.4. Adjusted mean number of new shoots per cut stem by species. ANOVA Prob. <0.0001. Error bars represent standard deviation, and letters illustrate significant differences in new shoot production between species.

Table 3.6. Adjusted and observed mean shoot production, upper and lower 95% confidence limit, and minimum and maximum value per cut stem by species.

Species	Adjusted mean	Observed mean	Upper 95% CL	Lower 95% CL	Min.	Max.
Trembling aspen	1.20	1.32	1.41	1.24	0.33	10
Paper birch	1.23	1.55	1.82	1.27	0.25	7
Pin cherry	1.15	1.27	1.39	1.15	0.33	8
Willow spp.	1.52	2.17	2.51	1.82	0.20	20
Alder spp.	2.82	3.91	4.49	3.32	0.33	19

3.4 Discussion

Black spruce and jack pine growth response following thinning

Thinning resulted in an overall positive growth response in both black spruce and jack pine. As indicated by other authors, by increasing growing space, light and nutrient availability for residual trees, thinning increases radial growth rates (Smith 1986; Vassov and Baker 1988; OMNR 1998 a,b). However, some residual trees experienced a decline in growth rates following thinning (4.4% of sampled black spruce and 25% of sampled jack pine trees). This may be due to over-thinning (excessive spacing), which could leave residual trees susceptible to wind, ice, snow, temperature stress, sun scalding, and photoinhibition (Janas and Brand 1988; Krishka and Towill 1989; Bell 1991; Aussenac 2000), damage to the tree as a direct result of the thinning operation itself (Vassov and Baker 1988), or crown closure of planted stands beginning at or around the time of thinning. We believe that crown closure occurred or was close to occurring in two of the sampled jack pine stands (site # 18 and 20 in annex 3.1) at the time of thinning application; all sampled trees within these stands exhibited a negative growth response following thinning (representing 10 trees out of the 16 jack pine trees exhibiting a negative growth response). These two sites were thinned relatively late (11-12 years following fire), had the highest stem diameters at the time of thinning when compared to all other sampled jack pine stands, and exhibited high lateral branch mortality at the time of sampling.

Timing of pre-commercial thinning operations

Our results indicate that for jack pine, a significantly greater growth response was observed in stands that were thinned between 4 and 9 years following disturbance. Due to increasing competition for nutrients, space, and light, pre-commercial thinning operations in jack pine stands generally coincide with the onset of the self-thinning phase, between 6 to 12 years following stand establishment (Vassov and Baker 1988). It is also more economical to thin stands at a younger age because less time and energy are required (Riley 1973; Smith et al. 1986). Stands thinned early also leave residual trees less vulnerable to stress and may improve stand stability (Aussenac 2000), making them less susceptible to over-thinning. Our results correspond well with observations made by these authors. Vassov and Baker (1988) found that 10 year-old jack pine stands typically exhibit a greater response to thinning than older age classes; additionally the 9-year age class was also identified as the most economical age class to thin (Riley 1973). Smith (1984) however, suggested jack pine stands be thinned between 10 and 15 years following establishment. It is important to mention that the studies conducted by both Riley (1973) and Smith (1984) examined 9, 22 and 33 year-old age classes, whereas our youngest jack pine stand examined was thinned 4 years following fire. Another argument for thinning earlier is that it will minimize stem taper, which lowers wood quality (Vassov and Baker 1988).

No significant difference among thinning dates was observed for black spruce although trees thinned at 6 years showed the lowest growth response. This may be due in part to its slow growth rate and it’s greater shade tolerance (Sims et al. 1990; Viereck and Johnston 1990); at the time of thinning, the canopy would have not yet closed so intense competition would have not yet begun, thereby minimizing growth response.

We suggest that thinning operations in jack pine stands not be employed beyond 9 years following fire, as is currently often the case. Indeed in our study area we observed black spruce and jack pine stands being thinned 16 years following fire. Based on this analysis, we are hesitant to provide a thinning schedule for black spruce, but given its slow growth rate and the fact that it appeared to exhibit the strongest growth response 7 and 8 years following fire (Figure 3.2), we suggest that thinning in black spruce stands should occur no earlier than 7 years following fire.

Growth response versus stem diameter, competitor density removed, competitor regrowth density, and thinning timing

The growth response of jack pine following thinning operations was significantly affected by pre-treatment stem diameter and the density of competitors removed by thinning operations, as well as post-treatment competitor regrowth density. In this approach, treatment age did not significantly affect growth response as it did in the non-linear approach (Figure 3.2); instead pre-treatment stem diameter exhibited the highest significance (Table 3.3). We hypothesized, however, that pre-treatment stem diameter would be dependent on both treatment age and competitor density removed so an additional multiple regression analysis was performed. The results supported this hypothesis (Table 3.4). So although treatment age did not appear to significantly affect growth response when considering other variables, it is directly linked to the most highly significant variable.

Our results show that growth response was inversely proportional to the stem diameter of dominant trees prior to thinning; i.e., smaller diameters resulted in a greater response. This supports Vassov and Baker’s (1988) suggestion that smaller trees (diameter) may exhibit higher post-thinning relative growth rates.

Jack pine is highly shade-intolerant (Benzie 1977; Rudolph and Laidly 1990; Viereck and Johnston 1990; Bell 1991). Additionally hardwood species such as cherry, willow, and alder compete heavily with jack pine and black spruce for light, nutrients, and especially water (Bell 1991). It is therefore not surprising that the greater the competition density removed, the greater the growth response. Indeed, Bell (1991) suggests that all overhead competition should be removed within one year following planting of jack pine.

With respect to competitor regrowth, the surviving root system of hardwood vegetation that regrows following thinning continues to use resources such as nutrients and water, and regrown stems may once again begin competing for light with residual trees if their growth rates are rapid. Indeed, trembling aspen root suckers and paper birch sprouts exhibit rapid growth following cutting, with the former growing up to two meters in its first year due to the availability of resources in parent roots (Steneker 1976; Haeussler and Coates 1986; Bell 1991). Additionally, if competing jack pine stems are thinned above the first living branch whorl, there is a high chance of regrowth (Splawinski et al. 2014b).

There was no significant relationship between black spruce growth response following thinning and competitor density removed, competitor regrowth density, age of thinning, or pre-treatment stem diameter; however stem diameter was close to significant (p-value = 0.0828). All sampled stands were dominated by black spruce before the fire, and due to poor conifer recruitment, were planted following salvage operations. We believe that the resulting low variation in competition density and composition (almost all hardwood) in the stands, as well as the slow growth rate and greater shade tolerance of black spruce (Sims et al. 1990; Viereck and Johnston 1990), explains this lack of relationship.

Hardwood mortality and regrowth

Both willow and alder species can reproduce quickly and vigorously following cutting (Richardson 1979; Habgood 1983; Haeussler and Coates 1986; Bell 1991). For example, although highly variable, individual stems of willow spp. that have been cut can produce up to 50-60 new sprouts (Haeussler and Coates 1986). Unless treated chemically, alder is not removed by cutting; indeed stem density may increase by approximately 63% depending on cutting season (Stoeckeler and Heinselman 1950).

The observed mortality rates varied significantly by species (here mortality refers to the death of the stem and does not take into account the production of root suckers). Of the species that exhibited the highest mortality rates following pre-commercial thinning (trembling aspen, paper birch, and pin cherry), those that regrew displayed the lowest shoot production per cut stem. Conversely, those that exhibited the lowest mortality rates (willow spp. 2%, alder spp. 3%) displayed the highest shoot production per cut stem (a maximum of 20 for willow spp. and 19 for alder spp.). If the density of these species is relatively low (especially willow and alder), it may be beneficial to avoid thinning. For example, the presence of alder may enhance conifer reproduction and growth, especially in black spruce, by increasing nitrogen and preventing grass growth (Stoeckeler and Heinselman 1950; Bell 1991), which has been identified as detrimental to early conifer establishment and growth (Bell et al. 2000). Birch and aspen presence may also improve nutrient cycling (Haeussler and Coates 1986; Bell 1991). This may improve growth rates and survival as well as provide some protection, especially in the case of black spruce (Bell 1991). For example, Légaré et al. (2004) observed that black spruce DBH was enhanced when aspen occupied between 0% and 41% of total stand basal area.

Study limitations and future research

In addition to the relative lack of variation in competition density in sampled black spruce stands, we provide another three factors that may explain some of the variability that was not accounted for by our statistical model: (1) We did not examine root suckering following pre-commercial thinning, however this is a common reproduction strategy in trembling aspen (Greene et al. 1999), pin cherry (Fulton 1974) and speckled alder (Brown and Hansen 1954). We observed, to varying degrees, this type of regeneration in almost all thinned stands where these species were present; in some cases the density (post- versus pre-treatment) increased at the stand level. (2) Residual tree spacing following pre-commercial thinning was not measured, however it is known to affect growth response (Smith 1984). (3) We did not examine the effect of ericaceous species presence on conifer growth. Numerous studies indicate that ericaceous shrubs can negatively affect conifer regeneration and growth (Bell 1991; Mallik 2003). This may include allelopathy, soil nutrient deficiency and imbalance due to phenolic compounds, direct competition, soil acidification, poor ectomycorrhization, changes in conifer myccorrhizae activities, site degradation, and water use (Bell 1991; Inderjit and Mallik 1996a, b, 2002; Mallik 2003).

Future research should focus on examining the effects of the pre-treatment density of individual hardwood species on the growth response of black spruce and jack pine following pre-commercial thinning, in order to identify their relative competiveness, and if and at what limit hardwood retention would be beneficial. To date, hardwood retention in Quebec has focused primarily on benefits for fauna and biodiversity (Legris and Couture 1999; Cimon and Labbé 2006), and not maximizing crop-tree growth.. High competitor density has a negative effect on the growth of black spruce and especially the shade-intolerant jack pine (Benzie 1977; Johnstone 1977; Rudolph and Laidly 1990; Viereck and Johnston 1990; Bell 1991; Bell et al. 2000). However companion species may improve nutrient cycling (for example, nitrogen fixation, Bell 1991), which can result in an overall positive effect of their presence in natural stands and commercial plantations if their densities are not too great. For example, in the absence of thinning, jack pine had a greater average DBH and volume when mixed with paper birch when compared to pure jack pine and mixed aspen stands (Longpré et al. 1994). Similarly, a positive effect of aspen presence on black spruce DBH and height growth has been reported (Bell 1991; Légaré et al. 2004). We know of only one study, Bell et al. (2000), that examines the relative competiveness of woody and herbaceous species on growth of planted seedlings of black spruce and jack pine, however it only focuses on the first 4 years following planting and not beyond.

This study focused on stands only subjected to pre-commercial thinning as a means for controlling density. Future research should aim to develop comprehensive intensive stand management regimes by examining the combined use of silvicultural approaches and on-site factors. This includes the above-mentioned hardwood retention strategy; chemical treatment, which has shown promise in controlling vegetation (Bell 1991); thinning timing (Riley 1973; Vassov and Baker 1988); thinning intensity (spacing) (Smith 1984; Vassov and Baker 1988); thinning height (Splawinski et al. 2014b); pre-treatment stand density (OMNR 1998b); disease and insect susceptibility (Vassov and Baker 1988); the possibility of multiple thinning treatments (Smith 1986; OMNR 1998b); and economic factors such as desired end-products (OMNR 1998b), current and future market value of products, and operational costs (OMNR 1998a).

3.5 Conclusion

Results of this study indicate that (1) thinning timing has a significant effect on the growth response of jack pine, and should be employed between 4 and 9 years following fire, (2) jack pine growth response following thinning is significantly affected by pre-treatment competitor density, post-treatment competitor regrowth density, and pre-treatment stem diameter, and (3) mortality rates and new shoot production vary significantly by hardwood species, however due to the high and dense regrowth potential of willow and alder, we recommend that stands exhibiting low densities of these species be left un-thinned.

3.6 Annex 3.1

The following table provides site details including: dominant species (BS = black spruce, JP = jack pine), drainage (M = mesic, X = xeric), site location within a specific fire (Cl = Closse, Cu = Cuvillier, We = Wedding), time since fire, years since thinning, mean diameter at stump height (DSH) prior to thinning with standard deviation, mean growth response (%) following thinning with standard deviation, mean competitor density prior to thinning (stems/ha) with standard deviation, mean competitor regrowth density following thinning (stems/ha) with standard deviation, and hardwood species present (A = aspen, B = birch, C = cherry, W = willow spp., and Al = alder spp.).

Site #	Species	Drainage	Fire	Time since fire (thinning timing)	Years since thinning	Mean diameter (DSH) prior to thinning (cm)	Std Dev	Mean growth response (%)	Std Dev	Mean competitor density (stems/ha)	Std Dev	Mean competitor regrowth density (stems/ha)	Std Dev	Hardwood species present
1	BS	M	Cl	7	9	2.82	0.34	121.2	34.7	1500	2236	500	1118	C, W
2	BS	M	Cu	9	7	3.84	0.96	196	56.5	26000	27928	22000	22804	A, C, W
3	BS	M	Cu	13	2	4.80	1.91	228.9	52.9	32000	19316	22500	19764	A, B, C, W
4	BS	M	We	7	5	3.24	0.3	378.6	81	5000	1768	4500	2092	A, B, C, W
5	BS	M	We	7	5	3.46	0.9	195	80.70	3000	2739	3000	2739	B, C, W
6	BS	X	Cl	8	8	2.64	0.63	397.8	158	20000	17589	18000	15350	A, B, C, W
7a	BS	X	Cl	8	8	3.00	1.26	160.9	69.6	15000	5863	10000	8478	A, C
8	BS	X	Cu	9	6	4.26	1.43	189.4	43.1	8500	4873	7000	4472	A, C
9	BS	X	Cu	8	8	2.40	0.74	296.6	149	25500	16808	12000	2739	A, C, W
10	JP	M	Cl	8	8	3.44	0.98	120.5	70.9	12000	8551	4000	2850	A, W
11	JP	M	Cu	9	6	2.40	0.82	243.6	84	67500	66685	23000	19072	C, W
12	JP	M	Cu	13	3	4.08	1.06	200.1	108	44500	27295	9500	6471	A, B, C, Al
13	JP	M	We	7	5	3.94	0.9	280.4	111	4500	5123	3500	4873	Al
14	JP	M	We	7	5	3.96	0.8	199.7	36.5	18000	6225	7000	5701	A, C, W, Al
15	JP	M	We	7	5	4.14	1.20	238.3	66.4	6000	4183	2000	3260	A
16	JP	X	Cl	6	9	1.96	0.48	436	152.90	24500	10216	16500	8404	A, B, C, W
17	JP	X	Cl	6	10	2.46	0.22	192.5	38	98500	47355	35000	25981	A, W
7b	JP	X	Cl	8	8	5.25	0.19	193.7	108	22500	14860	7500	6770	A, C
18	JP	X	Cu	12	3	9.52	0.70	63.57	6.56	2000	4472	2000	4472	W
19	JP	X	Cu	8	7	2.18	1.10	136.7	52.2	53000	34884	26500	37022	
20	JP	X	Cu	11	5	8.50	1.21	65.22	6.17	28500	7202	7500	5863	A, B, C
21	JP	X	Cu	9	7	3.56	0.89	373.9	153.30	116000	52933	24000	16826	A, B, C, Al

CHAPTER IV

THE IMPACT OF EARLY PRE-COMMERCIAL THINNING OF DENSE JACK PINE (*Pinus banksiana* Lamb.) STANDS ON THE MORTALITY OF THINNED STEMS

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4.1 Résumé

L'éclaircie précommerciale des peuplements de pin gris (*Pinus banksiana*) est une application sylvicole courante pour contrôler la densité et la croissance des peuplements forestiers boréaux sous aménagement. Si elle est appliquée trop tôt, la reprise vigoureuse de la croissance des conifères peut réduire la croissance radiale et le rendement potentiel des arbres résiduels, ce qui entraîne des coûts additionnels d'éclaircie tout en rallongeant la période de révolution. Nous avons étudié la proportion de la reprise de croissance chez le pin gris après éclaircie en tant que fonction des verticilles retrouvés sur la souche des tiges coupées et de la hauteur de l'éclaircie à la suite d'un feu et d'une coupe de récupération. Quatre peuplements ayant fait l'objet d'une coupe de récupération et d'une éclaircie précommerciale sur le site de deux feux de forêt survenus en 1995 dans la région de l'Abitibi-Témiscamingue au Québec ont été échantillonnés. Des relations significatives ont été relevées entre le nombre de verticilles présents sur chacune des tiges après l'éclaircie précommerciale et la proportion de la mortalité, ainsi qu'entre le nombre de verticilles présents sur chaque tige après l'éclaircie commerciale et la hauteur de souche moyenne. Nous suggérons que l'éclaircie précommerciale dans le cas de peuplements denses de pin gris soit réalisée entre 7 et 10 ans après l'établissement du peuplement et à hauteur de 10 cm à 13 cm au-dessus de la souche. De plus, nous identifions les différents indicateurs que les forestiers peuvent utiliser sur le site pour mieux planifier les opérations d'éclaircie.

Mots-clefs: Éclaircie précommerciale, pin gris, mortalité de la souche, verticilles, hauteur d'éclaircie, croissance, âge de révolution, feu de forêt, coupe de récupération.

Abstract

Pre-commercial thinning of jack pine (*Pinus banksiana*) stands is a common silvicultural method to control stand density and growth in managed boreal forest stands. If employed too early, vigorous conifer re-growth can reduce the radial growth and potential yield of residual trees, thus requiring additional costly thinning treatments and extended rotation period. We examine thinned jack pine re-growth proportion as a function of remaining branch whorls on the stump of cut stems, and of thinning height following fire and salvage. Four salvaged and pre-commercially thinned stands in two forest fires that occurred in 1995 in the Abitibi-Temiscamingue region of Quebec were sampled. Significant relationships were identified between the number of branch whorls remaining on individual stems following pre-commercial thinning and the mortality proportion, and between the number of branch whorls remaining on individual stems following pre-commercial thinning and mean stump height. We suggest that pre-commercial thinning in dense jack pine stands be applied at 10 cm - 13 cm stump height, between 7 and 10 years following establishment. In addition, we identify various indicators that foresters can use on-site to better plan thinning operations.

Keywords: pre-commercial thinning, jack pine, stump mortality, branch whorls, thinning height, tree growth, rotation age, forest fire, salvage logging

4.2 Introduction

Natural regeneration densities of jack pine (*Pinus banksiana* Lamb.), a serotinous, shade intolerant conifer (Fowells 1965, Rudolph and Laidly 1990, Sims et al. 1990, Lamont et al. 1991, Gauthier et al. 1993, Enright et al. 1998, Greene et al. 1999, Claveau et al. 2002), can be high (Bella 1974, De Groot et al. 2004), reaching up to 200,000 stems/ha following fire (Splawinski et al. Unpublished). For harvested areas, reforestation methods such as spot seeding, aerial broadcast seeding and the redistribution of cone-bearing slash through scarification can also result in relatively high stem densities (Van Damme and McKee 1990). While these over-stocked stands often require pre-commercial thinning treatments to reduce density and improve residual tree growth and volume (Vassov and Baker 1988), success is highly dependent on treatment timing (Riley 1973). Pre-commercial thinning of jack pine stands is a common silvicultural method to control stand density and growth in managed boreal forest stands in Canada (Vassov and Baker 1988), especially in dense, xeric post-fire stands (Riley 1973; Smith 1984).

Stem density will determine the timing of the onset of the self-pruning phase (Vassov and Baker 1988). The higher the stem density, the faster the self-pruning of lower branches will begin in order to minimize energy loss. Pre-commercial thinning is typically applied at the juvenile stage, 6 to 12 years after the stand origin, when intense competition for space, light and nutrients begins to reduce the radial growth of commercially important conifers, thereby reducing stem volume and extending rotation period (Vassov and Baker 1988). Its use must be carefully timed; if employed too early, vigorous hardwood and conifer re-growth can reduce the radial growth and potential yield of residual trees, thus requiring additional costly thinning treatments and extending rotation period; if delayed too long, treatment costs increase and radial growth decreases (Riley 1973).

In the event of top injury, and depending on the level of damage, vertical growth from the remaining living branches can occur. These then become the new leaders, allowing the tree to re-grow (Fig. 4.1) (Riley 1973). In a rough sense, the success of thinning is inversely proportional to the density of re-grown stems.

Figure 4.1. Observed re-growth of thinned stems in site 1 from the current study. Note the high density and height of re-grown stems, as well as the lack of crown closure.

Density, stocking, spacing, and diameter and height growth response of jack pine following pre-commercial and commercial thinning has been extensively studied (Skilling 1957; Cayford 1961, 1964; Buckman 1964; Steneker 1969; Riley 1973; Bella 1974, Bella and de Franceschi 1974; Benzie 1983; Smith 1984; Goble and Bowling 1993; Morris et al. 1994; Bulley et al. 1997; OMNR 1998a), and the problematic nature of whorl re-growth has been briefly outlined by Riley (1973). However, we know of no studies that examine thinned jack pine mortality percentage as a function of either the remaining number of branch whorls on the stump of cut stems or thinning height. Specific industrial guidelines for jack pine thinning height based on scientific studies are also lacking.

Riley (1973) determined that, while pre-commercial thinning was most economical in younger jack pine stands, timing was important. He observed that surviving whorls growing close to the ground led to dense re-growth of thinned jack pine stems in the two years following thinning. In the same study area, Smith (1984) examined jack pine stocking, density and height and diameter response to pre-commercial thinning, and found that thinning as close to the ground as possible resulting in minimal re-growth.

A study examining live limb survival and development on stumps following pre-commercial thinning in the closely-related lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm.) and coastal western hemlock (*Tsuga heterophylla* [Raf.] Sarg.) found variable stump survival depending on treatment (Forrester and von der Gonna 1990). Stumps thinned closest to the ground, with the fewest remaining live limbs, exhibited the greatest mortality. Gay (1987) also reported survival of stumps with live limbs following treatment in a lodgepole pine stand.

The objectives of this study on the pre-commercial thinning of jack pine are to: (1) examine the relationship between thinning height and the number of remaining branch whorls; (2) examine the relationship between the number of remaining branch whorls and the percent mortality of these thinned stems; (3) determine the thinning height that results in the greatest mortality of thinned stems; and finally (4) propose guidelines to improve thinning success based on thinning height and timing of operations in dense stands, thereby increasing growth of residual trees.

We propose the following hypotheses: (1) thinning treatments that leave no living branch whorls on the remaining stump will result in 100% stem mortality; and (2) the mortality of thinned stems will be inversely proportional to the number of remaining post-thinning whorls.

4.3 Methods

Study Area

We sampled four salvaged and pre-commercially thinned (by brush-saw) stands in two forest fires that occurred in 1995 in the Abitibi-Temiscamingue region of Quebec (Fig. 4.2). All four stands were dominated by jack pine, found on a surficial deposit of sand of glaciolacustrine origin, with no evidence of crown closure at the time of data collection; here, crown closure is defined as all available crown space being fully occupied (Fig. 4.1).

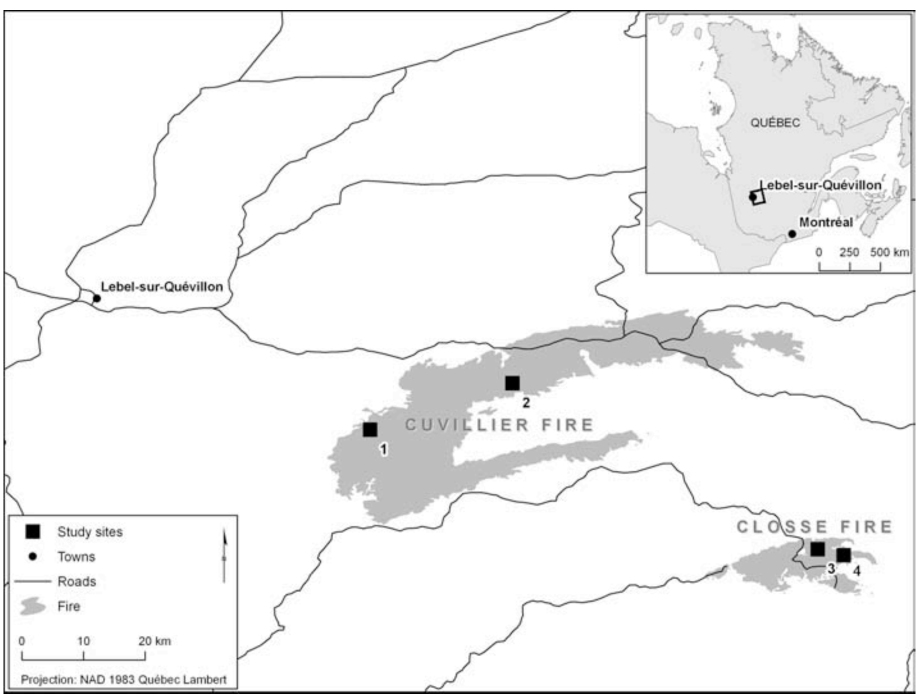

Figure 4.2. Map of study area and site locations.

Two sites (site 1 and 2) were established in the Cuvillier fire, which is located in northwestern Quebec 40 km southeast of the town of Lebel-sur-Quevillon (48°49.513'N, 76°37.224'W). Ignited accidentally by man on August 16, 1995, it burned 47 709 ha of forest before it was extinguished by rain on October 20.

Two sites (site 3 and 4) were established in the Closse fire, which is located in northwestern Quebec 100 km southeast of the town of Lebel-sur-Quevillon (48°41.242'N, 75°58.793'W). Ignited accidentally by man on August 20, 1995, it burned 6925 ha of forest before it was extinguished by rain on October 20.

Sites were identified in the summer of 2010 and data collection occurred over the summers of 2011 and 2012. Site details can be found in Table 4.1.

Table 4.1. Site details on drainage, organic layer depth, thinning year, density of stems removed, and mortality of thinned stems.

Site	Drainage	Organic layer depth (cm)	Pre-commercial thinning year	Thinned jack pine stems/ha	Sample size of thinned stems (n)	Mortality of thinned stems (%)
1 (Highly Xeric)	Excessive	2 cm	2004	54250	217	45.62%
2 (Mesic)	Moderate	12 cm	2005	74000	296	71.62%
3 (Xeric)	Well drained	5 cm	2002	93500	374	86.36%
4 (Xeric)	Well drained	3 cm	2002	60250	241	73.86%

Ten 4-m^2 plots spaced 10 m apart along a single transect were established on each site to determine both the pre- and post-thinning density of jack pine. In addition, the following data were recorded for each individual cut stem: stump height (rounded to the nearest centimeter); the number of branch whorls (dead or alive) remaining on the cut stump; and the living status of the stump (dead or alive) (if green needles were present on any of the remaining branches, the stump was considered alive). Based on our field observation we suggest that all stumps remaining after thinning were still present at the time of data collection. The stumps that were present showed low levels of decomposition; indeed, the great majority still had bark present, with clearly visible branch whorls. In order to determine site drainage and organic layer depth, 5 pits were dug per site (one every second plot), until the surficial deposit was reached.

Numerical and statistical analysis

ANOVA was used to compare the mean thinning height by site, the mean thinning height by site that would leave zero branch whorls on the stem, and the mean thinning height by site that would leave no more than one (data lumped) branch whorls on the stem. Levels of significant factors were compared using Tukey's HSD post-hoc method.

To study the effect of thinning height on the number of remaining branch whorls while controlling for sites, we used an analysis of covariance; model effects included the 4 sites stump heights (continuous), the sites, and the interaction between the two. Sites were compared using Tukey's HSD post-hoc method.

To study the effect of remaining number of branch whorls on the mortality frequency (all sites lumped) we used Chi^2. Branch whorl numbers were merged into classes when frequencies were too low to meet the requirement of an unbiased test.

Variables were log-transformed when ANOVA assumptions of normality and homoscedasticity were not met. A α value of 0.05 was used for all statistical analyses.

4.4 Results

Site data on stems thinned, sample size, and mortality % can be found in Table 4.1.

Mean cut height by site

ANOVA analysis indicates that the sites were thinned at significantly different mean cut heights (Prob. > F < 0.0001) (Fig. 4.3). Cut heights were significantly greater on sites 2 and 4 than on site 3, which in turn were greater than on site 1 (Tukey HSD). Variables were log-transformed as ANOVA assumptions of normality and homoscedasticity were not met.

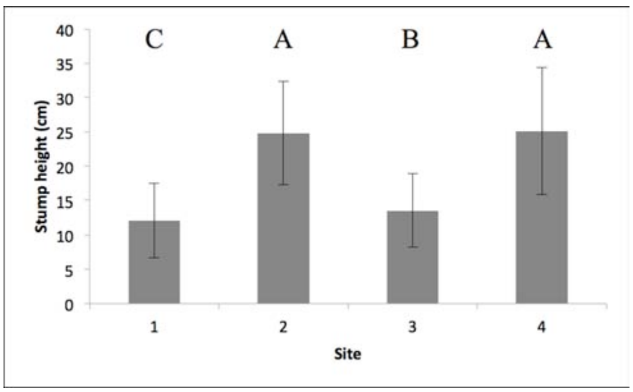

Figure 4.3. Mean cut height (cm) by site. ANOVA Prob. > F < 0.0001. Error bars represent standard deviation.

Number of branch whorls versus stump height

As stump height increased so did the number of remaining branch whorls. An analysis of covariance indicates significant differences in the number of observed branch whorls between sites (Prob. > F < 0.0001), and a significant relationship between stump height and number of remaining branch whorls (Prob. > F < 0.0001), but no significant difference among sites in the slope of this relationship (Prob. > F = 0.5408) (Fig. 4.4).

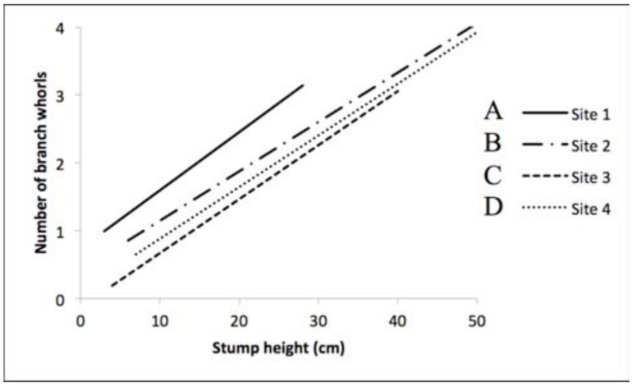

Figure 4.4. Analysis of covariance studying the effects of site and stump height on the number of remaining branch whorls. Letters illustrate significant differences in number of branch whorls between sites.

Mortality frequency and the number of remaining branch whorls

We observed that if thinning removed all branch whorls from the thinned stem, 100% stem mortality occurred. Fig. 4.5 illustrates the results of Chi^2 for lumped data. The relationship between mortality frequency and the number of remaining branch whorls was significant without significant differences among sites. Mortality was similar when zero or one whorl was left, and significantly higher than that of stumps with more than two whorls.

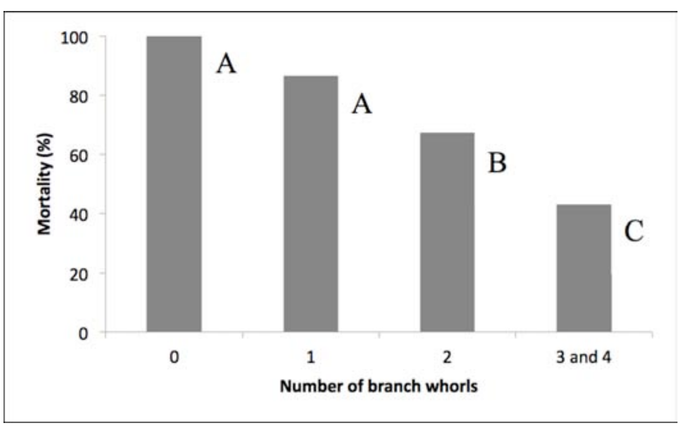

Figure 4.5. Percent stem mortality as a function of number of branch whorls for all sites lumped (Prob. > Chi^2 < 0.0001).

Thinning height

ANOVA analysis indicates that a significant difference exists in the mean cut height yielding zero branch whorls between sites (Prob. > F = 0.007). The mean thinning height required to leave no whorls observed on site 1 is significantly inferior to the other sites (Tukey HSD). Variables were log-transformed as ANOVA assumptions of normality and homoscedasticity were not met. Site 1 has a mean thinning height of 5 cm (95% CL of 2 cm and 9 cm), while the mean for sites 2, 3, and 4 lumped is 11 cm (95% CL of 10 cm and 11 cm).

When lumping cut height yielding zero and one branch whorl, the ANOVA analysis indicates that a significant difference exists in the mean (lumped) between sites (Prob. > F < 0.0001). The thinning height observed in site 1 is significantly inferior to the other sites, while the thinning height in site 3 is significantly inferior to sites 2 and 4 (Tukey HSD). Variables were log-transformed as ANOVA assumptions of normality and homoscedasticity were not met. Site 1 has a mean thinning height of 9 cm (95% CL of 8 cm and 10 cm), site 3 a mean thinning height of 12 cm (95% CL of 12 cm and 13 cm) and sites 2 and 4 a mean thinning height of 17 cm (95% CL of 17 cm and 18 cm).

4.5 Discussion

Mean cut height by site

The statistical analysis indicates that thinning operations were carried out at significantly different heights depending on the site. In Quebec, thinning height is regulated at a maximum of 20 cm with tolerance based on terrain obstacles (MRNF 2011). This analysis indicates that thinning was not implemented at the proper cut height in two out of the four sites sampled, and even when it was, re-growth of thinned stems was still observed. The high cut height observed in site 2 was due to the presence of dense ericaceous cover, which obstructed the regulated thinning height zone; however, no such obstructions existed in site 4, indicating poor treatment application. Therefore, a revision of existing practices is suggested.

Number of branch whorls versus cut height

Results show that the higher pre-commercial thinning is applied on a stem, the more branch whorls will remain. Although this is inherently obvious, it is still necessary to illustrate in the context of our argument. The analysis of covariance indicates significant differences in the Y-intercept but not the slopes among sites. The differences in the number of branch whorls observed at any given cut height can be explained by differing growth rates between sites. This is most likely due to on-site characteristics such as nutrient availability, quality of drainage, soil temperature, pH and moisture regime, light availability, or competition with other species. These characteristics are known to influence jack pine stem growth and stand productivity (Bonan and Shugart 1989, Rudolph and Laidly 1990, Bell 1991).

Mortality proportion versus the number of remaining branch whorls

The objective of thinning is to reduce competition and stem density; thus, treatments that result in 100% thinned stem mortality are considered highly successful. Jack pine is not capable of sprouting new shoots from the root collar or roots following pre-commercial thinning, and must rely on remaining living branches. We observed that if pre-commercial thinning removed all branches, 100% stem mortality occurred.

Chi^2 for all sites lumped indicated significant differences in mortality frequency based on the remaining number of branch whorls. Therefore, the more branch whorls left on the stem, the higher the survival rate.

Thinning height leaving 0 branch whorls on thinned stems by site

The only way to achieve 100% stem mortality following pre-commercial thinning of jack pine stems is to effectively remove all branch whorls with treatment application, but what cut height would achieve this objective? Results from ANOVA and Tukey HSD examining the mean cut height that yields zero branch whorls indicate that site 1, with a mean effective thinning height of 5 cm, is significantly different from the other three sites. This is most likely due to the excessive drainage and the shallow thickness of the organic matter (2 cm) (Table 4.1), which by extension would decrease nutrient availability and increase drought susceptibility, resulting in poorer stem growth. Low initial growth rates would result in a relatively higher proportion of branch whorls closer to the ground at the time of thinning (Fig. 4.4), thereby increasing survival. Stands that exhibit these characteristics should not be thinned until self-pruning has killed the branch whorls closest to the ground.

All other sites are similar, with a mean effective thinning height of 11 cm, which is not surprising given that jack pine displays optimal growth in moderate mesic to light xeric conditions (Rudolph and Laidly 1990, Beland and Bergeron 1996). The results indicate that among sites that did not show a statistical significance in terms of cutting height leaving zero whorls on the stem, a cutting height of 11 cm is sufficient. These results correspond very well with the minimum cutting height outlined by Forrester and von der Gonna (1990), who considered 10 cm to be the shortest stem thinning height without any loss in worker productivity. Treatment costs will increase in stands where thinning is carried out as close to the ground as possible (as would have to be done in site 1) due to the additional input of time required (Forrester 1989, Forrester and von der Gonna 1990).

In young stands where it may not be possible to thin close to the ground due to obstructions such as rocks, stumps, wood, a dense cover of ericaceous species, or high topographic variability, stand density could be a useful indicator of the timing of the onset of self-pruning in jack pine. This would allow foresters to better predict when the lowest branches experience the greatest mortality in order to better time pre-commercially thinning operations. As previously mentioned, self-pruning of lower branches in jack pine stands typically occurs between 6 and 12 years; however, it is density-dependent (Vassov and Baker 1988). The greater the stem density the faster self-pruning will begin. Thus, for very dense sites thinning operations could be scheduled earlier than less dense sites, because of higher mortality of lower branches. Excessively drained sites that lack a thick organic layer and surface vegetation tend to have limited nutrient resources and are more susceptible to drought. On these sites the growth of jack pine can be greatly reduced, thus potentially delaying the onset of self-pruning. Even though they may contain high stem densities (as observed on site 1) re-growth of thinned stems can remain high. In addition, jack pine is a highly shade-intolerant species (Fowells 1965, Rudolph and Laidly 1990, Sims et al. 1990, Claveau et al. 2002). Although this study did not examine the direct effects of thinning on stand solar insolation levels, it appears that stands thinned earlier, or stands that exhibit poor growth (as mentioned above), have crowns exposed to relatively more light than those thinned later due to the presence of relatively shorter un-thinned trees (Splawinski 2010, personal observation). Higher levels of insolation may decrease the mortality of the remaining branches on thinned stumps by providing enough energy through photosynthesis to survive; indeed on site 1 the survival of thinned stumps tended to be greater around relatively shorter residual trees.

Recent research has indicated that jack pine is capable of root grafting (Tarroux et al. 2010; Tarroux and DesRochers 2010, 2011), which allows for the sharing of resources among connected trees (Tarroux and DesRochers 2011). Grafting is minimal in the first 10 years; however, it increases to ~10% by a stand age of 11 to 20 years (Tarroux and DesRochers 2010). Surviving stumps constitute a resource drain on un-thinned grafted individuals, which results in decreased growth rates (Tarroux et al. 2010). Thinning at an earlier age would reduce or eliminate this issue.

Recommendations

We suggest that pre-commercial thinning in dense jack pine stands be applied between 7 and 10 years following establishment, similar to the recommendation made by Smith (1984) and Vassov and Baker (1988), to minimize treatment costs and maximize growth. In addition we recommend that pre-commercial thinning operations must cut trees at heights between 10 cm and 13 cm, given that 1) Chi^2 analysis revealed no significant difference in mortality frequency between zero and one remaining branch whorl (Fig. 4.5); and 2) a significant difference exists between site 3 and sites 2 and 4 when data are lumped for zero and one remaining branch whorl (employing the precautionary principle, we provide the upper 95% CL for site 3). However, if foresters wish to ensure maximum mortality of thinned stems, we suggest a thinning height of 10 cm. Workers should be instructed to follow this guideline, with emphasis placed on the importance of this factor on thinning success. In a study by Smith (1984) workers were instructed to thin as close to the ground as possible, resulting in re-growth of <1%.

The suggestions outlined here are meant as general guidelines to pre-commercial thinning. Final decisions should be based, if possible, on on-site observations made by foresters responsible for planning operations. Onset of the self-pruning phase (and by extension proportion of lower branch mortality), stand density, obstructions on the forest floor (rocks, wood, ericaceous species), and mean bole height of the first living branch whorl, are all useful indicators. For example, if branch whorls on individual trees are dead at >10 cm then it would be possible to apply thinning regardless of stand age. Similarly, if there is a heavy presence of ericaceous species, rocks, or wood that exceeds the 10 cm thinning prescription then it may be useful to delay treatment until self-pruning kills the branch whorls in the obstructed area.

4.6 Conclusion

Results of this study indicate that thinning height has a significant effect on the remaining number of branch whorls, which in turn affects the survival rate of thinned stems; the lower the cut height the greater the mortality. We suggest that pre-commercial thinning operations be delayed in excessively drained stands and in those with obstacles present (rocks, wood, ericaceous species) until self-pruning kills the branch whorls in the obstructed zone. In stands that do not exhibit this problem, a cut height of 10 cm to 13 cm should be employed to maximize the mortality of thinned stems. These stands should be thinned between 7 and 10 years after disturbance.

GLOBAL CONCLUSION

The principal aim of this doctoral project was to improve the state of knowledge on the natural regeneration dynamics of black spruce and jack pine following fire and salvage logging, and the employment of pre-commercial thinning operations, thereby improving the sustainable management of this important natural resource. This was accomplished by first addressing fundamental gaps in knowledge and then using this new information to provide forest managers with stand and landscape-level tools and silvicultural recommendations needed to decrease the need for post-fire interventions by relying on natural regeneration, increasing their success when employed, and minimizing the cost of investments.

The objectives of this project were as follows: (1) using a post-fire regeneration model to develop a stand-level tool for assessing natural regeneration potential of black spruce and jack pine following fire and salvage, in order to identify the proportion of good seedbeds necessary to yield adequate natural regeneration densities across a range of basal areas expected in the field; (2) linking a post-fire regeneration model with forest inventory maps to create a landscape-level tool for assessing natural regeneration density of black spruce and jack pine following fire and salvage, thereby allowing for the prescription of post-fire interventions such as planting and pre-commercial thinning, and identification of regions where fire is not likely to result in adequate natural regeneration; (3) examining the impact of the timing of pre-commercial thinning operations and stand composition on the radial growth response of black spruce and jack pine, and the effect of pre-commercial thinning on the mortality and re-growth density of hardwoods; and (4) examining the early pre-commercial thinning of dense jack pine stands following forest fire and salvage logging, and the impact of treatment height on the mortality and re-growth of thinned stems.

This conclusion summarizes the new knowledge attained, the results of the developed natural regeneration assessment tools, and the recommendations to foresters for improving pre-commercial thinning success.

Stand-level assessment tool

Two scenarios were simulated in order to create the stand-level natural regeneration assessment tool: (1) regeneration density of black spruce and jack pine in burned intact stands, and (2) in 100% salvaged stands. This was done for both an early and late season fire date (June and August). Simulations were carried out for basal areas ranging from 5 to 50 m^2/ha, in increments of 2.5 m^2/ha, representing the range of basal areas expected in the field. For every increment of basal area, the percentage of good-seedbeds yielding ≥ 1 seedling/m^2 was identified. Results indicate that a higher percentage of optimal seedbeds are necessary (1) for black spruce to regenerate adequately in burned, salvaged stands when compared to jack pine (i.e., planting of black spruce will almost always be necessary), (2) as basal area of the species of interest decreases, and (3) to adequately regenerate burned intact and salvaged stands in late-season fires compared with those from early-season fires.

This operational tool provides a novel approach for managers and foresters to quickly assess reforestation needs following fire and salvage at the stand level. Rapid planning of both salvage and planting operations will improve efficiency and response time, thereby increasing the sustainability of this resource while minimizing operational costs. Evaluation can also be used to suggest which sites should be given ameliorative prescriptions such as partial cutting of burned black spruce or direct seeding (Greene et al. 2006; Splawinski et al. 2014a).

Landscape-level assessment tool

This novel spatial operational tool used basal areas obtained from temporary plots and seedbed distributions from field data to simulate seedling densities for pure black spruce and jack pine stands under burned intact and 100% salvaged scenarios. Stands were grouped by age class, pre-fire stand cover, surficial deposit, and drainage. Following this classification scheme, simulated seedling densities were transferred onto forest inventory maps for the Lake Matagami lowland ecological region (6a) in the boreal forest of Quebec. The results illustrated that both black spruce and jack pine are well adapted to fire; conversely, it illustrated how salvage operations have a negative impact on the regeneration potential of black spruce, and to a lesser extent, jack pine, due to the removal of the aerial seedbank: only 36% of intact black spruce and 28% of intact jack pine stands needed to be planted following fire; however under the 100% salvage scenario 100% of black spruce and 74% of jack pine stands required planting.

This tool allows managers and foresters to better plan salvage operations and subsequent silvicultural treatment applications by identifying stands and regions where natural regeneration density will be expected to be inadequate or potentially excessive. Foresters and managers could use this tool to estimate potential costs of mechanical site preparation, planting, and aerial seeding in stands that are inaccessible for summer planting, as well as pre-commercial thinning in their management units, thereby aiding in determining future budget allocations. Additionally assessment of the vulnerability of management units to poor regeneration after fire and the identification of regions at particular risk is also possible, especially if the goal is to maintain or create productive stands that yield maximum potential volume for future harvesting.

One of the principal goals of both the stand and landscape-level tools is to limit the need for reforestation following fire and salvage logging by relying on natural regeneration, which provides clear economic and environmental advantages (presented in detail in Chapters 1 and 2, and Annex B). As previously mentioned, optimal seedbeds are crucial for the successful re-establishment of serotinous species in burnt stands. Although considered a high-quality seedbed for germination, sphagnum moss is considered a poor medium for conifer growth (Lavoie et al. 2007). Thus, it is important to reiterate that if the management end-goal is to maximize stand productivity and growth, it might be preferable to scarify and then plant sites that contain a significant presence of sphagnum (Lafleur et al. 2011).

Timing of pre-commercial thinning application, stand composition, and mortality of hardwood species

This study examined the effect of competition density, regrowth density, stem diameter, and the timing of thinning on the growth response of black spruce and jack pine saplings following pre-commercial thinning. It also examined the mortality rate of hardwoods following thinning and the number of new shoots produced per surviving thinned hardwood stem. Results indicate that (1) thinning timing has a significant effect on the growth response of jack pine, and should be employed between 4 and 9 years following fire, (2) jack pine growth response following thinning is significantly affected by competition density, regrowth density, and pre-treatment stem diameter, and (3) mortality rates and new shoot production vary significantly by hardwood species, however due to the high and dense regrowth potential of willow and alder, we recommend that stands exhibiting low densities of these species be left un-thinned. These results can be used to aid foresters in the identification of stands that require pre-commercial thinning and to modify current thinning strategies.

Pre-commercial thinning height and the mortality of jack pine stems

This study focused on examining the relationship between thinning height and the number of remaining branch whorls on jack pine stems, and the number of remaining branch whorls and the percent mortality of these thinned stems. Results of this study indicated that thinning height had a significant effect on the remaining number of branch whorls, in turn affecting the survival rate of cut stems; the lower the cut height the higher the mortality. This allowed us to determine the thinning height that resulted in the greatest mortality of thinned stems, and to propose guidelines to improve thinning success based on thinning height and timing of operations in dense stands, thereby increasing growth and yield of residual stems.

We recommend that pre-commercial thinning in dense jack pine stands be applied between 7 and 10 years following establishment, and carried out between 10 cm and 13 cm stump height in order to maximize mortality. Conversely, operations should be delayed in excessively drained stands and those with obstacles present (rocks, wood, ericaceous species) until self-pruning kills the branch whorls in the obstructed zone. Foresters could use the following on-site indicators to better plan and schedule pre-commercial thinning operations: the onset of the self-pruning phase (and by extension proportion of lower branch mortality), stand density, obstructions on the forest floor (rocks, wood, ericaceous species), and mean bole height until first living branch whorl.

Although this thesis focuses on two separate stages of development (establishment and juvenile stage) of black spruce and jack pine following fire and salvage, when considering the sustainable management of this resource, they are invariably linked. During the establishment phase it is crucial to assure adequate regeneration following both forest fire and salvage logging; indeed in Canada legislation mandates that harvested stands be properly regenerated (Natural Resources Canada 2011). If left undisturbed, these species generally regenerate to similar densities as existed prior to fire (Greene and Johnson 1999; Ilisson and Chen 2009), however salvage tends to reduce natural regeneration densities substantially, especially in black spruce stands (Greene et al. 2006; Splawinski et al. 2014a); they then often require planting. Jack pine is less affected, and can still exhibit high seedling densities if the pre-fire basal area was high and good post-fire seedbeds are abundant, due to its shorter seed abscission schedule (Splawinski et al. 2014a,b). Salvage also tends to promote the establishment and growth of hardwood species that take advantage of the open and warm conditions created; this often results in shifts in stand composition, from conifer dominated to hardwood dominated (Greene et al. 2006; Boucher et al. 2014).

During the juvenile stage, it is important to employ stand-tending techniques (here pre-commercial thinning) when an excessive softwood or hardwood density is present. Thinning is employed in order to maximize growth of residual trees and minimize rotation period (Smith 1986; Vassov and Baker 1988), to avoid plantation failure, which can be caused by severe deciduous competition (Carleton and MacLellan 1994), and to avoid/reduce stand compositional changes.

Thus a good understanding of both of these developmental stages, and the proper employment of the tools and recommendations presented in this thesis can increase the sustainable management of both black spruce and jack pine. Indeed, ensuring the proper regeneration of burnt and salvaged stands with emphasis on natural regeneration, identifying regions at risk of regeneration failure, and minimizing compositional changes following salvage logging and pre-commercial thinning would bring operations more in-line with an ecosystem management approach (Vaillancourt and Leduc 2009; Nappi et al. 2011).

Although maintaining forest composition following fire, salvage logging, and pre-commercial thinning operations plays a major role in sustainable forest management, maintaining a heterogeneous distribution of stand age-classes across the landscape is also crucial, a topic that was not examine in this thesis. As previously mentioned, fire is the dominant disturbance in the boreal forest (Payette 1992; Webber and Flannigan 1997; Stocks et al. 2002), and increases the proportion of young-aged stands across the landscape by resetting stand succession. With the expected future increase in fire frequency and area burned (Bergeron et al. 2010; Wotton et al. 2010), the proportion of younger age classes will also increase.

Current forestry management practices are centered on even-aged management (Burton et al. 2003), which is employed due to its perceived similarity to wildfire (Bergeron et al. 2002; Bergeron et al. 2001). Indeed, this method represents 93% of managed forests in Canada (CCFM 2009). Under this management scheme, clear-cutting is most frequently employed, making it the dominant harvesting method (Masek et al. 2011). Like fire, this practice leads to an increase in the proportion of younger-aged stands across the landscape (Bergeron et al. 2002, McRae et al. 2001); these stands will exhibit poor natural regeneration if subjected to fire before reaching reproductive maturity (Zasada 1971; Viereck and Johnston 1990; Gauthier et al. 1993; Viglas et al. 2013), as outlined in Chapter 2.

In the context of maintaining forest resilience to fire, the current even-aged management method, coupled with the expected future increase in fire frequency and area burned will play a detrimental role; the greater the proportion of young-aged stands across the landscape, the greater the chance of regeneration failure (Girard et al. 2009). It is therefore essential to ensure the adequate regeneration of stands and regions that are susceptible to fire. The landscape-level natural assessment tool presented in Chapter 2 could prove useful in quickly identifying these areas, thus resulting in the appropriate corrective measures being implemented.

Future research

This project has the potential to stimulate future research in a wide range of areas related to sustainable forest resource management and ecosystem response to fire and salvage. Concerning the establishment stage, additional research should focus on evaluating the applicability and success of both the stand and landscape-level assessment tools in estimating post-fire and post-salvage regeneration potential and silvicultural treatment application; a study aimed at validating their effectiveness should be relatively easy to implement. The initial purpose should be to strictly determine how often predictions are correct, and if incorrect, to what degree. For example, in the case of the landscape-level tool, a fire occurring in ecological region (6a) within the last decade that contains both salvaged and unsalvaged stands can be examined. Using GIS, the fire boundary can be delimited, and pure stands of black spruce and jack pine can be isolated. One could then compare how the stands actually regenerated (natural regeneration, planting, thinning) versus what the simulations prescribed. Attention should also be given to gathering further data on poorly understood model parameters such as post-fire granivory rates, the effect of fire severity on seed mortality, post-fire seedbed proportions, and improving inventory classification. Indeed, given the current lack of widespread data on post-fire seedbed proportions, and their importance in the modeling effort (one of the most sensitive parameters), it is imperative that future work focuses on seedbed quantification and projection from remote sensing data. Developing such an approach could provide rapid details on post-fire seedbed coverage, both spatially and temporally, and eliminate the need for tedious fieldwork (especially in hard-to-access stands).

Stand and landscape-level assessment tools can be created in other jurisdictions that possess the necessary data on stand attributes. They can also be used to link early regeneration stages to the growth and yield of young forest stands. Indeed, due to their novelty, both the existing regeneration model and tools can act as templates or a starting point for researchers wishing to create models and tools to assess regeneration following fire and salvage for their respective locations (not just other areas of the boreal forest but other biomes and species). All the main parameters crucial to the re-establishment of serotinous species following fire and salvage logging have been identified, therefore only minor fieldwork would be required to supplement missing data.

The stand and landscape-level tools can be modified to include scenarios that examine a delay in salvage logging and/or variation in the proportion of the stand that is salvaged in order to yield adequate natural regeneration densities. These results can then be used to develop more comprehensive forest management strategies to make sure that the forest recovers from the disturbances. Specifically, there is a current lack of cost-benefit analysis on the effect of delaying salvage or lowering the proportion of the stand that is salvaged (in terms of wood quality and value of the final product), and how this loss can be offset by reducing planting (relying on natural regeneration).

Besides assuring adequate natural regeneration, a delay in salvage timing or a reduction salvage proportion can provide pyrophilic species with the habitat and temporal window crucial for the completion of their life-cycles (Splawinski et al. 2014a). An ecosystem management approach to burnt forests can therefore be achieved by applying strategies that would greatly reduce the negative effects of salvage logging (Nappi et al. 2011).

With respect to pre-commercial thinning (juvenile stage), further research should focus on (1) examining the effects of the pre-treatment density of individual hardwood species on the growth response of black spruce and jack pine, in order to identify their relative competiveness, (2) if and at what limit hardwood retention would be beneficial, (3) the root suckering potential of hardwoods following pre-commercial thinning and how it affects post-treatment density, and (4) the development of comprehensive intensive stand management regimes by examining the combined use of silvicultural approaches and on-site factors. This knowledge can then be used to improve the assessment tools themselves, the main model used in their creation, and lead to further recommendations and revisions of pre-commercial thinning practices.

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ANNEX A

SEED ABSCISSION SCHEDULES AND THE TIMING OF POST-FIRE SALVAGE OF PICEA MARIANA AND PINUS BANKSIANA

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Abstract

For aerial seedbank species, the seed abscission schedule following fire is of practical interest as it affects the optimal timing of post-fire salvage operations designed to maximize natural regeneration. It is also of theoretical interest as we would expect that the rapid deterioration of the better (very thin duff or exposed mineral soil) post-fire seedbeds due to leaf-fall from regenerating plants ought to select for rapid dissemination of seeds following burning. Nonetheless, there are no published reports of the abscission schedule of an aerial seedbank species that include the full temporal range from the fire date to several years after. In northwestern Quebec, we used eight burnt, non-salvaged stands, four dominated by black spruce (Picea mariana) and four dominated by jack pine (Pinus banksiana), in three different fires to examine the seed abscission schedule of these aerial seedbank species for the first 3 years after fire. We found that (1) the abscission schedules of populations of each species differed between fires and (2) black spruce dispersed seeds from the cones at a significantly slower rate than jack pine at all fires. Extrapolating from the regressions (all fires lumped), we conclude that approximately 90% of jack pine and black spruce seeds will have been dispersed by 1 and 5 years, respectively, after a fire. Further, we argue that due to its protracted abscission schedule, early post-fire salvage will invariably require that black spruce be planted. The approach adopted here should be useful for optimizing post-fire salvage timing for all commercially valuable species with aerial seedbanks.

Keywords: fire; abscission; salvage; seed; regeneration; recruitment

Introduction

The species composition of boreal forest communities is highly dependent upon the initial recruitment dynamics following very large fires (Greene et al., 1999; Johnstone et al., 2004; Amiro et al., 2001; Stocks et al., 2003). The short fire return interval in the North American boreal forest has resulted in the regional dominance of fire-adapted tree species, especially in the western half of the continent where the return time is only 50–150 years (Enright et al., 1998; Lindenmayer and Noss, 2006; Gauthier et al., 1993b; De Groot et al., 2004; Scherer-Lorenzen et al., 2005).

The three most common tree species in the North American boreal forest are aspen (Populus tremuloides), black spruce (Picea mariana (Mill.) BSP) and jack pine (Pinus banksiana Lamb.), the two latter species possessing aerial seedbanks (Greene et al., 1999; De Groot et al., 2004; Gauthier et al., 1993a). For these two species, the density of their regeneration is positively correlated with their pre-fire tree density, and consequently there is seldom any dramatic post-fire change in species composition, at least in the absence of salvage (Greene and Johnson, 1999; Ilisson and Chen, 2009).

These two species have small (spruce: 1 mg; pine: 3.5 mg), wind-dispersed seeds, with relatively constant seed production from year to year (Messaoud et al., 2007; Rudolf, 1965). Black spruce usually has 3–6 seed cohorts on its branches while jack pine can have 10 or more (Enright et al., 1998; Greene and Johnson, 1999; Greene et al., 1999). With increasing time, however, seed viability declines (Greene et al., 1999; Rudolf, 1965).

Although in the absence of fire old cones of jack pine will slowly open when exposed to intense solar radiation, the great majority of cones are opened by the heat of flaming combustion as the resin beneath the scales is volatilized (Enright et al., 1998;

Lamont et al., 1991). By contrast, black spruce will release all the seeds of a cohort within a few years of attaining maturity regardless of fire occurrence (Enright et al., 1998; Greene et al., 1999), although Zasada (1979) showed that cone opening in black spruce in Alaska was modestly accelerated by fire.

Methods for studying seed abscission have been indirect. Charron and Greene (2002) measured the residual viable seeds per cone on branches along a chronosequence of stands with different times since fire. Others have tried to extrapolate seed abscission rates from seedling ages, although the difficulty of obtaining accurate seedling ages for slow-growing species can, along with temporal changes in seedbed-mediated mortality rates, obscure the relationship (St-Pierre et al., 1992; Sirois and Payette, 1989; Cayford, 1963; Charron and Greene, 2002).

We know of only three direct studies of abscission on these two species, each severely limited in the time span they record. Johnstone et al. (2009) used seed traps to examine black spruce seed rain and viability over a 2-year period following a late summer fire (August 2004) in Alaska, but the crucial first 10 months after fire were missing from the data. De Groot et al. (2004) used traps to follow the abscission of jack pine seeds only for the first 2–3 months following an experimental fire. Likewise, for black spruce Wilton (1963) monitored abscission in Newfoundland for only the first 2 months after fire, stopping because of a salvage operation. The only other serotinous tree species where the post-fire abscission rate has been closely followed was sand pine (Pinus clausa (Chapm. ex Engelm.) Vasey ex Sarg.); but again the study is problematic as observations were discontinued 3 weeks after the fire because of salvage (Cooper, 1951).

Post-fire salvage of burned stands is increasingly used to offset the economic loss resulting from otherwise foregone future harvests (Lindenmayer and Noss, 2006; Greene et al., 2004). Salvage occurs as rapidly as possible because foresters wish to (1) prevent damage to the timber from wood-boring beetles; (2) reduce checks (wood splitting) that typically develop as the standing dead trees dry; and (3) given windthrow, enhance the number of burnt trees that will still be standing when the harvesting machinery passes by Saint-Germain and Greene (2009). As a result of quick salvage, large numbers of seed-bearing cones are either deposited in slash piles at the edges of roads or end up on the ground where they cannot disperse their seeds more than a few cm (Greene et al., 2004; Lindenmayer and Noss, 2006). The studies alluded to earlier, both direct and indirect, make clear that jack pine releases seeds more rapidly than does black spruce, and thus it is not surprising that early salvage reduces the natural regeneration of black spruce far more than that of jack pine (Greene et al., 2004). In any case, a delay in salvage would benefit the regeneration potential of either species, as it would lead to a greater percentage of seeds abscising prior to the harvest. In turn, this would reduce the amount of post- fire planting required. But our ability to quantify the trade-off in the salvage timing—planting cost vs. reduced wood value—is hampered by our lack of detailed knowledge of the abscission schedule of these two common boreal species. Examining seed release of black spruce and jack pine in the first 3 years following three stand-replacing fires in northwestern Quebec, our first goal is therefore to understand at a fine temporal scale the abscission schedules, and therefore be able to suggest changes in the present approach to salvage that would minimize some of the negative effects of removing burnt trees too rapidly.

Our second objective is to examine the functional form of the abscission schedule for these two species. To our knowledge, this issue has never been broached for any plant species; instead the few abscission studies we have are simply empirical descriptions or, at best, regressions of number of seeds abscised vs time. A simple null hypothesis is that the probability of seed abscission is random with respect to time; this would result in a negative exponential loss rate. A more likely scenario however, especially for conifers, is that the abscission probability declines with time. This is because with most conifers (but not Abies or some Cupressaceae), scales must flex open to permit release of viable seeds, and the more distal the scale, the most resistant it is to opening widely (Dawson et al., 1997). A second reason is that the scales flex open in response to relative humidity, and this will be lowest in the first few months after the fire before regeneration can modify the initially low albedo of the charred organics (Lyons et al., 2008). We will fit the empirical data on abscission schedules to a two-parameter Weibull distribution; one of its two parameters expresses temporal changes in the loss rate.

Methods

We examined the abscission schedule of both species in three fires: Nemaska (2002), Mistissini (2006), and Senneterre (2007). All three are in the central boreal forest of Quebec, and were lightning-ignited, stand-replacing fires extinguished by rain. Within each fire all the stands we used to sample the post-fire seed rain had 100% tree mortality and were at least 100 m from a fire edge with surviving trees.

The Nemaska fire burned 60,000 ha from July 2 to July 12. Four 4 m^2 seed traps were installed in each of four stands (two dominated by pine; two dominated by black spruce) approximately 3 weeks after those parts of the area had been burned. The Senneterre fire (the joining of two burns: fire #193 and fire #254) started on 14 May 2007 and burned 64,000 ha in about 3 weeks. Two stands, one dominated by black spruce before the fire and the other by jack pine, were used. The Mistissini fire was ignited in the first week of June 2006, and burned 920 ha of forest before being extinguished on the 24th of June. Two stands, one dominated by black spruce before the fire and the other by jack pine, were chosen. At both Senneterre and Mistissini, seed traps were installed about 1 week after the fire was extinguished.

In order to estimate how many seeds had abscised in the brief period before seed trap installation, we used a coring tube to sample the organic layer next to the traps at Senneterre and Mistissini. The tube contents were dried in a lab; after sieving, the number of spruce and pine seeds per core was determined. One hundred samples were taken from each site (core aperture area = 12.6 cm^2), for a total area of 0.126 m^2 per stand. On a per area basis, for pine the seedfall in the first week was, averaging across those two fires, about 40% of all available seeds. For spruce, the average seedfall in the first week was only 10% of the total seeds available. For Nemaska, for the missing initial 3 weeks from fire to trap installation, we used estimates of the cumulative seed proportion lost by each species at the two other fires as of their third post-fire week.

Over the course of the study, seed trap contents were examined six times each at Nemaska and Mistissini, and seven times at Senneterre. In order to determine the cumulative proportion of seeds abscised by any date, we need to also know the total number of seeds remaining in cones when the study was terminated. At the end of this period (3 years after the fires at Nemaska and Mistissini, and 2 years after the Senneterre fire), 10 cones of black spruce and jack pine were taken from 10 separate trees of each species for a total of 100 cones per site. The remaining filled seeds within these cones were counted after drying at room temperature for several months to determine the final number of full-sized seeds not yet abscised. Based on the size of the imprint of absent but full-sized seeds on the scales of these cones we also estimated the original number of filled seeds available at the time of fire. On a per area basis, we estimated that pine still retained about 6% of its seeds at Senneterre (end of second summer since fire) and about 7% at Mistissini and Nemaska (end of third summer since fire). For black spruce these estimated values were 39% and 24%, respectively. The estimated total complement of full-sized seeds/cone at the time of fire was about 24 seeds for pine and 31 for spruce.

Expressing the cumulative proportion, F_t, of seeds abscised by time t as a two-parameter Weibull distribution, we have:

$$F_t = 1 - \exp(-[t/a]^b) \qquad (1)$$

where a is the scale parameter (time to lose 63% of seeds; an invariant property of the distribution), and b, the shape parameter, indicates whether the probability of abscission is increasing ($b > 1$) or decreasing ($b < 1$) with t. This equation can be manipulated into a linear form for least-squares regression.

To experimentally verify the rate of opening of jack pine scales we took 15 cones of jack pine from the Mont Laurier region (the transition between the boreal and eastern hardwood forest) of southern Quebec and boiled them to melt the resin. We then appended the cones upside down above a lab bench. After 30 days we checked to see how many filled (full endosperm as determined via a cutting test) seeds had fallen from the flexed scales. To determine how many seeds remained, we used pliers to open up the distal scales more fully so we could extract the remaining filled seeds.

Results

The parameter estimates from fitting the data to the Weibull are shown in Table 1; all correlations were significant ($p < 0.01$). Among pine at the four sites (three fires), slopes (b) ranged from 0.24 to 0.68. Three of the four slopes were significantly smaller than 1.0. A set of six pairwise comparisons showed that two of the slopes were significantly different from one another (Senneterre vs either JP2 or Mistissini; $p < 0.05$; t-test; a Kolmogorov–Smirnov test was first used to demonstrate the normality of the transformed data). The scale parameter (time to 63% seed loss), *a*, ranged from 0.16 to 5.13 months (time is expressed in months of 30.4 days); pairwise comparisons showed no difference among the *a* values ($p > 0.05$; t-test).

Table 1. Regression results for eight stands at four fires for jack pine (jp) and black spruce (bs). The fitted parameters (*a* and *b*) for the Weibull are shown, as well as the 95% confidence limits for *b*. The probability for the correlation is *p*. The expected time to abscise a percentage of the seeds is from the regression equation. The Nemaska fire has two separate stands (1,2) for each species.

Site	Fire/# months recorded	*n*	r^2	*p*	*a*	*b*	*b* 95% conf. interval	Time (months) to lose % seeds		
								10%	50%	90%
JP-1	Nemaska/37	6	0.7	0.024	2.459603	0.5	0.107–0.889	0.027304	1.181724	13.04057
JP-2	Nemaska/37	6	0.84	0.007	4.030697	0.66	0.307–1.013	0.133226	2.313165	14.26237
BS-1	Nemaska/37	6	0.86	0.005	19.89908	0.965	0.486–1.444	1.932253	13.61085	47.22653
BS-2	Nemaska/37	6	0.95	0.001	23.05537	1.066	0.761–1.371	2.792284	16.34755	50.41522
JP	Mistissini/35.5	6	0.91	0.002	5.126183	0.681	0.416–0.945	0.18822	2.992661	17.44544
JP	Senneterre/26.8	7	0.93	<0.0001	0.156971	0.236	0.169–0.303	1.13E−05	0.033216	5.378131
BS	Mistissini/35.5	6	0.99	<0.0001	15.65794	0.767	0.66–0.874	0.832761	9.709699	46.44986
BS	Senneterre/26.8	7	0.93	<0.0001	20.12823	0.471	0.371–0.666	0.16936	9.243902	118.2608
JP	All fires	25	0.68	<0.0001	2.05078	0.472	0.336–0.608	0.017431	0.943376	12.00398
BS	All fires	25	0.89	<0.0001	17.84131	0.633	0.54–0.726	0.509887	9.999221	66.62657

For spruce at the four sites, the smallest slope was 0.52 while the largest was 1.02. Two of the four slopes were significantly smaller than 1.0. Six pairwise comparisons of the four stands indicated that all three comparisons involving Senneterre were significantly different from the others, as well as the comparison of BS2 vs Mistissini ($p < 0.05$; t-test). None of the four slopes were significantly different from one another. The scale parameter, *a*, varied from 15.7 to 23.1 months. Pairwise comparisons indicated that no spruce *a* value was different from the others.

Combining all the data for each species, spruce was significantly slower at releasing seeds (i.e. had a smaller a value) than pine (Figure 1; $p < 0.001$); 17.8 vs 2.1 months, respectively. As well, combining fires, the slope, *b*, of spruce was significantly larger than that of jack pine (0.63 vs 0.47, respectively). Finally, for both species with fires combined, the two slopes were significantly smaller than 1.0.

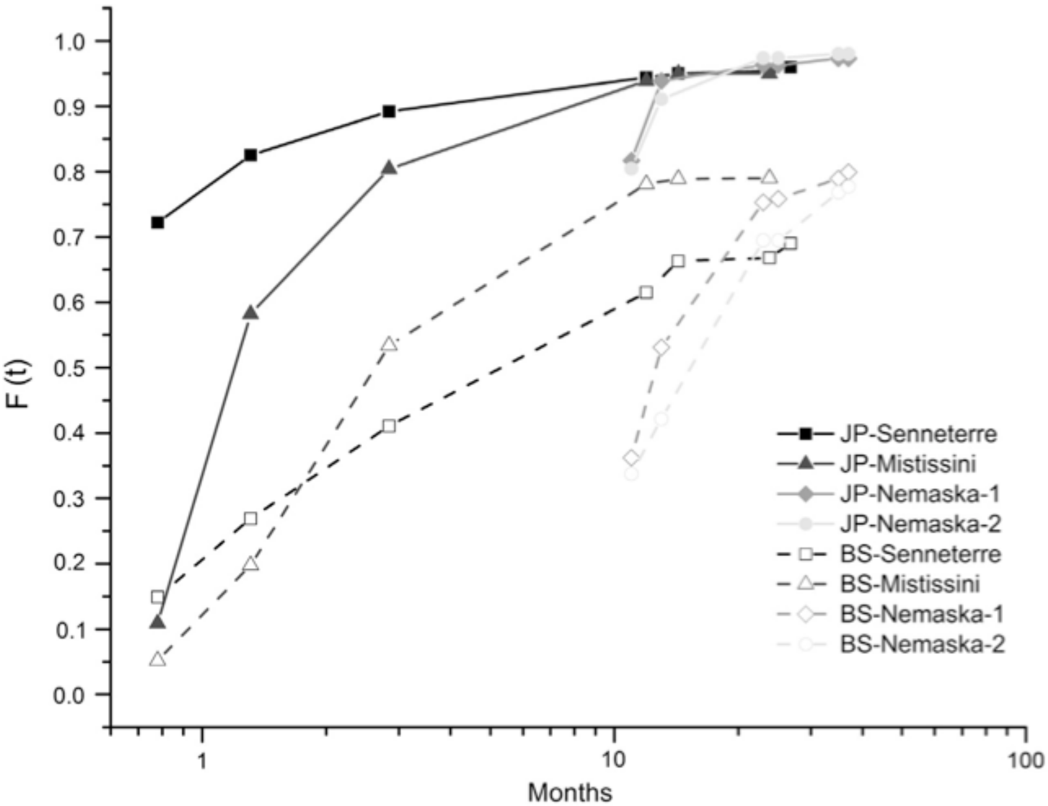

Figure 1. Seed abscission schedule of black spruce (bs) and jack pine (jp) following three wildfires (Nemaska, Mistissini, and Senneterre). $F(t)$ is the cumulative proportion of seeds abscised by time t (months; log scale). Nemaska has two separate stands (1,2) for each species.

For the 15 boiled jack pine cones, after 1 month in the absence of wind or vibration 72% of all filled seeds had abscised. By contrast, the Weibull expectation for seed loss after 1 month based on the pooled (three fires) regression in Table 1 would be 51%.

Discussion

The results indicate that black spruce released seeds far more slowly than jack pine; this is consistent with indirect observations made by Charron and Greene (2002). With data combined for all three fires, black spruce would take 10 months to abscise

50% of its seeds, while jack pine would require only about 1 month. Like- wise, the 90th percentile of seed release for pine would occur 1 year after the fire, but for spruce would occur, because of the high slope value, after more than 5 years. These latter results are remarkably similar to what Charron and Greene (2002) observed indirectly via a chronosequence of seeds/cone observations following wildfires in Saskatchewan; e.g. after about 24 months they found that 65% of the seeds of spruce and 97% of pine had abscised, whereas our regression results indicate that 70% and 96%, respectively, of the seeds had been released after 2 years.

For the combined data (and most cases of individual fires), the regression slope was significantly smaller than 1.0, indicating that the probability of abscission declined with time. Why would seed release be initially so rapid? There are two possibilities. The first is that the central scales open far more readily than the more apical and (especially) distal scales, a characteristic easily observed after boiling the pine cones. (Note that we are ignoring the unfilled and typically tiny seeds concentrated at the extreme distal and apical ends of the cone.) Almost 25% of the pine seeds fell from the appended cones in the lab in the absence of wind by the second day. Another 50% of the seeds required 27 more days to abscise. This is because only the most central scales were very widely flexed after a few days. Another reason for the decline in release probability with time is undoubtedly the increasing albedo of a burn as re-vegetation progresses (Lyons et al., 2008). Initially the blackened surface resulting from smoldering combustion of the organic horizon would make the air at canopy height quite warm. This decrease in the relative humidity around the appended cones would hasten the process of scale flexing. As plants recruit (most vigorously by asexual reproduction), the albedo would quickly rise over the first 2 years, increasing the relative humidity and therefore slowing the rate of cone opening following each precipitation event. Note that if this latter cause of slowing abscission is important, then seed release for these two species should exhibit slopes that are steeper than observed here (i.e. closer to 1.0) if non-burned sites are studied (and of course non-serotinous species should, therefore, generally have slopes near 1.0).

Why should pine abscise faster than spruce seeds? Without fire, very young jack pine will, before the serotinous trait is expressed, abscise essentially all seeds within about 1 year following the late-summer initiation of scale opening. By contrast, in the absence of fire, each cohort of black spruce tends to persist for several years after seed maturation before scales begin to open; indeed, at tree seed nurseries black spruce is notoriously the most reluctant of all the conifer species to abscise its full complement of seeds under any mechanical treatment (Haavisto et al., 1988). Fire melts the resin bonds in the serotinous pine cones and appears to modestly accelerate seed fall in black spruce (Zasada, 1979). It may be then that, following fire, pine behaves as if it were younger or simply non-serotinous (i.e. releasing almost all seeds within a year) while the abscission behavior of black spruce is hardly changed. Further, although there are no other studies on this, it follows then that each cone cohort of black spruce would be opening sequentially after fire over the course of several years.

Undoubtedly, the abscission process is not as temporally uniform as expressed by the Weibull. For example, rain will temporarily reverse the scale opening process. Also, the wind must play a major role in abscission. This role could be drag, proportional to the square of the speed, directly pushing a seed-wing unit from under a flexed scale, or it could be an inertial force as wind vibrates the branch to which the cone is appended. (Neither mechanism has been studied in conifers.) Differences between fires in the subsequent weather (rain and wind) would then be expected to lead to difference in, for example, the observed regression slope. Indeed, we do see significant differences among the three fires. In particular, Senneterre, where seeds were lost very rapidly, accounted for both of the comparisons where the slope for pine differed significantly between fires, and for three of the four examples of significant slope differences for spruce.

Both species avoid potentially problematic schedules where abscission is too hurried or too delayed. It has been argued by a minority of authors that the first-summer cohort of post-fire seeds of any species frequently has poor survival because germination-inhibiting ash deposits are still thick (e.g. De Groot et al., 2004; Thomas and Wein, 1985; Wang and Kemball, 2005). But even jack pine by September 1, 4 months after a late spring fire, would have about 25% of its crop still available for the second summer (Further, some fraction of seeds abscised in the late summer will delay germination until the next summer). In consequence, even a prohibitive depth of ash would not be catastrophic for jack pine as a great deal of the seed crop would still be available to germinate under more clement conditions. A fire that occurred later in the summer would pose even fewer problems. At the other extreme, the slow deterioration of the better seedbeds as broadleaf litter accrues (re- viewed in Greene et al., 1999) should not deleteriously affect the more slowly-releasing black spruce. Age-specific early survivorship on the best seedbeds (exposed mineral soil and thin humus) appears to not decline seriously until about the 4th year following fire (or even later if there are few broadleaved shrubs and trees: Charron and Greene (2002)). However, where angiosperm species grow rapidly from surviving perennating organs, this more lethargic abscission schedule of black spruce may lead to poor post-fire regeneration.

Our results indicate that the seasonal timing of both fire and salvage will impact the proportion of seeds available to germinate in the first summer. Salvage usually occurs as fast as possible, within a few months of the fire after road construction is completed. Despite our evidence that abscission occurs most rapidly in the first few months after fire, this will still not give black spruce, and to a lesser extent, jack pine, sufficient time to abscise enough seeds to adequately stock the burned stand, thus leading to poor natural conifer regeneration and, necessarily, expensive planting (Greene et al., 2004). Based on time of abscission only, our results suggest that salvage be delayed until the second winter following fire for stands dominated by black spruce, and until the first winter for jack pine stands. This would allow for a much greater proportion of seed abscission to occur (90% of the crop for pine after 1 year; 65% for spruce after 2 years) and thus greatly reduce or eliminate entirely the costs associated with planting (The situation is certainly less neat than imagined here). We are presently developing a model that includes not only these abscission schedules and the timing of both the fire and salvage operations, but complications such as (1) the expected fraction of germinants killed by harvesting after a delay, as well as (2) the fact that skid paths are often very good seedbeds because of mineral soil exposure.)

The quick removal of burnt trees affects not only conifer regeneration but also plants and animals that rely on these species for survival, and thus there are other, equally compelling, reasons to delay salvage. Many animals are attracted to burnt areas; for example, charred trees are used by woodpeckers and owls, carnivorous mammals, and saprophagous beetles (Lindenmayer and Noss, 2006; Nappi et al., 2004; Greene et al., 2006; Saint-Germain and Greene, 2009). Pyrophilous ground-dwelling insects are present only for 2–3 years following fire. This in turn limits the concentration of fire-associated animal species to the same temporal window between fire and salvage (Saint-Germain and Greene, 2009). Presumably a 2–3-year delay in salvage would therefore be quite beneficial for these species, and not just for the sexually-recruiting plants.

More generally, almost all of the species in the world with aerial seedbanks are associated with fire-prone environments (Lamont et al., 1991). For the fraction of these species of commercial value in forestry, we face the problem that while the probability of post- fire seed abscission will be greatest initially, there will still be too few seeds on the ground by the time forestry companies are ready to begin salvage. While the value of the burnt wood will be maximized by salvaging at the earliest possible date (Saint-Germain and Greene, 2009), the cost of the replanting necessitated by inadequate regeneration, on the order of $1000 USD/ha (Greene et al., 2006), must also be considered. For any of these species, understanding the abscission schedule will permit us to calculate the salvage date that leads to the lowest cost overall by avoiding costly artificial regeneration.

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ANNEX B

A MODEL OF THE POST-FIRE RECRUITMENT OF PICEA MARIANA AND PINUS BANKSIANA AS A FUNCTION OF SALVAGE TIMING AND INTENSITY

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Abstract

In this paper, we model the post-fire recruitment dynamics of two aerial seedbank species, *Picea mariana* and *Pinus banksiana*, in response to salvage logging. The model incorporates: (1) initial seed availability as a function of source tree basal area and proportion of stand salvaged; (2) seed abscission as a function of time; (3) seedling survivorship as a function of seed mass, seedbed proportion, and granivory; and (4) seedling and seed mortality as a function of salvage operations. We also elaborate a simulation of the effect of direct seeding via cone-bearing branches fed into a moving chipper. The model performed adequately when tested against data sets from two fires in Quebec and one in Saskatchewan. In particular, it showed that *P. mariana* was more adversely affected by early salvage than *P. banksiana* because of its far slower seed abscission rate. The model predicted that a delay in salvage or a decrease in salvage proportion would enhance tree regeneration densities, especially for *P. mariana*. Finally, model projections indicate that the use of a chipper to disseminate seeds during the harvesting would permit either species to be adequately regenerated cheaply even with low pre-fire basal area per area or very early salvage.

Keywords: fire; salvage; regeneration; recruitment; abscission; survivorship; STELLA

Introduction

Fire is the dominant disturbance in most of the boreal forest (Stocks et al. 2002; Schmiegelow et al. 2006; Weber and Flannigan 1997), driving the structure, composition, and function of boreal forest stands, and causing significant losses in viable timber. In Canada, the fire return time ranges from 100 years in much of the southern boreal to 250 years in the taiga, and this has resulted in the dominance of pyrophilic tree species adapted to this disturbance regime (Greene and Johnson 1999). Forestry companies and governments have responded to fire by increasingly using salvage to avoid a reduction in the annual allowable cut (Lindenmayer and Noss 2006; Saint-Germain and Greene 2009). However, large-scale post-fire salvage is such a new silvicultural practice that it is presently poorly regulated, and its effects on plants, animals, and soil properties have barely been broached by researchers (Saint-Germain and Greene 2009). In addition, in Canada, companies are spurred to salvage burns by provincial rules that both require and subsidize the practice. Indeed, subsidies are almost always necessary because most of the affected stands will not be at the optimal size (age) for profitable harvesting (Saint-Germain and Greene 2009).

Current salvage procedures generally remove all accessible timber in a burn, and can therefore be both more extensive and intensive than conventional harvest techniques where the emphasis is on the more marketable and larger stems, and where clearcut size is often limited by statute (Lindenmayer and Noss 2006). Salvage usually occurs as rapidly as the initial road network can be constructed, typically within a few months of the fire, and is normally completed within 6 to 10 months. Companies salvage so quickly because of the expected degradation of xylem due to wood-boring insects, stain fungi, wood-decay fungi, and checking (wood splitting due to drying of the boles) (Saint-Germain and Greene 2009). A more minor reason for celerity is that the standing dead trees continue to fall with time since fire (Angers et al. 2011).

These degradation agents vary in their effect on wood value; in particular, wood affected by checking, stain fungi, and insect damage can still be used for pulp.

Salvage negatively impacts the natural regeneration of *Pinus mariana* and *Pinus banksiana*, two common boreal forest tree species that rely on aerial seedbanks to re-establish after fire (Charron and Greene 2002; Greene et al. 2006; Saint-Germain and Greene 2009), as early salvage removes the aerial seedbank before many of the seeds have abscised (Greene et al. 2013). Further, up to 30% of the first-summer cohort of seedlings will be crushed by the machinery as the skidpaths created by the harvesters disturb about a third of the substrate (Greene et al. 2006). Additionally, Greene et al. (2006) speculated that the drier conditions resulting from removal of the shade-casting burnt stems were a contributing factor to the reduced recruitment in salvaged sites. While a seedling density of ~1/m^2 or greater is considered adequate to fully re-stock a stand (Greene et al. 2002), post-salvage natural regeneration densities of *P. mariana* and, to a lesser extent *P. banksiana,* are typically well below this density, and therefore forest companies are required to plant trees at an average cost of USD $750/ha (Saint-Germain and Greene 2009). In addition to delaying salvage to benefit natural regeneration, an unexplored alternative is partial cutting; e.g. parallel strips of burned trees might be left behind. This ought to benefit the conifer species that are so negatively affected by salvage-related seed removal.

Suitable seedbeds, which are crucial for the successful establishment of small-seeded species such as *P. mariana* and *P. banksiana* are affected by both the fire and subsequent salvage (Miyanshi and Johnson 2002; Greene et al. 2007). Fire increases the frequency of the better seedbeds by reducing organic layers (Miyanishi and Johnson 2002). Ironically, salvage can further increase the frequency of suitable seedbeds in an area now denuded of seed sources; Greene et al. (2006) observed five times more mineral soil and humus (both are very favorable seedbeds for small-seeded species) in salvaged stands than non-salvaged (but burned) because so much organic material had been pushed to the sides of the skidpath by the harvesting equipment. In other cases, of course, the harvesters might merely produce water-filled ruts.

There is at present no model of the effect of salvage timing on regeneration. While Greene and Johnson (1999) modeled post-fire tree regeneration and Greene et al. (2006) modeled the regeneration of trees after the salvage of burnt stands, neither could take into account the effect of the timing of the salvage operation because they did not know the seed abscission schedules of the species. Our primary objective is to simulate the impact of both salvage timing and the proportion of stand area salvaged on natural recruitment densities of two common aerial seedbank species, *P. mariana* and *P. banksiana*. We will first validate the model using data from three fires in the boreal forest of North America. Then, we will use the model to explore how the timing and proportion of salvage affects the subsequent recruitment density of each species. At one of these fires, we have experimentally used partial cutting to leave residual trees in parallel strips, and thus our second objective is to verify that partial cutting will increase the regeneration by leaving a fraction of the aerial seed-bank available. This silvicultural alternative has never been tested before. Lastly, we will use the model to examine the potential effect of redistributing seeds (by feeding cone-bearing branches into a chipper that follows the harvester) rather than either hauling them off-site along with the boles or simply leaving the branches on-site. Dispersal of seeds from branches left on-site on the ground is not effective because they tend to be spatially concentrated and there is little seed dispersal once the cones are at or very near the ground (Greene et al. 2004).

The model

General approach

This model simulates the establishment (density) of *P. mariana* and *P. banksiana* seedlings from aerial seedbanks following fire and salvage using the modeling software STELLA (Costanza et al. 1998). It models seed availability, the delay of germination until the spring, and age-specific juvenile survivorship as a function of seedbed type and proportion, seed mass, tree basal area per area, and granivory. Finally, the model includes the effect of salvage timing and proportion of stand area salvaged. This model ignores exogenous factors such as differences in weather from one year to the next, and competition with other plant species. It does not include cone-bearing branches (and thus seeds) that fall onto the ground as a direct result of salvage operations; indeed, it is assumed that all branches are hauled away along with the boles. A simulation period of 72 months (6 years) is used, which is expected to permit abscission of all post-fire seeds in the absence of salvage (Greene et al. 2013). The following sections address the assumptions and functions of the model, all of which are empirically documented and used solely for model calibration, and not in the model validation process.

Seed availability before and during the fire

As argued empirically by Greene and Johnson (1999) for these two species in Saskatchewan, seed production per m^2 (Q_D) is directly proportional to tree basal area per area (m^2/m^2):

(1) $Q_D = 163\,400\,(0.53)\,B_D^{0.95}$ (*P. mariana*)

(2) $Q_D = 35\,097\,B_D^{0.86}$ (*P. banksiana*)

While it is understood that *individual* basal area typically explains only about 20 to 50% of the variation in seed production among local conspecifics in any one year, it has been repeatedly emphasized that it is the only simple measure of seed production available (Calogeropoulos et al. 2003; Viglas et al. 2013). However, at the stand scale, as in our approach here, much of this individual variation is averaged out, and basal area/area is a very good predictor of seeds/area (Greene and Johnson 1999). In equation (1) we follow Greene and Johnson (1999) and De Groot et al. (2004) in assuming that only 53% of the seeds of *P. mariana* survive passage of the flaming front while the *P. banksiana* seeds are not harmed by the fire. It is further assumed that the overlapping dispersal curves of individual trees result in a spatially random distribution of deposited seeds.

Seed abscission

The seed abscission schedules of *P. mariana* and *P. banksiana* following fire have been empirically documented (Greene et al. 2013). Expressing the cumulative proportion, F_t, of seeds abscised by time t since fire as a two-parameter Weibull distribution, we have:

$$F_t = 1 - \exp(-[t/a]^b) \qquad (1)$$

where *a* is the scale parameter, and *b*, the shape parameter, indicates whether the probability of abscission is increasing or decreasing with t. With *t* expressed in months, Greene et al. (2013) found that the coefficients *a* and *b* in equation (1) were 17.84 and 0.633, respectively, for *P. mariana*, and 2.05 and 0.472, respectively, for *P. banksiana*. These values lead *P. mariana* to abscise seeds far more slowly than *P. banksiana*.

Seasonal availability of seeds for germination

While seed abscission occurs year-round, germination occurs only in late spring and summer. This model assumes that seeds abscised from June to August are able to germinate during this period while those abscised between September and May must wait until the following summer to germinate (Greene et al. 1999).

Granivory and cumulative juvenile survivorship

Substrates such as exposed rocks, firm logs, charred logs, and standing puddles are considered lethal for seeds. As for non-lethal seedbeds, we estimate the cumulative survivorship (S) of a cohort over its first three summers from deposited seed to seedling, following the approach of Greene and Johnson (1998), where they collated the results of numerous empirical studies (albeit the great majority were in clearcuts rather than burns). They divided seedbeds into good (with proportion, w) and poor (1-w), with the difference in the survivorship created by either type increasing rapidly and inversely with seed size. These two proportions sum to the total non-lethal proportion of the ground. For this study of a fire, the good seedbeds were similar to those of Greene et al. (2006): exposed mineral soil and living (surviving) mosses. The poor seedbeds had residual duff or a thick layer of leaves or dead mosses, or, more rarely, were lichens. We assumed that the survivorship on either type was dependent on germinant size, with the latter, in turn, dependent upon seed mass (m) in g. Their equation is:

$$S = gw[1 - \exp(-f_L m^b)] + g(1 - w)[1 - \exp(-f_H m^d)] \quad (2)$$

Seed mass was 0.0012 g for *P. mariana* and 0.0045 g for *P. banksiana* (Greene and Johnson 1999). As in Greene and Johnson (1998), b and d in equation (2) were set at 0.43 and 0.76, respectively; f_L and f_H are set at 1.83 and 0.33, respectively. Finally, g, the survivorship through the granivory stage, is set at 0.95 for the summer of the fire itself, following the observation of Charron and Greene (2002) that granivory is extremely rare initially in the boreal fire they studied when the site is far from the fire edge or from a residual stand. We know of no other study of first-summer granivory rates after wildfire in forests that makes clear the distance to a source of small mammal dispersants. Subsequent to that first summer, *g* is reduced to 0.43 (as in Greene and Johnson 1998) for the remainder of the simulation. Finally, it is assumed that after the third summer, the age-specific survivorship for any cohort is essentially 1.0 (Charron and Greene, 2002).

Salvage affects the seedbed proportions. Greene et al. (2006) observed a 30% increase in mineral soil and thin humus in a 100% salvaged site due to organic layer removal by harvesters. All of this increase was on the skidpaths; i.e. the skidpaths occupied about 30% of the burn. In the model we reduce both pre-salvage seedbed proportions (multiplying *w* and (1-*w*) by 0.70) and then add 0.3 to the category *w*. This is far too simple as in some cases the machinery is merely baring rocks (a lethal substrate) or creating depressions (ruts) that are filled with water part of the time. That is, the assumption that 30% is added to the "good substrate" category is optimistic, however it was chosen as this is the standard amount of area expected to constitute skid paths in Quebec if salvage operations are properly executed. Spacing of skid trails during the course of operations will undoubtedly vary from site to site; therefore, given the lack of empirical data, we use this estimate.

Seed removal by salvage

Seeds not yet abscised at the time of salvage are removed during the harvest. Thus, if for example, 50% of the stand area is salvaged, it is assumed that 50% of the remaining seeds have been removed. This approach does not take into account that some cone-bearing branches will be knocked off the boles during the operation, but as there are no data available on the number of seeds per area inside cones remaining on-site immediately after salvage, we can only acknowledge that this aspect of our model will underestimate the recruitment density.

Seedling and seed mortality from salvage

Seedling and seed mortality results from the passing of machinery along skid paths. It is set at 30%, the percentage of the burn covered by the parallel skidpaths (Greene et al. 2006). If for example there were 10 germinants/m^2 after the first summer and 100% salvage occurred between September and May, then the first summer cohort is reduced by 30% to 7.0 seedlings per m^2. As for seeds that fell onto the ground between September and the salvage date (and had therefore not yet germinated), these likewise were reduced by 30% because the machinery heaps the organic material into "windrows" along the two sides of the skidpath, and thus the vast majority of these seeds will be irremediably buried. When the salvage proportion is less than 1, then the mortality rates endured by first-summer seedlings and ungerminated seeds are reduced accordingly. Thus, for example, if 50% of the area is salvaged, then the deposited (but not yet germinated) seeds and post-germination recruits will be multiplied by 0.15 (i.e. 0.5 x 0.3).

Model validation

Simulated seedling densities were compared to observed densities obtained from (1) the present study conducted in the 2005 Lebel-sur-Quevillon (Quebec) wildfire, (2) the 1997 Val Paradis (Quebec) wildfire, (Greene et al. 2006; Greene et al. 2004), and (3) the 1989 Muskeg (Saskatchewan) wildfire (Greene and Johnson 1999); (Figure 1).

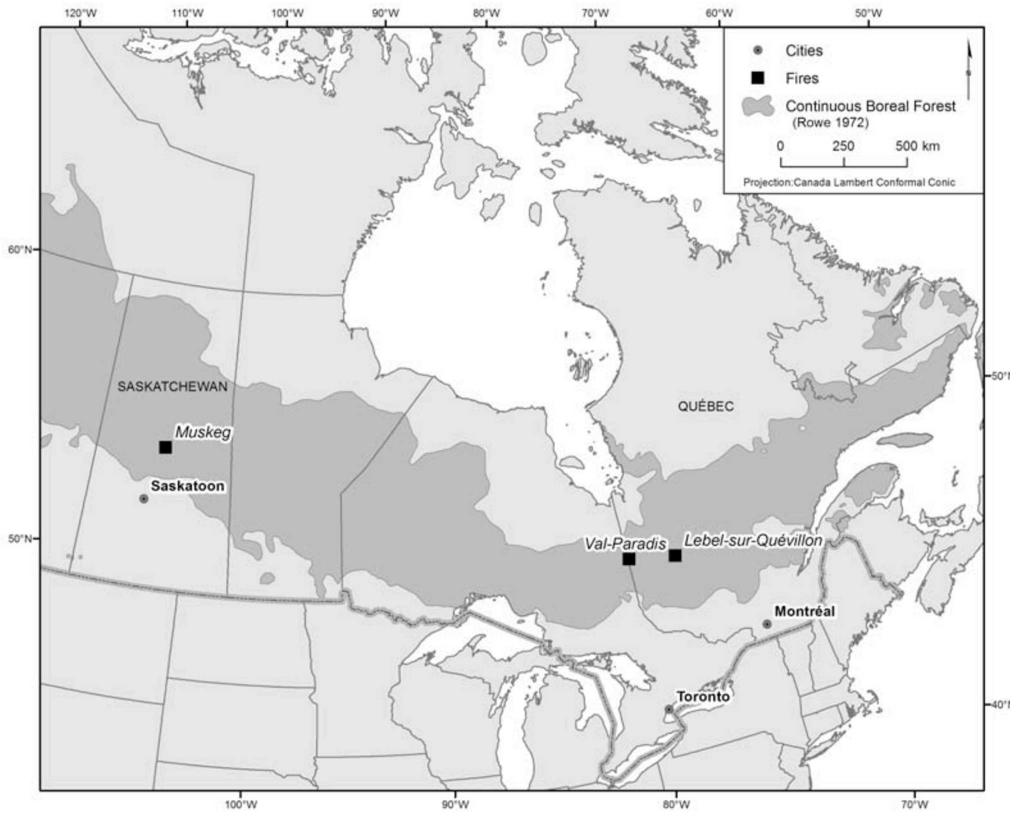

Figure 1. The location of the Lebel-sur-Quevillon, Val Paradis, and Muskeg fires.

Sensitivity analysis

A sensitivity analysis was performed for four parameters under two scenarios (burned intact and 100% salvaged). First, basal area per area for the species of interest was analyzed using a minimum value of $0.001 m^2/m^2$ and maximum value of $0.003 m^2/m^2$, reflecting the fact that below 0.001, the species is an increasingly minor component of a stand while values >0.003 are very unlikely to be encountered. Second, the seedbed-mediated survival from seed to germinant and granivory rate were analyzed using values of 0%, 25%, 50%, 75%, and 100% of the default value (as discussed above) as there are far too few studies to permit us to estimate the 95% confidence interval as a guide to the sensitivity analysis; and finally, seed mass was varied using the 95% confidence interval based on our original samples.

Field observations

The Lebel-sur-Quevillon fire was located in northwestern Quebec (48° 49.52’ N, 77° 00.07’ W) approximately 80 km from the town of Lebel-sur-Quevillon. Ignited by lightning in the early summer of 2005, it burned 4113 ha of forest until it was extinguished by rain. Salvage by the company Tembec began in October 2005 within the burn and continued until February 2006 with each month accounting for a specific area harvested. Prior to fire and salvage, selected stands within this fire were dominated by mature *P. mariana* or, more rarely, *P. banksiana*. Stands dominated by the former exhibited a large variation in organic layer depth depending on proximity to the water table; many had a ground cover dominated by *Sphagnum* while others were mantled with feathermosses (*Ptilium crista-castrensis*, *Hylocomium splendens*, *Pleurozium schreberi*) and *Dicranum* spp. The single *P. banksiana* stand had thinner and dryer seedbeds dominated by feathermosses and, in a few patches, lichens (mainly *Cladina* spp.). Ericaceous species were common understory components in almost all the stands, and consisted mainly of *Vaccinium* spp, *Kalmia angustifolia*, *Ledum groenlandicum*, and *Gaultheria procumbens*.

All stands sampled within the burn had 100% tree mortality. Seven sites were selected within the burn, five of these within the salvaged portion, and each representing a different month of salvage (October to February). The stand representing October salvage was dominated by *P. banksiana*. At Lebel-sur-Quevillon for the simulations, we used the salvage date that corresponded to the particular stand sampled after fire.

Tembec conducted a partial harvest in an area dominated by *P. mariana*. Salvage occurred in parallel strips: a 10 m wide portion of forest was salvaged leaving to the side a 10 m wide residual band. Thus, approximately 50% of the burned trees remained. One site was selected within this linear residual salvage zone for study (December salvage). Tembec also established some areas where they did not salvage. The seventh site was located in one of these intact burned areas.

At each of the seven sites, ten randomly oriented transects were established at the end of the summer of 2008. Each transect was 25 m long and 2 m wide. Along the transects we recorded seedling frequency, seedbed type (based on a point every 0.5 m along the centerline of the transect; n=51 per transect), and basal area for any bole more than 50% within the transect. Basal area was recorded at breast height in the burned intact stand whereas in the 100% salvaged stands it was recorded using tree stumps. In the linear residual stand basal area was recorded using the standing burned trees in the residual bands. Stump diameters were converted to the slightly smaller breast height diameters using the regression in Greene et al. (2006).

Seedbed proportions (lethal; *w*; and 1-*w* for the non-lethal proportion) were determined using field data from the Lebel-sur-Quevillon wildfire. These seedbed data were obtained from a burned intact black spruce site using transects. Seedbed data were unavailable for the salvaged stands (both *P. mariana* and *P. banksiana*); therefore, we substituted the values from the burned intact *P. mariana* site.

Details on study area and sampling design for the early summer Val Paradis fire are available in Greene et al. (2006) and Greene et al. (2004). The original studies and subsequent results included deciduous, coniferous and mixed stands subjected to low, moderate, and severe fire. For the purpose of this study we were only interested in mixed (i.e. >25% coniferous component) and pure coniferous stands subjected to moderate or severe fire. This gave us 16 intact and 19 salvaged *Picea mariana* stands, and 10 intact and 17 salvaged *Pinus banksiana* stands. Data on species-specific pre-fire basal area/area, recruit densities, seedbed proportions, and salvage and fire date were available. Seedling densities from the three-year study were corrected following the age-specific argument presented by Charron and Greene (2002); i.e. we included subsequent age-specific mortality for the germinant and 1-year-old cohorts; the expected cumulative survivorship (from the end of the first summer to the end of the third winter) on good seedbeds was 73.34% for *P. mariana* and 60.82% for *P. banksiana*, and 37.88% and 16.44%, respectively, on poor seedbeds. Average intact seedbed proportions for *Picea mariana* and *Pinus banksiana* stands were used for the sites that would subsequently be salvaged. Salvage month for the Val Paradis wildfire for use in the simulations was set at 9. In reality, salvage began in August and lasted until December; we chose October (the median month), since specific dates were not available.

The 5-year-old early summer Muskeg fire of Greene and Johnson (1999) occurred on much drier sites than the two Quebec fires. None of the 18 *P. mariana* and 19 *P. banksiana* stands they examined had been salvaged; and they developed regressions for the two conifer species relating seedling density (recruits/m^2) to pre-fire basal area per area. Their observed seedbed proportions were quite different from the two Quebec fires: mineral soil and humus 17%, living *Sphagnum* and feathermoss 0%, thick duff 74%, lethal substrates 9%, nonetheless if we regard these proportions merely as being good, poor, and lethal seedbeds, then they are similar to the Quebec fires. Complete methods for the Muskeg fire study are available in Greene and Johnson (1999).

Data was collected at the Lebel-sur-Quevillion fire specifically for use in this study. The data from both the Val Paradis and Muskeg fires were obtained from previous unrelated studies.

Statistical analysis

Linear regressions were used to compare simulated versus observed seedling densities, by fire and by species. This was done to test the accuracy of simulated densities by determining whether slopes were significantly different from 1 and intercepts significantly different from 0. At the Lebel-sur-Quevillion fire only one *P. banksiana* stand was sampled; for that stand we examined whether the simulated seedling density fell within the 95% confidence interval of the observed density.

Prescriptive simulations

Exploring the model, we conducted three additional sets of simulations. First, we ascertained for each species the effect of delaying salvage. We ask: what is the pre-fire basal area per area that will provide adequate stocking (>1 seedling/m^2) given a 100% salvage operation in the winter (December) within the first six years after fire. The second set of simulations was like the first except we additionally asked what would be the effect of reducing salvage intensity to values less than 100%. It is assumed for this second scenario that, with less than 100% salvage, residual stands will be in parallel rows and seed dispersal need not be explicitly examined. Third, we asked what would happen if cone-bearing branches were fed into a chipper that followed the harvester along the skid path and sprayed the mix of seeds and chips across the surrounding area *behind* the advancing harvester. In particular, for this third scenario we imagine that (1) the seeds are redistributed randomly across the site (including the good seedbeds created by the harvester) and (2) 75% of the residual seeds were available for redistribution, the remaining 25% being accounted for by seed mortality inside the chipper or by small branches that were not thrown into the machine.

In these simulations it is assumed that the species of interest is the only component of the stand that has commercial value and figures in the stocking calculation. We also assume the following post-fire (but pre-salvage) seedbed percentages: mineral soil 17%, living *Sphagnum* and feathermoss 10%, the poor seedbeds are solely high-porosity burnt duff 60%, and lethal substrates 13%. The total fraction of good seedbeds (mineral soil plus living mosses equals 27%) is higher than seen generally in the eastern North American boreal forest but lower than in the west (Greene et al. 2007).

For pre-fire basal area per area, we only examine the range 0.001 to 0.003. Below 0.001, the species is an increasingly minor component of a stand and one should not expect full stocking no matter the prescription. Meanwhile, values >0.003 are very unlikely to be encountered, especially for *P. mariana*.

Results

The Lebel-sur-Quevillon fire

Observed *P. mariana* and *P. banksiana* stand seedling densities, per-fire basal area per area, and salvage date can be found in Table 1. In all cases at Lebel-sur-Quevillion, there was insufficient basal area/area to warrant harvesting had these been unburned forests. All harvesting at these sites was done within 8 months of fire. In only two cases at Lebel-sur-Quevillion did recruitment exceed 1 seedling m^2, our normative threshold for adequate stocking.

Table 1. Observed seedling densities, treatments, and basal area/area at the stands sampled at the Lebel-sur-Quevillion wildfire.

Site	Treatment	Salvage month	Basal area/area (m^2/m^2)	Observed seedling density/m^2
P. mariana	Burned intact	N/A	0.0015	1.02
P. mariana	50% salvaged	December	0.001	0.23
P. mariana	100% salvaged	November	0.001	0.1
P. mariana	100% salvaged	December	0.001	0.07
P. mariana	100% salvaged	January	0.001	0.11
P. mariana	100% salvaged	February	0.001	0.06
P. banksiana	100% salvaged	October	0.002	1.16

Post-fire exposed mineral soil and thin humus did not occur at these low-lying sites. Living *Sphagnum* and feathermoss were relatively common with 11% coverage, while high-porosity burnt duff accounted for 76%. Lethal seedbeds (almost entirely charred or unburned but firm wood, the latter resulting from the splintering of wood during cutting) comprised 13% of the ground.

Model validation

The results of log-transformed regressions of the simulated versus observed seedling density for all fires and treatments are shown in Table 2. At the Lebel-sur-Quevillion fire the *P. mariana* sites were lumped due to the small sample size. Observed natural regeneration densities of *P. mariana* from non-salvaged, salvaged (100%) and partially salvaged (50%) treatments were well predicted by the simulations (r^2 = 0.901; p = 0.002) (Figure 2). The intercept was not significantly different from 0 and the slope not significantly different from 1. The single predicted *P. banksiana* seedling density of 1.09/m^2 from a 100% salvaged burn at Lebel-sur-Quevillion within the 95% confidence interval (0.80 - 1.52) of the observed value (1.16/m^2).

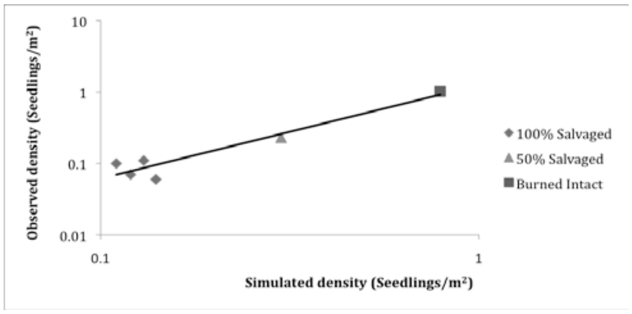

Figure 2. Log-log plot of observed vs simulated Lebel-sur-Quevillon *P. mariana* seedling densities (treatments lumped); detailed information on regression fit can be found in Table 2.

Table 2. Power law regression results for simulated versus observed seedling density. **Note:** The 95% confidence intervals are shown in parentheses for the intercept, α, and the slope, β. All correlations were significant at a probability of 0.05 except for the salvaged *P. mariana* and intact *P. banksiana* at the 1997 fire. a is the intercept and b the slope of the log-log regressions.

Fire	Species	Treatment	Fire year	α	β	df	r^2	p	*n*
Lebel-sur-Quevillion	*P. mariana*	Lumped	2005	0.225 (-0.722 - 1.172)	1.308 (0.774 - 1.841)	4	0.901	0.002	6
Val Paradis	*P. mariana*	Intact	1997	-0.477 (-1.410 - 0.456)	0.639 (0.111 - 1.167)	14	0.277	0.021	16
		Salvaged		-2.541 (-4.786 - -0.296)	0.018 (-0.806 - 0.841)	17	-0.059	0.964	19
	P. banksiana	Intact		0.060 (-1.108 - 1.228)	0.062 (-0.939 - 1.062)	8	-0.122	0.891	10
		Salvaged		0.053 (-0.543 - 0.649)	1.271 (0.455 - 2.087)	15	0.385	0.005	17
Muskeg	*P. mariana*	Intact	1989	0.841 (0.226 - 1.456)	0.978 (0.525 - 1.431)	16	0.54	0	18
	P. banksiana	Intact		0.553 (-0.212 - 1.318)	0.735 (0.357 - 1.113)	17	0.468	0.001	19

Observed seedling densities for *P. mariana* and *P. banksiana* from the Val Paradis wildfire (Greene et al. (2006) and Greene et al. (2004)) were compared to model predictions. The model predicted intact *P. mariana* densities reasonably well (r^2 = 0.277; p = 0.021) (Figure 3a), the intercept not significantly different from 0 and the slope not significantly different from 1. It failed however at predicting salvaged *P. mariana* densities (r^2 = -0.059; p = 0.964; Figure 3b). The mean observed recruit density for black spruce was 0.63/m^2 at the intact stands and 0.13/m^2 at the salvaged stands.

For *P. banksiana* at Val Paradis the opposite trend was observed. While the model failed to predict intact seedling densities (r^2 = -0.122; p = 0.891; Figure 3c), it predicted salvaged seedling densities relatively well (r^2 = 0.385; p = 0.005; Figure 3d), with the intercept not significantly different from 0 and the slope not significantly different from 1. The mean observed recruit density for jack pine was 2.12/m^2 at the intact stands and 1.69/m^2 at the salvaged stands.

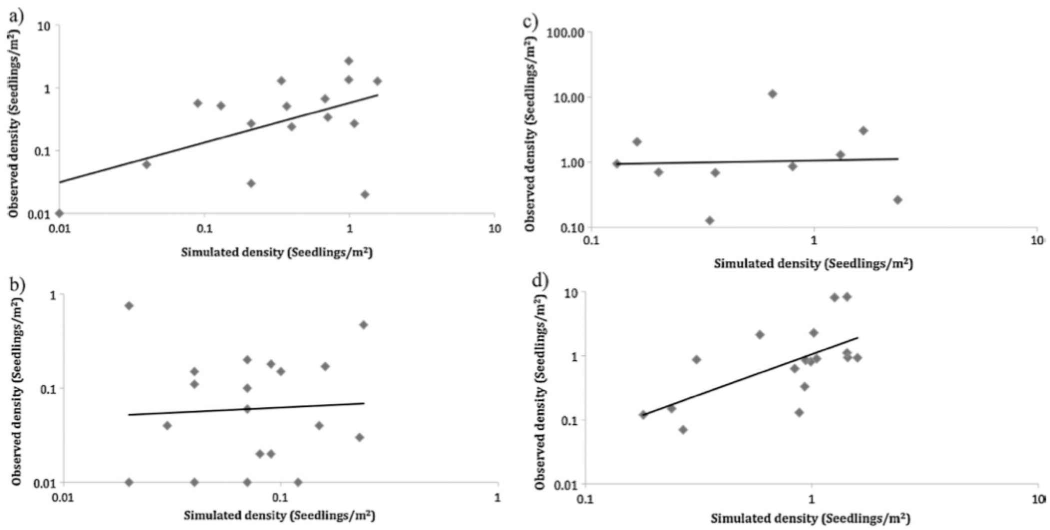

Figure 3. Simulated versus observed seedling densities for intact (a) and salvaged (b) *P. mariana*, and intact (c) and salvaged (d) *P. banksiana* stands at the Val Paradis wildfire; detailed information on regression fit can be found in Table 2.

The model performed reasonably well predicting seedling densities for both intact *P. mariana* (r^2 = 0.54; p = 0.000; Figure 4a) and *P. banksiana* (r^2 = 0.468; p = 0.001; Figure 4b) stands at the Muskeg fire in Saskatchewan. In the case of *P. mariana* the intercept was significantly different from 0 while the slope was not significantly different from 1, indicating that the model tended to under-predict. By contrast, for *P. banksiana* neither the intercept nor slope was significantly different from 0 or 1.0, respectively.

(a) (b)

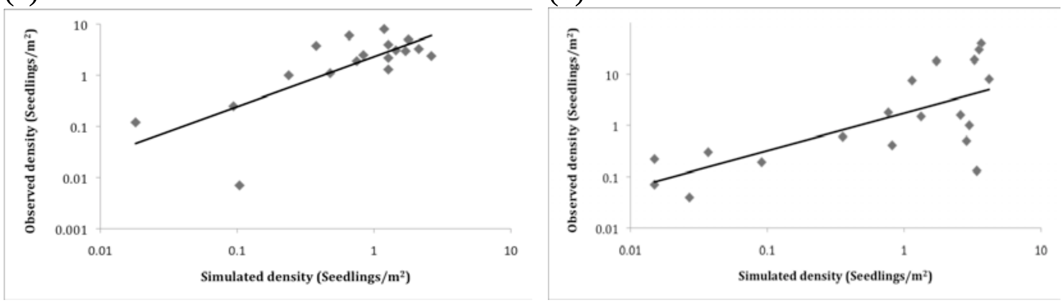

Figure 4. Simulated versus observed intact *P. mariana* (a) and *P. banksiana* (b) seedling densities for the Muskeg fire; detailed information on regression fit can be found in Table 2.

Prescriptive simulations

The simulations indicated that, not surprisingly, delaying salvage increased the regeneration density. For *P. mariana* to minimally achieve full stocking (>1.0 seedling/m^2) with 100% salvage required a delay in harvesting until the fourth winter with basal area per area as low as 0.00125; below this basal area 100% salvage would never result in minimal stocking (Figure 5). A delay until only the third winter permitted full stocking with a minimum basal area per area of 0.00175. First winter salvage did not provide full stocking at any reasonable (<0.003) value of basal area per area. By contrast, *P. banksiana* required no delay to achieve adequate stocking (Figure 5). A basal area per area of only 0.001 would fully stock the site with a December (i.e. first winter) salvage (Figure 5).

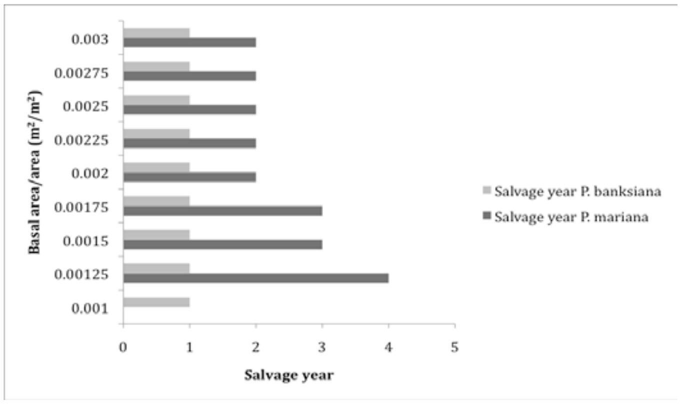

Figure 5. The year of 100% winter salvage in which minimally full stocking can be obtained given the pre-fire basal area/area.

The second set of simulations looked at the additional factor of salvage intensity. Of course, as the intensity of salvage decreased, the regeneration was augmented because fewer seeds were removed from the site and better seedbeds were available after the passage of the harvesters. For *P. mariana* only a basal area ≥ 0.00175 will allow for partial salvage in the first winter following fire; anything lower will require a delay until the second or third winter (Figure 6). For *P. banksiana*, full stocking could be achieved at any pre-fire basal area from 0,001 to 0.003 with 100% salvage.

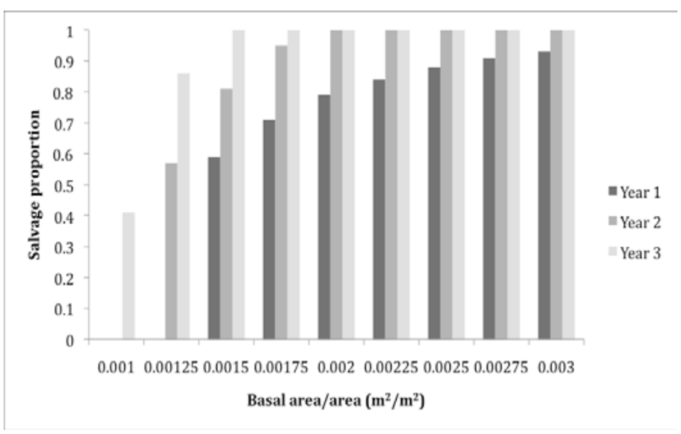

Figure 6. The maximum proportion of a stand that can be salvaged for *P. mariana* to achieve 1 seedling/m^2 given a winter salvage date (first through third years) and the prefire basal area per area.

The third and final simulations examined the effect of the redistribution of seeds (via a chipper) on final seedling density. The expected amelioration is more pronounced for *P. mariana* (Figure 7a) than *P. banksiana* (Figure 7b) because there were more seeds to redistribute due to its slower abscission schedule. For both species, any basal area per area value as low as 0.001 was sufficient to achieve adequate stocking, even with a first winter harvest.

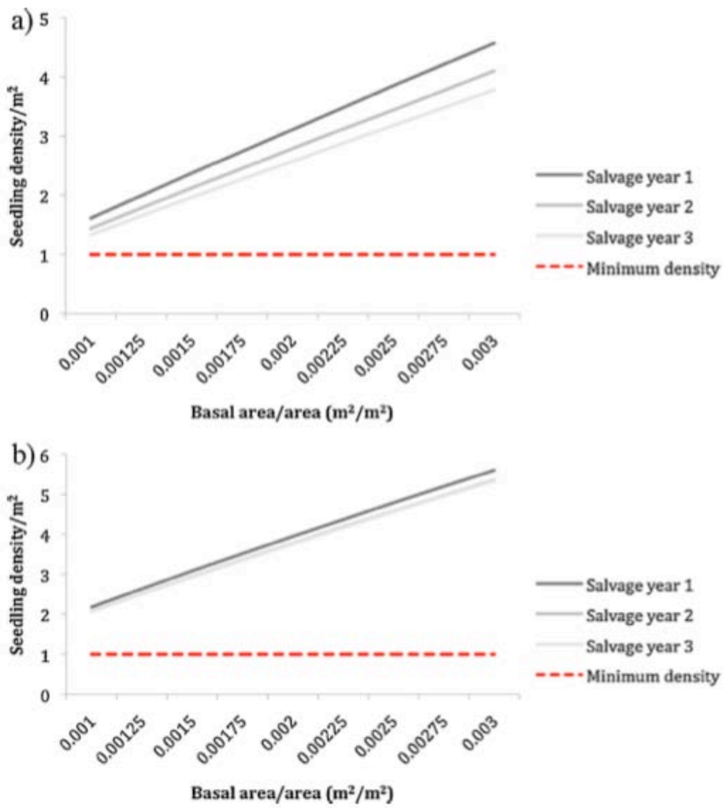

Figure 7. (a) *P. mariana* and (b) *P. banksiana* seedling density vs the dimensionless basal area/area following 100% salvage and 75% re-dispersal of salvaged seeds in the first 3 winters following fire (note: for *P. banksiana* year 3 has similar values to year 2 and is therefore masked).

Sensitivity analysis

A sensitivity analysis was performed for three parameters: basal area per area, seedbed-mediated survival from seed to germinant, and the granivory rate. In these three cases, the parameter values ranged from 0.25% of the expected mean to 4 times the expected mean. In all cases, the output (seedlings m^{-2}) was merely a linear function of the parameter value. For a fourth parameter, seed mass, we calculated the 95% confidence interval based on our original samples, and examined the range of seedling densities as mean seed mass varied from about two standard deviations to either side of the mean mass. Not surprisingly, given the relatively invariant nature of seed mass within a species, there was only an 8% difference in seedling density over this range.

Discussion

Generally, the model performed well, for either species and for the range of 0 to 100% salvage. As expected, both observed and simulated seedling densities declined as the proportion of the forest that was salvaged increased, there was no tendency for the model to over-predict or under-predict. In two cases (both at Val Paradis; Figures 3b and 3c) the regression between observed and simulated densities was not significant. In both these cases however the mean simulated density was close to the observed value; the problem was that neither pre-fire basal area per area nor seedbed quality seemed to greatly affect the observed recruit densities. What other factors were masking the effect of these two drivers?

There are five likely causes of the unexplained variation in the observed recruitment densities. The first involves seed mortality occurring during the fire. This remains a poorly explored topic, with experiments ranging from the use of a blowtorch to placing cones within a campfire to direct observations before and after an experimental burn (Beaufort 1960; Despain et al. 1996; De Groot et al. 2004). A more systematic study than attempted to date may reveal a great deal of variation, due perhaps to differences in cone moisture as this will greatly affect the thermal connectivity, within and between stands in the seed survival during flaming front passage.

A second potential source of the unexplained variation is undoubtedly that basal area/area is a poor estimator of the pre-fire seeds per area. While it has the merit of being a quick measure (e.g. one could appeal to pre-fire inventory maps), nonetheless field measurements have shown that the r^2 values for seed density vs. basal area/area are typically only around 0.3 (Calogeropoulos et al. 2003; Viglas et al. 2013).

A third likely source of variation in recruitment densities is that the rainfall in the first summer will undoubtedly greatly affect the first-summer age-specific survivorship of each cohort. This lack of realism in our model will be mitigated somewhat by the fact that each species at each site has more than one cohort.

A fourth and quite serious source of variation in the final seedling density is the assumption that an invariant amount of granivory occurs within each stand. In reality, even given equal distances from a source of dispersants, small mammal granivory rates can vary enormously (e.g. Cote et al. 2003; Greene and Johnson 1998).

A final source of error in the modeling effort is that the survivorship conferred by seedbed types are on a gradient and not so easily reduced to our categories of good, bad, and lethal. Likewise, even the same seedbed type may be on a southern vs. northern aspect and thus differ greatly in moisture availability in the first summer for a cohort (Alexander 1983). Finally, the same seedbed may differ markedly in how rapidly angiosperm leaf litter accrues (and thus changes the expected survivorship) or even if the litter has allelopathic effects (e.g. Interjit and Mallik 2001).

As a cautionary example, Greene and Johnson (1998) showed that, even with a single species (*Picea glauca*, white spruce) on a single seedbed type (mineral soil) and known seed input (hand sowing), 30 separate studies of juvenile survivorship from across North America revealed a range of almost 3 orders of magnitude. Further, they found that a single study with repeated annual sowings at the same site revealed almost as much variation as their cross-continental survey. Nonetheless, while seedbed type and basal area per area are both easily measured, they also can be used simply as givens (with the former taken from regional averages of seedbed type proportions as in Greene et al. (2007) and the latter read from inventory tables). By contrast, for the additional sources of variation listed above, we have neither default values nor easy field methods. In short, whatever the shortcomings of our approach, it is clear that more research is needed before the model can be elaborated further.

Turning now to the exploratory simulations, we saw that *P. banksiana* was much less harmed by early salvage than was *P. mariana*, a conclusion that tallies with observations made by Greene et al. (2006). For example at Lebel-sur-Quevillon, for the 100% salvage stands, and with similar pre-fire basal area per area, the former had 10 times more seedlings per m^2 than the latter. This is to be expected because, as expressed in our abscission function, much of the aerial seedbank of *P. mariana* is still on the tree when early salvage occurs, whereas *P. banksiana* will have few seeds left in the cones by that point (Greene et al. 2013).

While there are many commercially valid reasons to salvage early (St. Germain and Greene 2009), according to our model one cannot obtain adequate regeneration of *P. mariana* unless salvage is delayed until at least, depending on pre-fire basal area per area, the second or third winter following fire. By contrast, *P. banksiana* can be fully stocked after a first winter salvage with all but the very lowest basal area/area values. We cannot however recommend delay to foresters until there is a direct comparison of the cost of artificial regeneration vs the cost in lost or devalued wood given that delay. There is at present no published work useful for making such a comparison.

Salvage negatively affects other species such as saproxylic beetles and woodpeckers (Lindenmayer and Noss 2006; Morissette et al. 2002). More than 80% of saproxylic insects, and most pyrophilous ground-dwelling insects, are abundant only for two to three years following fire. Predators such as woodpeckers have rapid increases in population abundances in these recent burns (Saint-Germain and Greene 2009). Not surprisingly, Schmiegelow et al. (2006) observed that the woodpecker species common to burned areas were absent from recently salvaged sites. As previously explained, however, the goal of forestry companies is to harvest as quickly as possible; i.e. to truncate the already-short interval in which many animal species would normally sharply increase their abundances. A delay in salvage would therefore permit more of the fire-dependent insect taxa to successfully complete their life cycles, with consequent benefits for predators such as woodpeckers.

An alternative (or addition) to the strategy of delaying would be to harvest a fraction of the area. This should be done in parallel strips so that dispersal of seeds is not a constraint. As we saw, the recruitment from our partially salvaged stand at Lebel-sur-Quevillion was intermediate between intact and 100% salvaged *P. mariana* stands. With partial stands, the good seedbeds created by the harvester would be available for a diminished but nonetheless *on-site* seed source. Ideally, the care is taken to minimize rutting: we over-predicted the recruitment at our partially salvaged stand because much of the skidpath surface was reduced to water-filled ruts. For example, for *P. mariana*, a basal area per area of 0.0015 would have very low recruitment and require planting if it was 100% salvaged in the first winter, while a 59% salvage under these same circumstances would lead to full stocking.

Finally, while never tested in the field, the redistribution of seeds via a chipper is a promising method that would encourage high seedling densities of both species even when initial pre-fire basal area per area was low. Especially this technique could be useful with *P. mariana* as this species, when mature, clusters the cones at the top of the stem. Our suggested technique would require that the harvester remove the top of the tree before skidding the trunk to the landing. Subsequently an individual walking behind the chipper on the skidpath would grab individual cone-laden tops and throw them into the chipper. The machine will easily scatter the material across 20 m, more than enough to insure adequate dispersion of seeds across adjacent pairs of skidpath and inter-skidpath areas. Note however that our guess concerning the seed loss during passage through the chipper was unsupported by any empirical evidence and thus a field experiment is called for. Further, one would need to calculate the cost of the chipping operation relative to the cost of delay, partial salvage, and artificial regeneration.

In summary, our model offers a promising method for exploring recruitment following wildfire. Introducing salvage intensity and timing permits the model to generate silvicultural prescriptions. Indeed, the most obvious and quick utilization would be to couple the model with pre-fire GIS-based inventory maps and an assumption of seedbed-type coverage from the regional values of Greene et al. (2007) so that, for example, stands requiring planting could be identified early in the salvage planning process. For example, sparse *P. mariana* stands would be salvaged after three years (or perhaps not at all), while denser *P. mariana* and sparse *P. banksiana* stands would be salvaged at a shorter interval, and finally the most dense *P. banksiana* sites could be salvaged immediately. The model would further be useful for depicting how delays could be shortened as the salvage became partial rather than complete.

Acknowledgments

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