University of Alberta

Keystone Processes Affect Succession in Boreal Mixedwoods – the Relationship Between Masting in White Spruce and Fire History

By ©

Vernon Scott Peters

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment
of the requirements for the degree of Doctor of Philosophy

in

Environmental Biology and Ecology
Department of Biological Sciences

Edmonton, Alberta
Spring 2003

National Library
of Canada

Acquisitions and
Bibliographic Services

395 Wellington Street
Ottawa ON K1A 0N4
Canada

Bibliothèque nationale
du Canada

Acquisisitons et
services bibliographiques

395, rue Wellington
Ottawa ON K1A 0N4
Canada

Your file Votre référence
ISBN: 0-612-82155-2
Our file Notre référence
ISBN: 0-612-82155-2

University of Alberta

Library Release Form

Name of Author: Vernon Scott Peters

Title of Thesis: Keystone processes affect succession in boreal mixedwoods – the relationship between masting in white spruce and fire history

Degree: Doctor of Philosophy

Year this Degree Granted: 2003

Permission is hereby granted to the University of Alberta Library to reproduce single copies of this thesis and to lend or sell such copies for private, scholarly or scientific research purposes only.

The author reserves all other publication and other rights in association with the copyright in the thesis, and except as herein before provided, neither the thesis nor any substantial portion thereof may be printed or otherwise reproduced in any material form whatever without the author's prior written permission.

Vernon Scott Peters
6030 107A Street
Edmonton, AB T6H 2Y5
Canada

January 21st/03
Date

University of Alberta

Faculty of Graduate Studies and Research

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled *Keystone processes affect succession in boreal mixedwoods – the relationship between masting in white spruce and fire history* submitted by Vernon Scott Peters in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Environmental Biology and Ecology.

Dr. Mark R.T. Dale (Supervisor)

Dr. S. Ellen Macdonald (Supervisor)

Dr. Vic J. Lieffers (Committee Member)

Dr. David Hik (Committee Member)

Dr. James C. Cahill (Examining Committee)

Dr. John Zasada (External Examiner)

January 3rd / 2003

Date

ABSTRACT

Wildfires reinitiate the process of forest succession in boreal mixedwood forests; however, the timing of white spruce (*Picea glauca* Moench Voss) regeneration post-fire, which greatly influences the successional development of stands, varies greatly between fires. I investigated whether fire history attributes in conjunction with masting (the intermittent and synchronized production of abundant seed crops over large areas) of white spruce affected the timing and density of spruce regeneration, and ultimately the successional pathways of mixedwoods. I also determined whether: 1) aging errors occur, 2) hare browsing causes missing rings, 3) a delayed regeneration pulse occurs, and if so, when? 4) what factors affect the successional pathway of mixedwood stands post-fire, and 5) the concordance between pre- and post-fire density of white spruce. I studied 17 fires in northeastern Alberta that occurred during mast years (high seed production) as well as non-mast years (low seed production).

Burn timing relative to mast years had a long-lasting effect on regeneration. Significantly more spruce regeneration occurred in mast year fires than non-mast year fires. The greatest decline in density occurred between a mast year fire and fires with a one year delay before a mast year. Crossdating verified that a large mast cohort occurred on all mast year fires, and that most initial regeneration occurred within 5 years of the fire on recent fires. Ground-level age significantly underestimated the true age of spruce (up to 27 years in 40-year-old trees), and aging errors increased as stands aged. Clipping experiments indicated that browsing like that inflicted by snowshoe hares could lead to substantial age underestimation in white spruce. Delayed regeneration peaked 38 to 44 years after fire, and occurred primarily on decayed logs. Out of 20 stands from 1941 and

1942 fires, 7 stands were dominated by initial regeneration, 7 had "even" mixtures of initial and delayed regeneration, and 6 were dominated by delayed regeneration. Significant variability in spruce age structure occurred between the oldest fires despite similar masting history, burn dates, and seed availability. Finally, the likelihood of concordance between pre- and post-fire populations of white spruce was greater on mast and one-year-delay fires, than fires with longer delays. Our results indicate that masting is a keystone process that interacts with fire history to affect the persistence of white spruce in mixedwood landscapes.

ACKNOWLEDGEMENTS

In addition to the numerous researchers whose hard work have made the questions addressed in this study possible, there are many people that have contributed in many ways. Firstly, thank-you Ellen and Mark for your phenomenal support throughout the past five years. Your advice, personal involvement, and friendship have not only improved this thesis greatly, but have also made my time in your labs enjoyable. To committee member Vic Lieffers, thank-you for generously providing lab space and access to equipment, and to committee member Dave Hik, thanks for many insightful comments throughout my program. I also owe a lot to Gitte Grover, my enthusiastic industry advisor from Alberta Pacific Forest Industries. Thank-you for making me aware of key research issues, and for the financial support you secured.

Many people have been instrumental in data collection and in sharing their knowledge along the way. Field assistants Gunther Tondelier, Eric Paton, Rich Hart, and Paul Fuelbrandt withstood many grueling days working at remote field sites – your hard work and companionship were invaluable. Special thanks to my super tree ring sleuths Line Blackburn and Lana Laird – your attention to detail and dedication is admirable. I am indebted to Annie Desrochers for her instruction in dendrochronology – thank-you for the many hours of assistance that you gave. I have learned much from fellow graduate students – discussions with the Dale lab and Macdonald lab were always beneficial. Thanks too for all the computer tricks many of you taught me, and the enjoyable times we shared.

I'm especially thankful to Canadian society for the research funds that they have made available. Without the financial support of the Sustainable Forest Management Network, Natural Sciences and Engineering Research Council, Challenge Grants in Biodiversity, and Canadian Circumpolar Institute, this research would not have been possible.

Finally, I would like to thank friends and family for their consistent support and encouragement throughout my education. In particular, I am so fortunate to have had the love and companionship of my wife Sue Peters throughout this program. Thank-you for your patience, and for the countless ways you pinched in along the way. Thanks to the many people at McKernan Baptist Church for your fellowship and many prayers. I am

also grateful to God for the opportunity to learn a little more about His creation in the course of this work. I sincerely hope that people will benefit from the information in this thesis, and use it to promote good stewardship of Canada's forests.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF ABBREVIATIONS

ANOVA:	analysis of variance
df:	degrees of freedom
GLM:	generalized linear model
K-S:	Kolmogorov Smirnov
MYB:	mast year burns
NMYB:	non-mast year burns
YD:	year delay
YOS:	year-old stands

CHAPTER 1

Introduction

1.1 Fire History and Forest Development

In ecosystems that are frequently disturbed by fire, plant population dynamics are closely tied to fire behavior. The characteristics of fire in the boreal forest that affect these dynamics include fire intensity, size, frequency, and the amount of residual organic matter on the forest floor (Johnson 1992). Boreal forests have a fire regime characterized by very large crown fires that cause high mortality in tree populations (Heinselman 1981; Dix and Swan 1971; Rowe and Scotter 1973; Johnson 1992). Tree species that lack reproductive adaptations to fire must recolonize burned areas from adjacent unburned seed sources or from unburned residuals remaining within fires (Eberhart and Woodard 1987; Turner and Romme 1994). The limiting effects of dispersal distance on tree regeneration after fire have been observed in many forest ecosystems (Hill and Read 1984; Oliver 1981; Greene and Johnson 2000; Galipeau *et al.* 1997).

An aspect critical for regeneration is that seed availability and suitable microsites must coincide in space and time (Dix and Swan 1971; Zasada and Wurtz 1990). Unsuitable conditions for establishment after fire may greatly reduce the contribution of proximal seed sources (Purdy *et al.* 2002). Abiotic and biotic conditions after fire must also favor recruitment and subsequent seedling survival (Zasada and Gregory 1969; Purdy *et al.* 2002). Thus, the timing of regeneration, and ultimately the successional patterns exhibited by forest communities, may be affected by the interaction of regeneration niche and fire behavior.

Chronosequence studies have frequently been used to infer natural patterns of forest succession following fire in boreal forests (Dix and Swan 1971; Bergeron and Dubuc 1989; Simard *et al.* 1998). In such studies, the timing of regeneration, growth rate, and canopy dominance of species have been used to designate them as early, middle, or late succession species (Gutsell and Johnson 2002). Forest communities in which all tree species establish immediately after fire (i.e. most boreal communities) readily fit into the initial floristics succession model proposed by Egler (1954). The initial floristics model describes communities where the presence of a species is dependent on immediate colonization after disturbance because the conditions for establishment and survivorship are most favorable at that time (Egler 1954). In contrast, forests with species that require substrates that are not available after fire (i.e. decayed logs) and therefore dominate the canopy only later in succession, fit better in the relay floristics succession model (Egler 1954). The relay floristics model involves colonization and replacement of early successional species by later successional species that are more adapted to conditions in older disturbances (Egler 1954).

Mixedwood forests characterized by white spruce (*Picea glauca* Moench Voss) and either aspen (*Populus tremuloides* Michx.) or birch (*Betula papyrifera* Marsh.), occur on upland sites throughout the Mixedwood Ecoregion (Strong and Leggat 1992). Development of white spruce canopies is the principle driver of successional change in mixedwood communities because it modifies abiotic conditions and increases structural diversity (Stelfox 1995). Previous studies have suggested several tree successional pathways are possible depending on stand history attributes (Dix and Swan 1971; Kabzems and Louisier 1992; Youngblood 1995; Lieffers *et al.* 1996b; Kneeshaw and Bergeron 1996; Galipeau *et al.* 1997; Bergeron 2000); however, these studies lacked empirical evidence regarding these attributes. Hence, a study addressing the relative importance of factors that may exert the greatest influence on spruce establishment timing is necessary.

1.2 Timing of Regeneration – Conflicting Paradigms

Studies of white spruce recruitment have demonstrated that burned seedbeds are receptive (i.e. suitable for seedling establishment) for only three to five years after fire (Zasada and Gregory 1969; Zasada 1985; Coates *et al.* 1994) and receptivity declines during this period (Purdy *et al.* 2002). Fires must be of sufficient intensity to expose mineral soil, because thick organic substrates are unsuitable for regeneration (Nienstaedt and Zasada 1990; Purdy *et al.* 2002). Many studies have shown that most white spruce seeds are dispersed within 100 m of parent trees (Dobbs 1976; Zasada and Lovig 1983; Nienstaedt and Zasada 1990; Coates *et al.* 1994; Greene and Johnson 2000). White spruce requires living seed sources for regeneration because it lacks a seedbank (Heinselman 1981), and fires kill previously dispersed seed (Johnson 1992). Seedling survivorship increases dramatically after the first year, such that little mortality occurs after three to five years (Zasada *et al.* 1978; Wurtz and Zasada 2001).

Retrospective studies are useful in determining important regeneration periods over long time intervals (Pickett 1989). Age structures in mixedwood stands older than 60 years indicate that spruce regeneration may occur immediately after fire, gradually over time, or after delays exceeding 25 years (Dix and Swan 1971; Kabzems and Louisier 1992; Youngblood 1995; Lieffers *et al.* 1996b; Kneeshaw and Bergeron 1996; Galipeau *et al.* 1997; Bergeron 2000). An apparent discrepancy exists, however, between many of these studies of older forests and studies conducted up to five years after fire. Studies in older stands have reported apparent delays of five years before any spruce regeneration occurred (Youngblood 1995; Kneeshaw and Bergeron 1996; Lieffers *et al.* 1996b; Galipeau *et al.* 1997; Bergeron 2000), followed by increasing levels of ingress over time. In contrast, seedling recruitment studies show that immediate regeneration after fire generally ends after five years. It is unlikely that further regeneration occurs between 6 to 14 years after fire because organic seedbeds predominate and vegetation cover is higher (Purdy *et al.* 2002). This discrepancy has not been addressed and may be attributable to potential aging errors in older stands (Peters *et al.* 2002). Aging discrepancies may lead to the appearance of regeneration lags if assumptions about aging methodology are inaccurate (Desrochers and Gagnon 1997).

An important technique for the verification of aging errors is crossdating, which is the practice of identifying and correcting a lack of synchrony in ring sequences (Swetnam and Thompson 1985; Fritts and Swetnam 1989). Crossdating permits the confirmation of missing rings by visual and statistical comparison of ring width series with "dated" samples (i.e. trees where the origin date is known) (Swetnam and Thompson 1985). Crossdating has rarely been used in tree regeneration studies. Age underestimation of young trees has only recently been shown (Parent *et al.* 2000; Peters *et al.* 2002), and most regeneration studies analyze broad age classes rather than identifying individual cohorts. With the recent recognition that missing rings frequently occur in understory conifers such as black spruce (*Picea mariana* (Mill) BSP) (Desrochers and Gagnon 1997), balsam fir (*Abies balsamea* L.) (Parent *et al.* 2000), and white spruce (Peters *et al.*

2002; Gutsell and Johnson 2002), investigation into factors contributing to missing rings is warranted.

1.3 Importance of Masting

One aspect critical to seed availability after fire is the inter-annual variability in white spruce seed production. White spruce exhibits widespread and synchronous production of large seed crops at varying time intervals (Rowe 1955; Nienstaedt and Zasada 1990; Coates *et al.* 1994), which is a characteristic inherent to masting species (Silvertown 1980). Historical records demonstrate that there is significant synchrony during mast years (high cone crop years) in Alberta (Kemp and Keith 1970) and at distances up to 2500 km apart among species within the genus *Picea* (Koenig and Knops 1998). Dispersed seed within a mature white spruce stand can range between 2.5 and 4000 seeds / m^2, while cone production can range from 0 (pers. obs.) to 12,000 cones / tree (Waldron 1965; Nienstaedt and Zasada 1990). In mast years, most trees within a stand are producing cones, and many trees are producing large numbers of cones (Coates et al. 1994). Seed production can vary considerably between high seed years, as indicated by a 13-year study by Zasada (in Nienstaedt and Zasada 1990). Dispersed seed ranged between 1000 and 4000 seeds / m^2 (Zasada in Nienstaedt and Zasada 1990) in four years that could potentially be considered mast years, depending on regional synchrony and cone production in the year after masting.

The short period of seedbed receptivity after fire suggests that fire timing relative to mast years may greatly affect regeneration density. Little regeneration of white spruce may occur in non-mast years because masting species experience very high seed losses from seed predators (Peters 2000; Alden 1985; Coates *et al.* 1994). Short-term studies on natural regeneration of white spruce in cutblocks have shown that larger cohorts may occur in mast years than non-mast years (Lees 1963; Alden 1985; Wurtz and Zasada 2001). There is a dearth of information on natural regeneration after fire, and direct comparisons between fires and cutblocks are difficult. Fires differ from cutblocks in seedbed characteristics and vegetation recovery (Ehnes 1998), and seed predators may decline after fire (Sato 2000). If a mast year does not occur during the receptive period following fire, most spruce regeneration may occur much later, when substrates such as decayed logs become available or light increases. No previous study has determined whether fire timing relative to mast years affects long term regeneration patterns.

Considerable research has been done on the proximal trigger of masting in plants (e.g. drought) (Eis 1967; Piovesan and Adams 2001) and the evolutionary causes such as enhanced pollination and satiation of seed predators (Silvertown 1980; Nilsson and Wastljung 1987; Kelly and Sullivan 1997; Shibata *et al.* 1998). Surprisingly, there is little empirical evidence that masting is important to plant population dynamics. Studies that have investigated recruitment, have focused on seedling dynamics (Taylor and Aarssen 1989; Ida and Nakagoshi 1996; Sato 2000), thereby preventing conclusions about the long-term importance of individual mast cohorts to population age structure. The masting species in other studies have not had as specific substrate requirements as white spruce. The short window of opportunity for spruce regeneration after fire may mean a single mast cohort accounts for much of the regeneration that occurs. The persistence of spruce populations in mixedwood landscapes may hinge on a dynamic relationship between fire and mast events.

1.4 Successional Development of Mixedwoods

Patterns of ecological succession are frequently distinguished by when species assemblages occupy a site following disturbance (Egler 1954; Noble and Slatyer 1980). Different mechanisms are involved in mixedwood succession if trees establish on substrates that are available immediately after fire, versus substrates that become available later on. A delay in white spruce regeneration may occur between the time that post-fire microsites become unfavorable, and when logs are sufficiently decayed to support recruitment. Log decay in forests is facilitated over time by canopy closure and microclimate shifts (Cornett *et al.* 2001). The predominance of white spruce on post-fire substrates (initial regeneration) versus logs (delayed regeneration) could be used as an indication of whether initial floristics or relay floristics (characterized by facilitation processes) more accurately describes succession in mixedwoods.

Previous studies have suggested that the age structure of white spruce may be due to stand history attributes such as fire intensity, distance from seed sources (Lieffers *et al.* 1996a; Lieffers *et al.* 1996b; Kabzems and Lousier 1992), or the occurrence of mast years while post-fire seedbeds are receptive (Dix and Swan 1971). None of these hypotheses have been tested in boreal mixedwoods because stand history attributes were not known. A study of spruce regeneration in relation to stand history attributes is needed in order to distinguish the relative importance of substrate versus seed availability on age structure.

1.5 Persistence of Spruce Populations After Fire

A fundamental tenet of evolutionary theory is that organisms are adapted to their environment because natural selection favors the survival of individuals with advantageous traits (Darwin in Keeton and Gould 1986). Most boreal tree species are adapted to a severe and frequent fire regime, which is evident by little change in species composition within stands over many fire events (Johnson 1992; Greene and Johnson 1999). In contrast, white spruce lacks the typical adaptations for persistence in fire prone environments (such as serotiny or below-ground meristems) (Whelan 1995). Light, wind-dispersed seeds appears to be its primary mechanism of persistence, but regeneration is usually seed-limited beyond 100 m from surviving trees. The lack of a seedbank, high seed predation, and late onset of reproduction would appear to place it on a trajectory for extinction in the boreal forest where fires occur frequently.

The persistence of white spruce in mixedwoods is even more perplexing considering fire ignition and spread data which show it burns more than other species (Cumming 2000). One factor that may permit white spruce persistence is that it frequently occurs in aspen-dominated stands, which have extremely low susceptibilities of burning. Cumming (2000) hypothesizes that seed dispersal, regeneration, and growth of white spruce determine the amount of white spruce in mixedwoods, which in turn affects fire behavior and fire spread in mixedwoods. Currently, there is no evidence to indicate whether white spruce establishes better after fire on sites that were dominated by aspen or spruce before the fire, or whether pre-fire populations of spruce are usually replaced by spruce itself.

1.6 Thesis Outline and Objectives

This research was prompted by the apparent contradiction in the timing of white spruce regeneration between seedling recruitment studies and retrospective studies, and the need to reconcile previous research. Furthermore, there was a lack of empirical data on the importance of stand history influences on stand age structures. Rigorous hypothesis tests were needed to determine the underlying mechanisms of succession in mixedwoods. Finally, little attention has been given to the influence of masting on plant population dynamics despite considerable speculation that mast years are more important than non-mast years for regeneration.

The research contained in this thesis is presented in five main sections, followed by a concluding chapter. In Chapter 2, I address whether ground-level ring counts underestimate the true age of white spruce and whether aging errors increase with stand age. Fire selection criteria and sampling were designed so that stand history attributes would strengthen the identification of aging errors and show the effects of errors on the interpretation of age structure. I used rigorous crossdating techniques to verify aging accuracy. This aging work provided the foundation for chapters 3, 4, and 5. Browsing damage on aged trees prompted my investigation in Chapter 3 of snowshoe hares as a factor contributing to missing growth rings and underestimation of stem age. I used experiments with two intensities of clipping to simulate browsing.

In Chapter 4, I test whether burn timing relative to mast years and non-mast years has a lasting effect on white spruce density. This test addresses the importance of substrate deterioration on regeneration. I used fires up to 300 km apart to ensure that masting effects were tested at a regional level rather than locally. Age structures were used to verify the importance of mast cohorts. Chapter 5 tests the implications of work described in preceding chapters for the importance of immediate post-fire regeneration of white spruce to the successional development of mixedwoods. First, I established that a delayed regeneration pulse occurs on fire-killed logs. I then use age structures to test whether factors related to burn intensity, substrate suitability, or seed availability influence age structure, and ultimately successional pathway. In Chapter 6, I determine the concordance between pre- and post-fire populations of spruce. In this chapter, the importance of a dominant mast cohort to spruce replacement after fire is tested. I conclude the study with a review of my main findings, of the implications for mixedwood succession and mixedwood management, and of discussion topics requiring further research.

1.6.1 Use of terms

Throughout the thesis, I have used the term regeneration instead of recruitment when referring to trees that survived up until the time of sampling, thereby preventing confusion with seedlings that recruited after fire but subsequently died. These terms are frequently used interchangeably or only loosely in the literature. I have been careful to use the term cohort to refer to trees originating from individual years (e.g. mast year cohort). Frequently, cohort is used to refer to broad age classes spanning more than 20 years (e.g. initial cohort versus delayed cohort). In these cases, I used the terms initial regeneration and delayed regeneration instead. When referring to findings in other studies, I have been careful to use the appropriate terms as defined above, rather than what the authors used themselves.

1.7 Literature Cited

Alden, J. 1985. Biology and Management of White Spruce Seed Crops for Reforestation in Subarctic Taiga Forests. Fairbanks, Alaska, Inst. North. For., Agric. For. Exp. Sta., School of Agric. Land Res. Mgmt., University of Alaska, Fairbanks, AK.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology **81**: 1500-1516.

Bergeron, Y., and Dubuc, M. 1989. Succession in the southern part of the Canadian boreal forest. Vegetatio **79**: 51-63.

Coates, D.K., Haeussler, S., Lindeburgh, S., Pojar, R., and Stock, A.J. 1994. Ecology and silviculture of interior spruce in British Columbia. For. Canada, B.C. Min. For., B.C., Canada, FRDA Rep. 220.

Cornett, M.W., Puettmann, K.J., Frelich, L.E., and Reich, P.B. 2001. Comparing the importance of seedbed and canopy type in the restoration of upland *Thuja occidentalis* forests of northeastern Minnesota. Res. Ecol. **9**: 386-396.

Cumming, S.G. 2000. Forest type, fire ignition, and fire frequency in boreal mixedwood forests. Edmonton, Sust. For. Mgmt. Net. Working Paper 2000-11.

Desrochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? Can. J. For. Res. **27**: 1263-1267.

Dix, R.L., and Swan, J.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Can. J. Bot. **49**: 657-676.

Dobbs, R.C. 1976. White spruce seed dispersal in central British Columbia. For. Chron. **52**: 225-228.

Eberhart, K.E., and Woodard, P.M. 1987. Distribution of residual vegetation associated with large fires in Alberta. Can. J. For. Res. **17**: 1207-1212.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old field vegetation development. Vegetatio **4**: 412-417.

Ehnes, J.W. 1998. The influences of site conditions, age, and disturbance by wildfire or winter logging on species composition in naturally regenerating boreal plant communities and some implications for community resilience. PhD. Thesis, University of Manitoba, Winnipeg, MB.

Eis, S. 1967. Cone crops of white and black spruce are predictable. For. Chron. **43**: 247-252.

Fritts, H.C., and Swetnam, T.W. 1989. Dendroecology: A tool for evaluating variations in past and present forest environments. Adv. Ecol. Res. **19**: 111-187.

Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. **27**: 139-147.

Greene, D.F., and Johnson, E.A. 2000. Tree recruitment from burn edges. Can. J. For. Res. **30**: 1264-1274.

Gutsell, S.L., and Johnson, E. A. 2002. Accurately ageing trees and examining their height- growth rates: implications for interpreting forest dynamics. J. Ecol. **90:** 153-166.

Heinselman, M.L. 1981. Fire and succession in the conifer forests of North America. Pages 374-405 *In* D.C. West, H.H. Shugart, and D.B. Botkin, (eds.). Forest succession: concepts and application. Springer-Verlag, New York, N.Y., USA.

Hill, R.A., and Read, J. 1984. Post-fire regeneration of rainforest and mixed forest in western Tasmania. Aust. J. Bot. **32**: 481-493.

Ida, H., and Nakagoshi. 1996. Gnawing damage by rodents to the seedlings of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* in a temperate *Sasa* grassland-deciduous forest series in southwestern Japan. Ecol. Res. **11**: 97-103.

Johnson, E.A. 1992. Fire and Vegetation Dynamics: Studies from the North American boreal forest. Cambridge University Press, Cambridge, Great Britain.

Kabzems, R.D., and Lousier, J.D. 1992. Regeneration, growth and development of *Picea glauca* under *Populus* spp. canopy in the Boreal White and Black Spruce Zone, For. Canada, and B.C. Min. For., Victoria, B.C., FRDA Rep. 176.

Keeton, W.T., and Gould, J.L. 1986. Biological science. 4th ed. W.W. Norton & Company Inc., New York, N.Y., USA.

Kelly, D., and Sullivan, J.J. 1997. Quantifying the benefits of mast seeding on predator satiation and wind pollination in *Chionochloa pallens* (Poaceae). Oikos **78**: 143-150.

Kemp, G.A., and Keith, L.B. 1970. Dynamics and regulation of red squirrel

(*Tamiasciurus hudsonicus*) populations. Ecology **51**: 763-779.

Kneeshaw, D.D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. **26**: 888-898.

Koenig, W.D., and Knops, J.M.H. 1998. Scale of mast-seeding and tree-ring growth. Nature **396**: 225-226.

Lees, J.C. 1963. Partial cutting with scarification in Alberta spruce-aspen stands. For. Res. Branch. Dept. For., Ottawa, ONT., Pub. No. 1001.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K. and Stewart, J.D. 1996a. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. **72**: 286-292.

_____, Stadt, K.J., and Navratil, S. 1996b. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. **26**: 1002-1007.

Nienstaedt, H., and Zasada, J.C. 1990. *Picea glauca*. Pages 165-185 *In:* R.M.Burns and B.H. Honkala, (eds.). Silvics of North America. Vol. 1, Conifers. U.S. Dept. Agric. For. Serv., Agric. Handbook 654.

Nilsson, S.G., and Wastljung, U. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica* patches). Ecology **68**: 260-265.

Noble, I.R., and Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio **43**: 5-21.

Oliver, C.D. 1981. Forest development in North America following major disturbances. For. Ecol. Manage. **3**: 153-168.

Parent, S., Morin, H., Messier, C. 2000. Effects of adventitious roots on age determination in balsam fir (*Abies balsamea* (L.) Mill.) regeneration. Can. J. For. Res. **30**: 513-518.

Peters, S.H. 2000. The impact of small mammals on natural regeneration of white spruce after logging. M.Sc. Thesis, University of Alberta, Edmonton, AB.

Peters, V.S, Macdonald, S.E., and Dale, M.R.T. 2002. Aging discrepancies of white spruce affect the interpretation of static age structure in boreal mixedwoods. Can. J. For. Res. **32**: 1-6.

Pickett, S.T.A. 1989. Space-for-time substitution as an alternative to long-term studies. Pages 110-135 *In* G.E. Likens, (eds.). Long-term studies in ecology: approaches and alternatives. Springer-Verlag, Berlin.

Piovesan, G., and Adams, J.M. 2001. Masting behaviour in beech: linking reproduction and climatic variation. Can. J. Bot. **79**: 1039-1047.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fenn. **36**: 289-306.

Rowe, J.S. 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Ottawa, Dept. North. Affairs. Nat. Res., For. Res. Div. Tech. Note 3.

Rowe, J.S., and Scotter, G.W. 1973. Fire in the boreal forest. Quat. Res. **3**: 444-464.

Sato, T. 2000. Effects of rodent gnawing on the survival of current-year seedlings of *Quercus crispula*. Ecol. Res. **15**: 335-344.

Shibata, M., Tanaka, H., and Nakashizuka, T. 1998. Causes and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. Ecology **79**: 54-64.

Silvertown, J. 1980. The evolutionary ecology of mast seeding in trees. Biol. J. Linn. Soc. **14**: 235-250.

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

Stelfox, J. B. 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. AB Env. Centre, Can. For. Serv., Edmonton, AB, No. 001A.

Strong, W.L., and Leggat, K.R. 1992. Ecoregions of Alberta. AB For. Lands and Wild., Land Inf. Serv. Div., Edmonton, AB, T/245.

Swetnam, T.H., and Thompson, M.A. 1985. Using dendrochronology to measure radial growth of defoliated trees, USDA For. Serv., Handbook 639.

Taylor, K., and Aarssen, L. 1989. Neighbor effects in mast year seedlings of *Acer saccharum*. Am. J. Bot. **76**: 546-554.

Turner, M.G., and Romme, W.H. 1994. Landscape dynamics in crown fire ecosystems. Land. Ecol. **9**: 59-77.

Waldron, R.M. 1965. Cone production and seedfall in a mature white spruce stand. For. Chron. **41**: 316-329.

Whelan, R.J. 1995. The Ecology of Fire. Cambridge University Press. Cambridge, Great Britain.

Wurtz, T.L., and Zasada, J.C. 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. Can. J. For. Res. **31**: 999-1011.

Youngblood, A.P. 1995. Development patterns in young conifer-hardwood forests of interior Alaska. J. Veg. Sci. **6**: 229-236.

Zasada, J.C. 1985. Production, dispersal, and germination of white spruce and paper birch and first year seedling establishment after the Rosie Creek fire. University of Alaska, Fairbanks, Misc. Publ. 85.

Zasada, J.C., Foote, M.J., Deneke, F.J., and Parkerson, R.H. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination, and seedling survival. USDA. For. Serv., Pac. NW For. Exp. Sta., Gen. Tech. Rep. PNW-65.

Zasada, J.C., and Gregory, R.A. 1969. Regeneration of white spruce with reference to interior Alaska: a literature review. For. Serv., Pac. NW For. Exp. Sta. Gen. Tech. Rep. PNW-79.

Zasada, J.C., Lovig, D. 1983. Observations on primary dispersal of, *Picea glauca*, seed. Can. Field-Nat. **97**: 104-106.

Zasada, J.C. and Wurtz, T.L. 1990. Natural regeneration of white spruce on an upland site in interior Alaska. *In*: Hamilton E. (ed.). Vegetation management: an integrated approach. B.C., Canada, FRDA Rep. 109.

CHAPTER 2[1]

Aging Discrepancies of White Spruce Affect the Interpretation of Static Age Structure in Boreal Mixedwoods

---

2.1 Abstract

Post-fire regeneration of *Picea glauca* (Moench Voss) on boreal mixedwood sites appears to be highly variable over time because of wide ranges in size and ring counts amongst trees. Our objectives were to determine whether ground-level ring counts underestimate root collar age of understory *Picea glauca* and whether aging errors increase with stand age. Trees were collected from 7 to10 stands in each of three fires occurring in mast years between 1961-1991. Trees were cut at ground level, and the below-ground stumps were excavated, sectioned, and internally crossdated with skeleton plots after identifying the root-collar location. Ground-level disks were visually crossdated with a master chronology, which was constructed using the dendrochronology program "Cofecha". Crossdating demonstrated that ground-level ring counts underestimate age by a mean of 2.4 years (range of 0 - 6), and 6.3 years (range of 0 - 13) in 20 and 38-year-old stands respectively. Age-underestimation was significantly greater at the root collar than ground level due to more missing rings. Crossdated age structures showed that apparent regeneration lags in 20 and 38-year-old stands were artifacts of ground-level ring counts, and that the first year following fire was the most important year for establishment in all stand age classes. We conclude that errors in aging suppressed trees can lead to an inaccurate depiction of the timing of regeneration during early mixedwood stand development. Our results portray a different picture of *Picea glauca* succession and have important implications for forest management.

---

[1] This chapter has previously been published in a more abridged version. The paper's citation is: Peters, V.S., Macdonald, S.E., and Dale, M.R.T. 2002. Aging discrepancies of white spruce affect the interpretation of static age structures in boreal mixedwoods. Canadian Journal of Forest Research. 32: 1496-1501.

2.2 Introduction

Studies of forest regeneration dynamics frequently rely on retrospective approaches due to the long lifespan of trees (Harper 1977; Coates *et al.* 1994). Counts of annual growth rings at the base of felled trees are widely accepted as an accurate means of determining important establishment periods (Villalba and Veblen 1997). These techniques have been broadly applied in age or growth-related studies on white spruce (*Picea glauca* Moench Voss), particularly because its nonporous ring structure facilitates identification of annual rings (Phipps 1985), and it previously did not appear subject to biotic and abiotic factors that cause missing rings (locally absent rings) in other tree species. An apparent discrepancy exists, however, amongst studies on spruce regeneration timing which have examined mature to old mixedwood stands (60 to 160 years post-disturbance), versus studies conducted one to five years post-disturbance. Studies in mature stands in Alberta (Lieffers *et al.* 1996), Quebec, (Kneeshaw and Bergeron 1996; Galipeau *et al.* 1997; Bergeron 2000) and Alaska (Youngblood 1995) have reported apparent delays of 5 to 25 years before any spruce regeneration occurred after fire, followed by increasing levels of ingress over time. In contrast, seedling recruitment studies show that immediate post-fire regeneration generally ends after five years, irregardless of good seed production from nearby seed sources (Rowe 1953; Quaite 1956; Zasada 1985; Wurtz and Zasada 2001; Kabzems and Lousier 1992; Coates *et al.* 1994; Purdy *et al.* 2002).

The apparent discrepancy in the pattern of initial post-fire regeneration of white spruce in mixedwoods could arise from later recruitment on organic substrates (i.e. downed logs, leaf litter), as well as the same factors proposed to explain regeneration lags in black spruce: mortality of the initial cohort (Groot and Horton 1994) or potential aging errors in older stands (Black and Bliss 1980; Gagnon *et al.* 1992; Desrochers and Gagnon 1997). White spruce seeding trials on substrates similar to those found five or more years post-disturbance, have demonstrated that establishment and survivorship rates are very low (Delong *et al.* 1997; Stewart *et al.* 2000; Purdy *et al.* 2002). It is improbable that all initial recruits die, because seedling survivorship increases dramatically after the first year (Zasada *et al.* 1978; Wurtz and Zasada 2001; Purdy *et al.* 2002). Most authors consider a seedling which is alive after three to five years to be established, with only unusual disturbances (predation by herbivores, fire, etc.) accounting for subsequent mortality (Coates *et al.* 1994;

Aging discrepancies may lead to the appearance of regeneration lags if assumptions about aging methodology are inaccurate (i.e. the root collar is located at ground level [forest floor] and ring count equals age) (Desrochers and Gagnon 1997; Gutsell and Johnson 1999). Desrochers and Gagnon (1997) demonstrated that age at ground level underestimated true age in black spruce growing on upland boreal sites because root collars were located below ground level, and reverse taper (missing and compressed rings) prevented an accurate estimate of true age from a single location. The accumulation of leaf litter in mixedwoods could contribute to the same difficulties in locating the root collar zone of white spruce (Bergeron 2000), magnifying aging errors over time. In mixedwood stands white spruce may be suppressed because it faces sub-optimal light environments for growth (Coates *et al.* 1994; Constable and Lieffers 1996), competition (Kneeshaw and Bergeron 1996; Landhausser and Lieffers 1997; Kobe and Coates 1997; Landhausser and Lieffers 1998; Comeau pers. com.), and snowshoe hare browsing of saplings (Sinclair *et al.* 1993). Reductions in radial growth during extended periods of suppression (Kobe and Coates 1997) could increase the likelihood of annual growth rings failing to reach ground level with stand age (Villalba and Veblen 1997).

These potential sources of aging error, which are not accounted for with standard aging techniques, motivated this study. We carefully aged white spruce trees, including below-ground aging and crossdating, in mixedwood stands of varying time-since-fire and compared these to ground-level (humus soil level) ring counts. Our objectives were: 1) to determine the extent of aging errors associated with ground-level ring counts and whether aging errors increase with stand age, and 2) whether aging errors influence our interpretation of the timing of white spruce regeneration, and therefore of boreal mixedwood successional dynamics.

2.3 Study Area

The study area consisted of a 60,000 km^2 area in East central Alberta, North of Lac la Biche (54°46'N 111°8'W), and Athabasca (54°43'N 113°17'W)(Fig. 2.1). This area is situated within the Boreal Forest Natural Region and contains the Central

Mixedwood and Wet Mixedwood Natural Regions (A.E.P 1999). The canopies of study stands were dominated by trembling aspen (*Populus tremuloides* Michx.) or balsam poplar (*Populus balsamifera* L.), although paper birch (*Betula papyrifera* Marsh.) and jack pine (*Pinus banksiana* Lamb.) were present in several stands (Table 2.1). White spruce was the most abundant tree species in the understory of most stands, while black spruce (*Picea mariana* (Mill) BSP), paper birch, and balsam fir (*Abies balsamea* L.) were occasionally present.

The predominant soils on upland sites in this region are Gray Luvisols and Eutric Brunisols, which overlay a moraine landform of glacial till (Strong and Leggat 1992). Topography was undulating with a mean slope of 6 degrees, and a mean elevation of 647 m. Mean summer temperature is 13.5°C (May - August) while mean winter temperature is –13.2°C (November - February) (Strong and Leggat 1992). The mean annual precipitation is 397 mm, with most of the moisture falling as rain in July (240 mm) (Strong and Leggat 1992).

2.4 Methods

2.4.1 Fire selection and sampling

Fire selection criteria and sampling were designed so that stand history attributes would strengthen the identification of aging errors (Lorimer *et al.* 1999) and show the effects of errors on the interpretation of age structure. Aging techniques varied with stand age, thereby permitting more detailed aging approaches in older stands. Aging methodology is broken down into: 1) below-ground crossdating, in which the root collar is located, missing rings between ground level and the root collar are quantified, and contributing factors identified, and 2) above-ground aging, which identifies rings failing to reach ground level by making a master chronology, visually crossdating trees, and using "Cofecha" to assist crossdating decisions. Collection and aging methods of trees were refined after the 1998 field season when we realized that aging errors might occur. Some data from 1998 are included in this chapter because they provide evidence that standard aging techniques are inadequate for white spruce, and that this is a widespread problem. Throughout this chapter, we clearly identify which aging methods were used for samples collected in different years.

Fires occurring in 1991, 1979, and 1961 were selected from the Provincial Fire Database (Alberta Forest Management Division), and located using provincial fire maps (Delisle and Hall 1987; see Fig. 2.1), Phase 3 Forest Inventory Maps and ARC INFO fire coverages (Department of Environmental Protection 1996), and air photos (1961 - 1998). The fire years selected were synchronized to white spruce mast years to ensure a good seed supply in the year of the fire. Effects of burn timing relative to mast years on regeneration are being explored separately (see Chapter 4). Historical mast years in Alberta were identified using provincial cone collection records (Palamarek pers. com.), cone crop indices (Kemp and Keith 1970), Alberta based forestry publications, and provincial red squirrel trapping records (Todd 1979) which are significant correlates of cone crop ($r^2 = 0.911, p < 0.01$) (Kemp and Keith 1970). Peaks in red squirrel populations coincide with mast years (Kemp and Keith 1970). Additional fire selection criteria included a minimum size of 200 ha, seasonal occurrence between June 1 to Aug. 31, and canopy kill exceeding 95% in sampled stands. These criteria ensured that only crown fires with the potential to expose mineral soil microsites were sampled. Fires sampled ranged from 389 ha to 2845 ha.

Nine stands were sampled in both the 1991 and 1979 fires during the summer of 1998. These stands will henceforth be referred to as 7 and 19-year-old stands (YOS). In 1999, we sampled one additional stand from the 1979 fire, as well as 6 stands from a 1961 fire. These stands will henceforth be referred to as 20 and 38-year-old stands (YOS). All stands were comprised primarily of aspen and white spruce pre-fire. Burned stands were adjacent to unburned spruce seed sources containing trees which were seed producing at the time of the fire (seed sources were ≥ 55 years of age at breast height at the time of the fire). Stands were located between 300 m to 5 km apart, and originated primarily from independent seed sources. Three 2 m x 2.5 m plots were randomly located at both 20 m and 100 m from the seed source in each stand. Duff thickness and herb, shrub, and tree percent cover estimates were recorded in the plot. Five live post-fire origin spruce (all sizes) located nearest to the plot center were collected for aging, for a total of 30 trees per stand. The height of collected trees was measured, and trees exhibiting clipped leaders or branches from snowshoe hare browsing were noted.

2.4.2 Aging methods (root collar estimation)

In 1998, organic litter was removed from the base of trees in 7 and 19 YOS, and a disk was taken at the estimated root collar for aging (Table 2.2). In 7 YOS, the hypocotyl was usually visible above ground level; consequently, ground level closely approximated the root collar (base of the hypocotyl) and both ages were assumed to be the same. Counts of terminal bud scars were also used to age trees in 7 YOS. Initial budscars were not apparent on trees in 19 YOS so the root collar was estimated as the base of trees in the field. Preliminary analysis of below-ground tissues in the lab revealed that field estimates of the root collar location were not accurate; consequently, additional sampling and aging methods were included for the 20 and 38 YOS in 1999 (see Below-ground crossdating).

All disks under one centimeter in diameter were entirely scored with a fine razor blade and rubbed with chalk to improve cellular contrast (Desrochers and Gagnon 1997). Larger trees were first sanded with grits up to 200, and then two radii containing the greatest number of visible rings were scored and chalked (as above). When counts differed between radii due to partial rings, or when rings were unclear, specimens were rescored until all rings could be counted consistently. A binocular dissecting microscope (18 - 110 X magnification) was used for ring counts.

Below-ground crossdating

The 20 YOS and two 38 YOS (stands 2 and 3 were randomly chosen from all 38 YOS), were selected for below-ground crossdating (Table 2.2). Trees were cut at ground level and the entire below-ground portion of the trunk and main roots were collected. Ground level was defined as the top of the humus soil layer (i.e. recent leaves were flattened). In the lab, a disk was removed every two cm along the below-ground portion of the trunk. Below-ground crossdating of disks with skeleton plots was performed according to the procedures of Desrochers and Gagnon (1997), to determine if earlier growth years were located below ground (buried years), and the precise location of the root collar. The location of the root collar was determined by noting the shift from a pith (stem) to a central vascular cylinder with a diarch stele (root) (Esau 1960; Desrochers and Gagnon 1997) (Fig. 2.2). The actual root collar was usually situated within a disk;

therefore, the last disk exhibiting a pith on the upper surface was considered to be the root collar disk. Root collar ring count was obtained on this disk. Below-ground crossdating was performed at the tree level; thus disks were compared solely within individual trees (internal crossdating).

Growth rings that fail to deposit in the root collar region will also prevent the true age of a tree from being obtained by a ring count at the root collar (Desrochers and Gagnon 1997). Below-ground crossdating permitted the identification of missing rings. To determine if the number of missing rings at the root collar increase with stand age, missing rings were recorded for each tree. The failure of the most recent growth rings (outer rings) to deposit at the root collar is referred to as reverse taper (Desrochers and Gagnon 1997). Reverse taper was quantified by recording the number of outer rings (most recent years) that were missing in the root collar disk (Fig. 2.3). Rings missing above ground level (see Above-ground crossdating) were also missing in all below-ground sections, and were thus included in estimates of missing rings. To determine whether the length of buried trunk and adventitious rooting increased with stand age, we measured the distance of the root collar to the most distal adventitious root, and to ground level, along the curvature of the trunk midline.

Above-ground crossdating

To determine whether rings failed to reach ground level, trees from 38 YOS were crossdated above ground level. Visual crossdating was performed on ground-level disks from trees in 38 YOS (stands 2 and 3) using qualitative ring features (Swetnam and Thompson 1985) and a master ring width chronology according to Lorimer *et al.* (1999). Trees from the 20 YOS had insufficient signature years to warrant crossdating ground-level disks with a master chronology. A Parker's instrument micrometer (100 X magnification) was used for ring width measurement of ground-level disks from these stands. Ring width was measured to the nearest micron (0.001 mm), along the radius that contained the greatest number of rings and avoided the most compression wood. A value of zero was assigned to partial rings that were not bisected by the measured radius.

Due to the short time interval of ring sequences in 38 YOS, as well as the varying levels of suppression, a master chronology was constructed by using ring widths of ground-level disks from 14 trees in a 57 YOS (1942 origin) white spruce stand. The 57 YOS was located within 2 km of the sampled 38 YOS. This was a suitable reference stand because trees were exceptionally large, showed less suppression (greater likelihood of containing complete ring sequences), and were not producing cones yet, so annual growth sequences were not affected by mast crop history (Eis *et al.* 1965; Koenig and Knops 1998). Signature years (exceptionally wide and narrow rings) were identified from mean ring width plots (log transformed) of all reference trees (Lorimer *et al.* 1999). Dating errors were corrected in the master chronology by visual crossdating, and by verification with the dendrochronology software program "Cofecha", using the minimum segment length specifications (Holmes 1994). In 38 YOS, a 20-year segment length lagged 10 years, and a correlation level of 0.4, were used for identifying sections with potential dating errors relative to the master chronology. These parameters were lower than the minimum recommended parameters for Cofecha due to the short ring series analyzed; consequently, Cofecha was used solely to assist visual crossdating of trees with the master chronology. Several large trees in the 38 YOS dated back to the first year post-fire, and therefore contained a complete ring history (dated trees). These trees matched the master chronology as well as recommendations of Cofecha. Suppressed trees did not match the master chronology well and cannot be accurately crossdated with Cofecha; consequently, ring-width plots were also visually compared between dated trees and suppressed trees, working from the largest to the smallest (Lorimer *et al.* 1999). Trees at 20 and 100 m plots in each stand were crossdated separately in case additional variability occurred between sites. Poor matches with signature years prevented us from crossdating many of these trees; therefore, our estimates of missing rings are conservative.

2.5 Data Analysis

To test whether root collar depth below ground level, and the length of adventitious root development increased with time-since-fire, these values were compared between 20 and 38 YOS using one-tailed independent t-tests, for distributions with unequal homogeneity. One-way ANOVAS were used to test whether variability in duff thickness among stand ages could be a contributing factor. To test whether aging discrepancies changed with time-since-fire, two sample Kolmogorov-Smirnov tests (K-S tests) (two-tailed) were used to compare: age structure based on ground-level ring counts versus crossdated age, age structures among stand ages, ground level versus root collar ring count, and number of missing rings in 20 versus 38 YOS. Ground-level ring counts in 7 YOS were compared to the number of terminal bud scars with a paired t-test to compare similarity of age estimates. To test whether age structures in stands selected for crossdating were representative of other stands sampled, multiple comparisons were made between the 20 YOS (ground-level age) and seven of the nine 19 YOS (age at the estimated root collar); insufficient trees were found and aged in two 19 YOS to warrant statistical comparisons). K-S tests were used for pairwise comparisons of stands. Multiple comparisons of ground-level ring counts between the six 38 YOS stands were also conducted with K-S test. The appropriate Bonferroni corrections were applied to maintain an alpha level of 0.05 for all tests. This was the alpha level for detecting significant differences in all tests. Standard error of the mean is depicted by error bars in figures, and by the variation reported for mean values in tables. All statistical analyses were performed using SPSS version 10.0 (SPSS 1999).

2.6 Results

2.6.1 Location of root collar in relation to stand age

The root collar was located near ground level on white spruce trees in 7 YOS, but was located below ground in older stands. Most spruce seedlings in 7 YOS were located on mineral soil microsites with thin organic layers that rarely exceeded the height of the first year of growth (< 2.0 cm). Age estimates were significantly higher in 7 YOS when seedlings were aged by ground-level ring counts versus terminal bud scars (5.6 versus 5.2 years old respectively; $t = 2.840$, $df = 73$, $p = 0.006$). This may be attributable to difficulty identifying the first terminal bud scar on large seedlings that had greater bark development and no lateral branches until the second year. Ground-level ring count underestimated root collar age (based on skeleton plot only) by 2.4 years in 20 YOS, and by 3.8 years in 38 YOS. As many as 6 years of growth were buried below ground on trees in 20 YOS (range 0 - 6), and as many as 10 years on trees in 38 YOS (range 0 - 10). The root collar zone was located an average of 7.1 cm below ground level in 20 YOS (range = 0 to 15.6 cm), and an average of 11.1 cm (range = 2.2 to 44.1 cm) below ground in 38 YOS. The distance of the root collar below ground level was significantly greater in 38 YOS than 20 YOS ($t = 3.469$, $df = 73$, $p < 0.001$; not measured in 7 YOS).

The location of the root collar zone in 20 and 38 YOS was obscured by adventitious root development that occurred along buried portions of spruce trunks. Fallen fire-killed snags and snags of self-thinned aspen regeneration were observed on the lower stem of many spruce saplings, thereby compressing a portion of the trunk against the ground. Leaf litter subsequently covered this portion of trunk (pers. obs.). Trees that had resumed height growth, exhibited a bent stem below ground (Fig. 2.2) and had increased compression wood on the lower side of the trunk. Adventitious roots developed to within a mean of 1.5 cm from ground level on trees in 20 and 38 YOS. The distance from the most distal adventitious root to the root collar was significantly greater on trees in 38 versus 20 YOS ($t = 3.375$, $df = 73.2$, $p < 0.001$), although there were no significant differences in duff thickness among any of the stand ages ($F = 1.370$, $df = 46$, $p = 0.265$). Adventitious root development frequently corresponded to the portion of bent trunk below ground; however, trees with erect growth forms also showed some adventitious root development. In a number of cases where more than a quarter of the total stem length was bent and below ground level, adventitious roots near the ground provided the main rooting structure. Lateral roots just below the root collar were underdeveloped, and in some cases were already decomposing (Fig. 2.2).

2.6.2 Ground level age versus root collar age and crossdated age

An additional source of age underestimation at ground level in 38 YOS occurred from the failure of growth rings to deposit at ground level (missing rings). Prior to crossdating, correlation values of trees in most 38 YOS were low, with a mean of 62.2% flagged sections (sections with non-significant correlation to the master chronology). These values suggested that many trees were missing rings, and that the wide variation in growth between trees within stands reduced correlation (Table 2.3 and Appendix 2.1). After accounting for missing rings, correlation values improved at both locations in stand 2. In stand 3, correlation values decreased in the 20 m plot and did not change in the 100 m plot. The 20 m plot of stand 3 matched poorly with the master chronology; we noted that 73.3% of these trees had been browsed by snowshoe hare. Trees in stand 2 exhibited no browsing among live trees, and less growth variation between trees within the stand.

Visual crossdating with the master chronology indicated that 74.5% of trees in 38 YOS were missing an average of 2.5 rings (range 0 to10) at ground level (Table 2.3). An average total underestimation of 6.3 years (including 3.8 buried years from root collar to ground level) occurred with ground-level ring counts in 38 YOS (range 1 to 13).

The number of missing rings was greater at the root collar than it was at ground level. Rings missing at ground level in 38 YOS were missing in all below-ground sections. The frequency of trees with missing rings increased from 51.7% in 20 YOS to 90.9% in 38 YOS. Significantly more missing rings occurred at the root collar in trees from 38 YOS (4.5 ± 0.54 years) than 20 YOS (0.93 ± 0.32 years) ($t = 5.342$, $df = 78.7$, $p < 0.001$). Of these, a mean of 0.60 (0 - 7) and 0.03 (0 - 1) outermost rings were missing at the root collar in 38 and 20 YOS respectively. A reduction in stem diameter at the root collar versus ground level sections occurred in these trees due to missing rings and reduced radial growth of outer rings below ground. The mean number of missing rings was significantly greater in 38 YOS than 19 YOS ($Z = 2.038$, $n = 84$, $p \leq 0.001$). Overall, age underestimation was significantly worse at ground level than at the root collar (6.3 versus 4.7 years respectively; $t = -4.436$, $df = 54$, $p < 0.001$) in 38 YOS, despite a narrower range of age underestimation (0 to 13 versus 0 to 16 years, respectively) (Fig. 2.4).

Tremendous size variation occurred among trees recruiting at the same time. Trees aged 20 years old trees ranged in height between 22.7 - 165.6 cm in 20 YOS, while in 38 YOS, trees aged 36 years old ranged in height between 42.8 to 498.3 cm. A twenty-fold magnitude of variation occurred in mean ring widths between trees, which made ring counting very difficult in suppressed trees. Only trees aged 34 years old, and older had mean heights exceeding 1.3 m. This is typically regarded as the mean height of 14 or 15 year-old white spruce natural regeneration in Alberta's mixedwoods (Johnstone 1976b; Alberta Forestry Lands and Wildlife 1985; Alberta Forestry Lands and Wildlife 1991).

2.6.3 Aging error effects on determination of regeneration timing

There were significant differences in age distribution between ground-level ring counts and crossdated age estimates in 20 YOS ($Z = 2.232$, $n = 58$, $p < 0.001$), and 38 YOS ($Z = 2.670$, $n = 110$, $p < 0.001$). These differences reflect a shift in mean tree age and in the shape of the age distribution. Ground-level estimates of age suggested that regeneration commenced one year following fire on 7 and 20 YOS (Figures 2.5a and 2.5b respectively), while a 4 year delay was observed in the 38 YOS (Fig. 2.5d). After crossdating, the age distribution suggested a one year delay in regeneration for both the 20 and 38 YOS with the cohort arising from the mast year coinciding with the fire (seeds germinate the following year after cold stratification) now containing the greatest frequency of recruits (Figures 2.5c and 2.5e respectively). Without crossdating, only the 7 YOS showed an age structure dominated by a strong mast year cohort corresponding to the year following fire. Below-ground crossdating of trees in 20 YOS shortened the apparent regeneration period from 10 to 5 years. The timing of establishment on 20 YOS no longer differed significantly from any of the 7 YOS ($p > 0.05$ in all cases). Crossdating did not affect the apparent duration of regeneration in 38 YOS (32 versus 31 years for ground level and crossdated ages respectively); however, the period over which 80% of the regeneration appeared to occur decreased from 20 years to 11 years (55 trees sampled). Trees that established 20 or more years post-fire (crossdated age), accounted for 10.9% of regeneration. The two 19-year-old trees in 38 YOS (Fig. 2.5e) showed similar aging errors (2 and 4 years) to trees in 20 YOS.

Ground-level age distributions of stands randomly selected for determination of aging error, were representative of all other stands sampled in their respective age class. Age distributions did not differ significantly among any of the seven 19 YOS and the 20 YOS. Mean age of spruce regeneration based on ground-level ring counts ranged between 15.8 and 17.4 years (the outermost ring was omitted in the 20 YOS to standardize sampling period post-fire); however, age distributions did not differ significantly among any of the stands. In the 38-year-old stands, mean age of regeneration based on ground-level ring counts ranged between 18.4 and 27.8 years. A significant difference in age distribution existed between stand 1 and stand 7 ($Z = 1.716$,

$n = 59, p = .004$) (Table 2.4). Proportionately more spruce were recent seedlings in stand one than all other stands.

2.7 Discussion

2.7.1 Aging discrepancies in white spruce

The age of white spruce can not be precisely obtained by ring counts at ground level in young mixedwood stands in Alberta. Growth increments of naturally regenerating seedlings average less than two cm / year in the first three years (Coates *et al.* 1994); consequently, the first several years of height growth will be covered by leaf litter accumulation over time on mixedwood sites. Previous studies on black spruce and balsam fir in eastern boreal forests have documented that the root collar is located below the humus layer (Desrochers and Gagnon 1997; Ghent 1958). Organic matter accumulation over time led to as much as 19 and 35 years of age underestimation in 70 and 110-year-old stands of black spruce respectively (Desrochers and Gagnon 1997; Gagnon *et al.* 1992), and an error of 20 years in balsam fir (Parent *et al.* 2000) when these species were aged at ground level. While humus thickness did not increase significantly with time in our stands, it appeared more evenly distributed in 20 and 38 YOS than in 7 YOS, which still had some visible mineral soil (pers. obs.). The increase in length of buried stem tissue and number of buried growth years with time-since-fire may be due to snags falling on seedlings and saplings. Many burned snags were still suspended between 1 - 50 cm above ground in 20 YOS (17% cover in this stratum), while all burned snags were on the ground in 38 YOS. Furthermore, self-thinned aspen in the 38 YOS were heavy enough to compress portions of trunk against the ground. Organic matter accumulation and the development of large supporting adventitious roots obscured the length of buried trunk until trees were excavated. Adventitious roots prevented the accurate identification of the root collar in the field (Fig. 2.2).

Age estimation in white spruce is further complicated by the frequent occurrence of missing rings. Higher numbers of missing rings in older stands may be attributable to trees remaining in a suppressed state for a longer period of time (Villalba and Veblen 1997). Higher numbers of missing rings at the root collar than at ground level may be explained by the basipetal wave of ring formation failing to proceed all the way to the root collar in some years (Esau 1960; Knight 1961; Parent *et al.* 2000). Knight (1961) found that ring development is considerably delayed below ground. Buried stem portions in vigorous trees showed a 10 - 25% reduction in radial growth versus above-ground stem portions (Fayle 1968). Reduced radial growth below ground appeared to contribute to the number of missing rings at the root collar in white spruce. Reverse taper prevented the true age from being obtained at the root collar in black spruce and balsam fir, accounting for up to 20 missing rings (Desrochers and Gagnon 1997; Parent *et al.* 2001). In contrast, reverse taper accounted for only a small number of missing rings in white spruce. Missing outer rings can be identified easily; however, it became difficult to identify distinctive ring sequences that were critical for matching years between successive sections when narrow marker years disappeared (some of which were inner rings; see Fig. 2.4)

Limitations of skeleton plotting and crossdating techniques on suppressed trees can prevent the true age of trees from being determined (Cherubini *et al.* 1996; Desrochers and Gagnon 1997; Villalba and Veblen 1997; Mäkinen and Vanninnen 1999). We regard our crossdated age estimates as conservative for several reasons: 1) skeleton plots of successive sections did not match well in severely suppressed trees due to excessive compression wood and true age could not be determined; 2) within-stand master chronologies were constructed from ground level sections rather than from root collar sections (see methods); therefore, our ability to identify all missing rings by using skeleton plots could not be confirmed; 3) suppressed trees did not match master chronologies adequately to identify all missing rings by visual crossdating. Using Cofecha, we identified the same number of missing rings on the largest trees as visual crossdating (see methods), but can not be relied on for identifying the number of missing rings on suppressed trees (Lorimer *et al.* 1999). Mäkinen and Vanninen (1999) found dominant trees had greater ring width synchrony than smaller trees in tree ring chronologies. Factors contributing to suppression do not affect all trees evenly (i.e. asymmetric competition with size, only small trees are browsed by hares) (Parker 1984; Stoll *et al.* 1994). These factors may reduce radial growth for several years and prevent affected trees from responding to environmental conditions that synchronize annual ring widths (i.e. length of growing season, temperature, precipitation) (Fritts and Swetnam 1989; Mäkinen and Vanninen 1999). The apparent regeneration periods would likely be shorter if the "true age" of severely suppressed trees could be obtained. Age estimates obtained using these techniques must be regarded as minimums rather than true age (Desrochers and Gagnon 1997).

Missing rings are most frequently reported to occur in trees that are suppressed (Black and Bliss 1980; Carleton 1982; Cherubini *et al.* 1996; Lorimer *et al.* 1999). According to the standard correction factor of 15 years for white spruce to reach breast height, all trees in 20 YOS were suppressed because no trees reached breast height in this time period. Variations in suppression levels were evident in the tremendous height variability exhibited by trees of the same age (up to 11 fold even for adjacent trees). Highly suppressed trees (smallest mean ring widths) had the greatest number of missing rings. In mixedwood forests, such trees are below their light compensation point for a considerable portion of the summer (Man and Lieffers 1997; Messier *et al.* 1998), and depend heavily on photosynthetic gains in the deciduous leaf-off periods for growth (Constabel and Lieffers 1996). Height growth of understory conifers in aspen-dominated ecosystems is greatly reduced until the overstory breaks up (Palik and Pregitzer 1995).

Severe defoliation has been identified as an additional cause of missing rings (Ghent 1958; O'Neil 1963; Morin and Laprise 1997). Snowshoe hare browsing can keep white spruce crowns below winter browsing height for up to 60 years (Sinclair *et al.* 1993; pers. obs.). Simulated hare browsing of vigorous spruce in 20 YOS, caused failure to deposit a ring in up to 50 percent of trees (see Chapter 3, section 3.5). We propose that light limitation, coupled with severe clipping by snowshoe hare during cycle peaks (Sinclair *et al.* 1993), could be mechanisms that contribute to widespread missing ring occurrence in white spruce.

The average age underestimation of trees in 38 YOS (6.3 years) could account for the regeneration lags and extended regeneration duration observed in several non-crossdated older stands in previous studies (e.g. Youngblood 1995; Lieffers *et al.* 1996). Additional delays of up to two years would be expected depending on fire timing relative to the masting cycle (see Chapter 4, section 4.6.3). We suspect that aging errors are greater in older stands, and that they contribute to much of the variability that has been reported in regeneration timing; however, we do not believe that aging errors account for all regeneration lags (i.e. stands lacking seed sources at the time of the fire). Crossdating substantially shortened the time period over which most initial white spruce regeneration (trees establishing on immediate post-fire substrates) appeared to occur. Gagnon *et al.* (1992) also found that careful crossdating compressed regeneration periods dramatically for black spruce. It is likely that all stands in our study are subject to aging discrepancies, since stands selected for crossdating exhibited similar ground- level age distributions as most other sampled stands (section 2.6.3). Greater variation in age observed in 38 YOS than other age classes was likely due to the occurrence of some delayed seedling establishment on decayed logs (see Chapter 5, section 5.6.1), as was the case in several previous studies (Rowe 1955; Kabzems and Lousier 1992; Lieffers *et al.* 1996; Simard *et al.* 1998).

2.7.2 Interpreting static age structure

The usefulness of static age structures for inferring regeneration dynamics of any population is affected by the technical difficulty of obtaining the true age of individuals (Harper 1977). Our results clearly demonstrate that these difficulties apply to white spruce. The aging technique used, and the stand age, both influenced the apparent regeneration pattern. Ground-level ring counts in young stands (up to 7-years-old) can accurately identify the short duration of initial regeneration, the importance of individual mast years for regeneration, and the decline in seed bed receptivity with time (e.g. Quaite 1956; Wurtz and Zasada 2001; Coates *et al.* 1994; Purdy *et al.* 2002). Our results support the importance of these processes. Ground-level ring counts are inadequate in 20 YOS; they suggest that seedbed receptivity does not decline rapidly, and that more years contribute substantially to regeneration (e.g. Johnstone 1976a). We regard below-ground crossdating as adequate to accurately portray factors affecting regeneration in this age class because establishment patterns post-fire resembled those of 7 YOS. Ground-level aging is misleading in 38 YOS, and is likely worse in older stands. Ground-level ages may lead to false conclusions that immediate post-fire substrates were not suitable, a seed source was not available, or all seedlings establishing in the first three years died. Ground-level ages do not show the stem exclusion phase (6 to 20 years post-fire) observed in the 20 YOS, nor do they accurately show the period of greatest regeneration. Marked increases in missing rings between 20 and 38 YOS suggests that this is an important time for missing ring occurrence in suppressed spruce. We recommend that intensive crossdating both above and below ground be used to obtain accurate estimates of white spruce age structure in boreal mixedwood stands greater than 20 years of age.

Previous studies on the regeneration ecology of white spruce have not highlighted the contradiction between regeneration lags and continuous regeneration patterns. Acceptance of these different patterns may be attributable to uncertainty regarding seed source presence at the time of the fire, masting history, adequate substrate availability following disturbance, and disturbance date (Kabzems and Lousier 1992; Lieffers *et al.* 1996). By ensuring that these factors were known, our test of aging error effects on apparent regeneration lags was strengthened. We recommend that studies that use tree ages to understand regeneration dynamics, in addition to following the crossdating procedures described here, control for as many abiotic and biotic factors as possible. This will help to eliminate erroneous conclusions.

2.8 Conclusions

The magnitude of age underestimation occurring at ground level in young white spruce trees demonstrates why considerable uncertainty exists in its regeneration timing. Crossdating demonstrated that an immediate post-fire cohort of white spruce dominates the age structure in young mixedwood stands when intense burns coincide with mast years, and seed sources are nearby. Age structures probably vary under different conditions, however aging errors will also be prevalent. Successional models of mixedwood development need to use crossdated age structures to distinguish the importance of initial regeneration from subsequent ingress on log substrate. Ring counting at ground level and the root collar does not provide an accurate age in young stands between 19 to 38 years old. Ring count at breast height is very likely far worse, and errors may magnify the older a stand gets (see Chapter 4, Table 4.9). Given the reliance of the softwood industry on white spruce, we advocate that additional crossdating studies be performed in different stand types and geographic locations to assess the prevalence of age underestimation. Our results suggest that provincial growth and yield curves based on fire-origin stands (Alberta Forestry Lands and Wildlife 1985) need to be adjusted, and harvesting cycles may need to be lengthened in order to reflect juvenile development periods that are considerably longer and more variable than currently assumed.

Table 2.1: Mean basal area of canopy tree species (± 1 standard error) in study stands based on prism counts at breast height level (1.3 m). White spruce regeneration did not occur in prism counts.

Fire●	Number of stands	Aspen (m^2/ha)	Balsam poplar (m^2/ha)	Paper birch (m^2/ha)	Jack pine (m^2/ha)	Balsam Fir (m^2/ha)
1991	9	0.51 ± 0.28	0.26 ± 0.26			
1979	1	3.44		3.44	1.15	
1961	2	0.57 ± 0.57	35.59 ± 13.82	6.89 ± 1.15		0.57 ± 0.57

● Basal area values are for the sub-sample of stands that were crossdated. Crossdating was not performed in 1991 origin stands and all stands sampled were included in basal area values.

Table 2.2: Number of stands aged using different methods for each stand age. For many stands, trees were cut at a location estimated to be the root collar in the field, and were then aged (see■). The remaining stands were aged at ground level and also crossdated below ground. A sub-sample of stands 38-years-old and older were crossdated above ground.

Fire*	Stand Age (years-old)	**Number of Stands** Aged at ground level	 Crossdated with below-ground skeleton plots	 Crossdated above ground with reference stand□
1991	7	9■	0	0
1979	19	9■	0	0
1979	20	1	1	0
1961	38	6	2	2
●	57	1	1	1

---

* The 1991 fire was sampled in 1998 (7 years old), and nine stands from the 1979 fire were also sampled in 1998 (19 years-old). The remaining stands were sampled in 1999 on the same 1979 fire, a 1961 fire, and a fire that occurred in 1942 or earlier (20, 38, and 57 years old).

● Reference stand containing complete ring sequence between 1961 - 1999 (master chronology). oldest spruce measured; there was no fire evidence to confirm exact stand age.

■ Cut at the estimated root collar in the field

□ Accuracy verified with Cofecha

Table 2.3: Number of missing rings and mean ring width at ground level in 38-year-old stand that were visually crossdated with the master chronology. Within stands, crossdating was performed separately for trees in plots located 20 m versus 100 m from the seed source.

Stand # - Distance (m)	Mean # of missing rings	Mean ring width (mm)
2-20	2.9 ± 2.6	0.329 ± 0.068
2-100	0.6 ± 0.8	0.318 ± 0.050
3-20	3.1 ± 3.2	0.281 ± 0.052
3-100	3.2 ± 2.8	0.271 ± 0.081
Master●	0.36 ± 0.24	1.12 ± 0.189

● Reference stand used for master chronology (approximately 57 years old)

Table 2.4: Mean age estimate of white spruce regeneration in 38-year-old stands, based on ground-level ring counts.

	Stand 1	Stand 2	Stand 3	Stand 4	Stand 6■	Stand 7
Mean age (years)	21.9 ± 1.1●	25.2 ± 1.5	23.9 ± 1.0	24.0 ± 1.7	18.4 ± 2.1	27.8 ± 0.9●
Sample size (trees)	29	29	29	30	15	30

● Significant difference between stands ($p \leq 0.05$)

■ Stand 6 was omitted from statistical analysis due to insufficient sample size

Note: Stand 5 was omitted because it originated prior to 1961

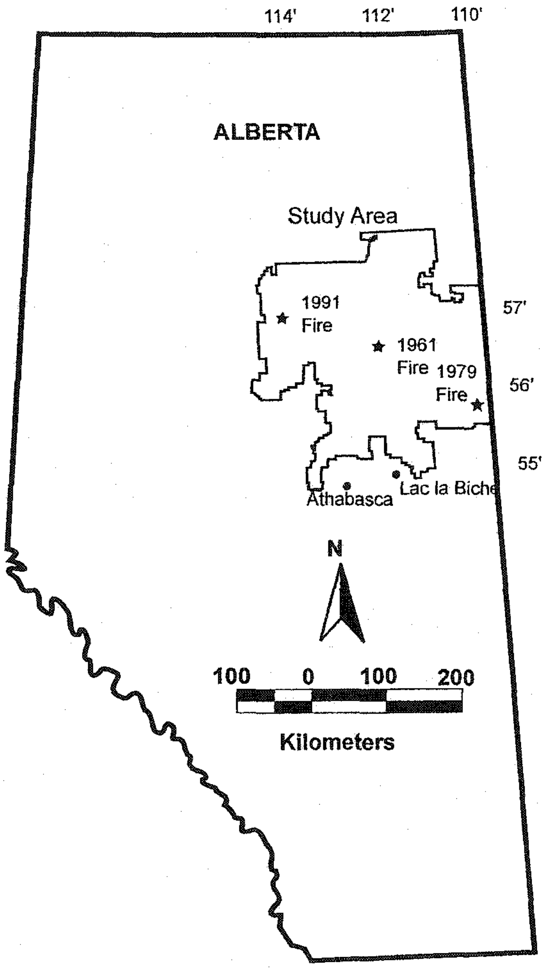


Figure 2.1 Map of study area in Eastern Alberta showing location of fires (stars).

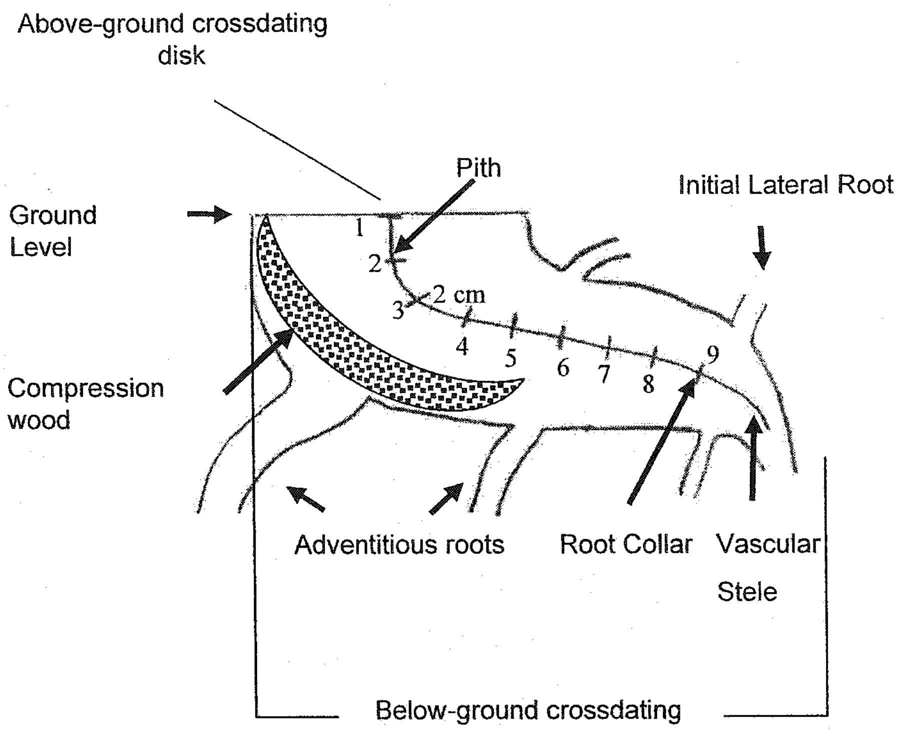


Figure 2.2: Stem position below ground on a tree exhibiting a bent growth form. Aging techniques used are shown relative to location of stem sections. Numbers 1-9 show location of sectioned disks (Modified from Desrochers and Gagnon 1992).

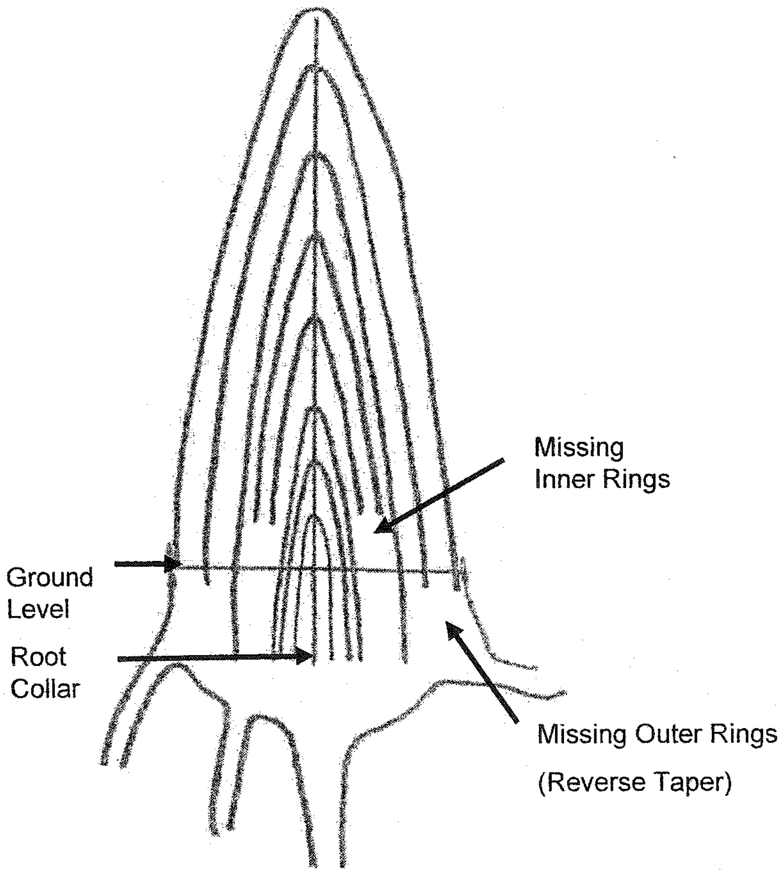


Figure 2.3: An example of missing rings and their location relative to ground level and the root collar (Modified from Desrochers and Gagnon 1997).

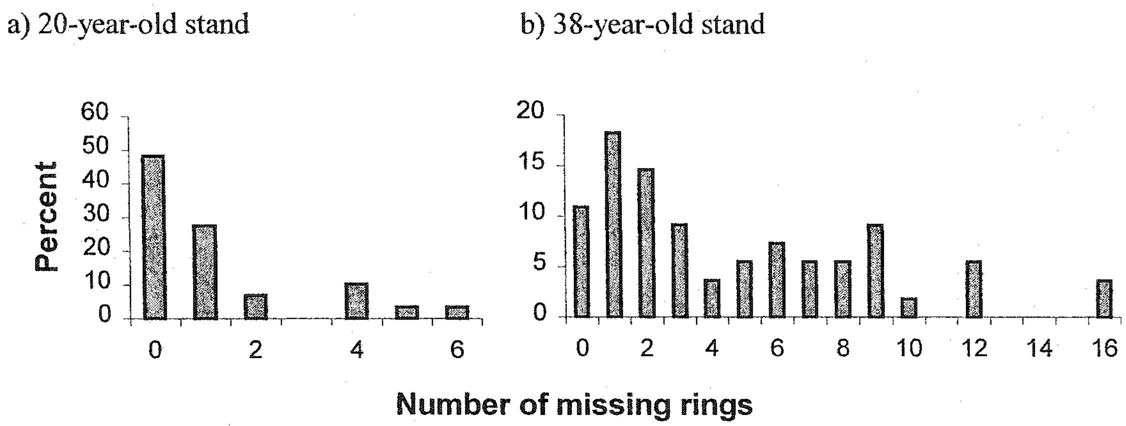
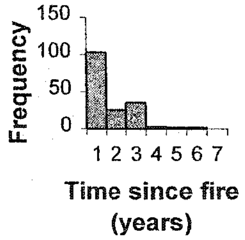


Figure 2.4: Frequency of missing rings occurring at the root collar in 20 YOS (Stand 10, n = 29 trees) and 38 YOS (stands 2 and 3, n = 55 trees). Below-ground crossdating was performed in all stands, while above-ground crossdating was also performed in 38 YOS.

Ground Level Timing (ring counts) **Crossdated Timing**

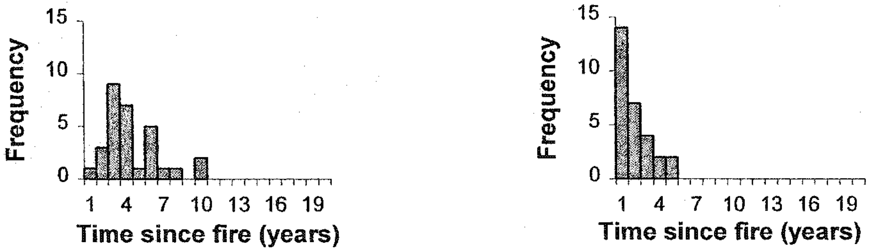
7-year-old stands (stands 1 - 9), n = 172 trees

a)



20-year-old stand (stand 10), n = 29 trees

b) c)



38-year-old stands (stands 2 and 3 combined), n = 55 trees

d) e)

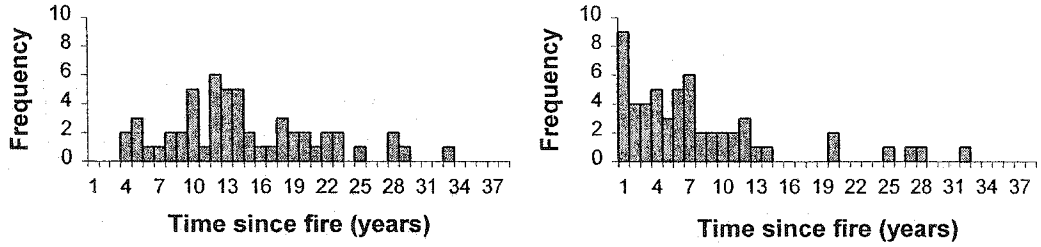


Figure 2.5: Comparison of white spruce regeneration timing as inferred from ground-level ring counts in a) nine 7 YOS, b) one 20 YOS, and d) two 38 YOS, versus c) below-ground crossdating in one 20 YOS, and e) below and above-ground crossdating in two 38 YOS.

2.9 Literature Cited

Alberta Environmental Protection. 1999. Natural regions and sub-regions of Alberta. AB. Nat. Heritage Inf. Centre, Edmonton, AB.

Alberta Forestry Lands and Wildlife. 1985. Alberta phase 3 forest inventory - An Overview. AB. For. Serv., Edmonton, AB.

Alberta Forestry Lands and Wildlife. 1991. Alberta vegetation inventory standards manual version 2.1. Land Inf. Serv. Div., Resource Inf. Branch.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology. **81**: 1500-1516.

Black, R.A. and Bliss, L.C. 1980. Reproductive ecology of *Picea mariana* (Mill) BSP at tree line near Inuvik, Northwest Territories. Ecological Monographs. 50: 331-354.

Carleton, T.J. 1982. The pattern of invasion and establishment of *Picea mariana* (Mill) BSP at tree line near Inuvik, Northwest Territories. Ecol. Monogr. **50**: 331-354.

Cherubini, P., Piussi, P., and Schweingruber, F. 1996. Spatiotemporal growth dynamics and disturbances in a subalpine spruce forest in the Alps: a dendroecological reconstruction. Can. J. For. Res. **26**: 991-1001

Coates, D.K., Haeussler, S., Lindeburgh, S., Pojar, R. , and Stock, A.J. 1994. Ecology and silviculture of interior spruce in British Columbia. For. Canada, B.C. Min. For., B.C., Canada, FRDA Rep. 220.

Comeau, P. 2001. Competition dynamics and competition management in young mixedwood stands. Oral presentation, Landscape ecology seminar series, Jan. 11. University of Alberta, Edmonton, AB.

Constable, A.J. , and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. of For. Res. **26**: 1008-1114.

Delisle, G.P., and Hall, R.J. 1987. Forest fire history maps of Alberta, 1931 to 1983. Can. For. Serv., Northern Forestry Centre, Edmonton, AB.

Delong, H.B., Lieffers, V.J., and Blenis, P.V. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can. J. For. Res. **27**: 1452-1457.

Department of Environmental Protection. 1996. Fire Incidence Database. AB. Land and For. Serv., For. Prot. Div., Edmonton, AB.

Desrochers, A. , and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? Can. J. For. Res. **27**: 1263-1267.

Eis, S., Garman, E.H., and Ebell, L.F. 1965. Relation between cone production and diameter increment of douglas fir (*Pseudotsuga menziesii* (Mirb) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and western white pine (*Pinus monticola* Doug.). Can. J. Bot. **43**: 1553-1559.

Fayle, D.C.F. 1968. Radial growth in tree roots; distribution - timing - anatomy. Faculty of Forestry, University of Toronto, Toronto, ONT, Tech. Rep. No. 9.

Esau, K. 1960. Anatomy of seed plants, John Wiley & Sons, Inc., New York.

Fritts, H.C., and Swetnam, T.W. 1989. Dendroecology: A tool for evaluating variations in past and present forest environments. Adv. Ecol. Res. **19**: 111-187.

Gagnon, R., Villeneuve, G., Morin, H., and St-Pierre, H. 1992. Dating mistake of mature black spruce (*Picea mariana*) after fire and their impact on population dynamics studies. In Disturbance Dynamics in Boreal Forest Workshop, 10-14 Aug. 1992, Umea, Sweden, University of Umea.O. *Edited by* Engelmark and R. Bradshaw. Umea.

Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. **27**: 139-147.

Ghent, A.H. 1958. Studies of Regeneration in Forest Stands Devastated by the Spruce Budworm. For. Sci. **4**: 135-146.

Groot, A., and Horton, B.J. 1994. Age and size structure of natural and second-growth peatland *Picea mariana* stands. Can. J. For. Res. **24**: 225-233.

Gutsell, S.L., Johnson, E. A. 1999. Testing the assumptions of methods used to infer patterns of forest succession. *In* Proceedings of the Sustainable Forest Management Network Conference, Science and Practice: Sustaining the Boreal Forest, 14-17 Feb. 1999, Edmonton AB. *Edited by* Terrence S. Veeman, Daniel W. Smith, Brett G. Purdy, Fional J. Salkie, and Gillian A. Larkin. Sustainable Forest Management Network, Edmonton, AB. pp. 500-506.

Harper, J.L. 1977. Population Biology of Plants, Academic Press, London

Hogg, E.H., and Schwarz, A.G. 1999. Tree-ring analysis of declining aspen stands in West-Central Saskatchewan. Edmonton, Northern Forestry Centre, Can. For. Serv. Inf. Rep. NOR-X-359.

Holmes, R.L. Cofecha Software Program. The Laboratory of Tree-Ring Research. University of Arizona. http:www.ltrr.arizona.edu/software.html.

Johnstone, W.D. 1976a. Ingress of lodgepole pine and white spruce regeneration following logging and scarification in west-central Alberta. Edmonton AB, Inf. Rep. NOR-X-170.

_______, W.D. 1976b. Juvenile height growth of white spruce and lodgepole pine following logging and scarification in west-central Alberta. Env. Canada, Can. For. Ser. Edmonton, AB, Inf. Rep. NOR-X-171.

Kabzems, R.D., and Lousier, J.D. 1992. Regeneration, growth and development of *Picea glauca* under *Populus* spp. canopy in the boreal white and black spruce zone. Forestry Canada and B.C. Min. For., Victoria, B.C., FRDA Rep. 176.

Kemp, G.A., and Keith, L.B. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology **51**: 763-779.

Kneeshaw, D.D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest Can. J. For. Res. **26**: 888-898.

Knight, R.C. 1963. Taper and secondary thickening in stems and roots of the apple. East Malling Res. Stn. Ann. Rep. 1960.

Kobe, R.K., and Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can. J. For. Res. **27**: 227-236.

Koenig, W.D., and Knops, J.M.H. 1998. Scale of mast-seeding and tree-ring growth. Nature **396**: 225-226.

Landhausser, S.M., and Lieffers, V.J. 1997. Seasonal changes in carbohydrate storage and regrowth in rhizomes and stems of four boreal forest shrubs applications in Picea glauca understorey regeneration. Scand. J. For. Res. **12**: 27-32.

Landhausser, S.M., and Lieffers, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Can. J. For. Res. **28**: 396-401.

Lieffers, V.J., Stadt, K.J., and Navratil, S. 1996. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. **26**: 1002-1007.

Lorimer, C.G., Dahir, S.E., and Singer, M. 1999. Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. Plant Ecology. **143**: 189-202.

Mäkinen, H., and Vanninen, P. 1999. Effect of sample selection on the environmental signal derived from tree-ring series. For. Ecol. Manage. **113**: 83-89.

Man, R., and Lieffers, V.J. 1997. Seasonal photosynthetic responses to light and temperature in white spruce (Picea glauca) seedlings planted under an aspen (Populus tremuloides) canopy and in the open. Tree Physiol. **17**: 437-444.

McBride, J. 1983. Analysis of tree rings and fire scars to establish fire history. Tree-Ring Bull. **43**: 51-67.

Messier, C., Parent, S., and Bergeron, Y. 1998. Effects of overstory and understory vegetation on the understory light environment in mixed boreal forests. J. Veg. Sci. **9**: 511-520.

Morin, H., and Laprise, D. 1997. Seedling bank dynamics in boreal balsam fir forests. Can. J. For. Res. **27**: 1442-1451.

Noble, D.L., and Ronco, F.J. 1978. Seedfall and establishment of Engelmann spruce and subalpine fir in clearcut openings in Colorado, USDA For. Serv., Rocky Mountain For. Range Exp. Sta., Res. Paper RM-200.

O'Neil, L.C. 1963. The suppression of growth rings in jack pine in relation to defoliation by the Swaine jack-pine sawfly. Can. J. Bot. **41**: 227-235.

Palik, B.J., and Pregitzer, K.S. 1995. Height growth of advance regeneration under an even-aged bigtooth aspen (*Populus grandidentata*) overstory. Am. Midl. Nat. **134**: 166-175.

Parent, S., Morin, H., Messier, Christian. 2000. Effects of adventitious roots on age determination in balsam fir (*Abies balsamea* (L.) Mill.) regeneration. Can. J. For. Res. **30**: 513-518.

Parker, G.R. 1984. Use of spruce plantations by snowshoe hares in New Brunswick. For. Chron. **60**: 162-166.

Phipps, R.L. 1985. Collecting, Preparing, Crossdating, and Measuring Tree Increment Cores. U.S. Geological Survey, Water Resources Investigations, Lakewood, CO, Rep. 85-4148.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fenn. **36**: 289-306.

Quaite, J. 1956. Survival of white spruce seedlings resulting from scarification in a partially cut mixedwood stand. For. Res. Div., Calgary, AB, Tech. Note 44.

Rowe, J.S. 1953. Delayed germination of white spruce seed on burned ground. For. Branch Dep. Resources and Development, Winnipeg, MB. Silvicultural Leaflet 84.

Rowe, J.S. 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Ottawa, Dept. North. Affairs. Nat. Res., For. Res. Div. Tech. Note 3.

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

Sinclair, A.R.E., Gosline, J.M., Holdsworth, G., Krebs, C.J., Boutin, S., Smith, J.N.M., Boonstra, R. , and Dale, M. 1993. Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. The Am. Nat. **141**: 173-198.

SPSS 1999. SPSS for windows release version 10.0. Chicago, IL.

Stewart, J.D., Landhausser, S.M., Stadt, K.J., and Lieffers, V.J. 2000. Regeneration of white spruce under aspen canopies: seeding, planting and site preparation. West. J. App. For. 15: 177-182.

Stoll, P., Weiner, J., and Schmid, B. 1994. Growth variation in a naturally established population of *Pinus sylvestris*. Ecology **75**: 660-670.

Strong, W.L., and Leggat, K.R. 1992. Ecoregions of Alberta. AB For., Lands and Wild., Land Inf. Serv. Div., Edmonton, AB, T/245.

Swetnam, T.H., and Thompson, M.A. 1985. Using dendrochronology to measure radial growth of defoliated trees, USDA For. Serv., Handbook 639.

Todd, A.W. 1979. A Review of Alberta Fur Production and Management 1920-21 to 1977-78. AB. Energy and Nat. Resources, Fish and Wild. Div.

Villalba, R., and Veblen, T.T. 1997. Improving estimates of total tree ages based on increment core samples. Ecoscience **4**: 534-542.

Wurtz, T.L., and Zasada, J.C. 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. Can. J. For. Res. **31**: 999-1011.

Yamaguchi, D.K. 1991. A simple method for cross-dating increment cores from living trees. Can. J. For. Res. **21**: 414-416.

Youngblood, A.P. 1995. Development patterns in young conifer-hardwood forests of interior Alaska. J. Veg. Sci. **6**: 229-236.

Zasada, J.C. 1985. Production, dispersal, and germination of white spruce and paper birch and first year seedling establishment after the Rosie Creek fire. University of Alaska, Fairbanks, Misc. Publ. 85.

Zasada, J.C. and Gregory, R.A. 1969. Regeneration of white spruce with reference to interior Alaska: a literature review, U.S. Dep of Agriculture Forest Service. Pac. NW For. Exp. Sta. Gen. Tech. Rep. PNW-79.

Zasada, J.C., Foote, M.J., Deneke, F. J., and Parkerson, R. H. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination, and seedling survival. USDA For. Serv., Pac. NW For. Exp. Sta., Gen. Tech. Rep. PNW-65.

Zasada, J.C. and Wurtz, T.L. 1990. Natural regeneration of white spruce on an upland site in interior Alaska. In: Hamilton E. (ed). Vegetation management: an integrated approach. B.C., Canada, FRDA Rep. 109.

CHAPTER 3[2]

Effects of Simulated Snowshoe Hare Browsing on Annual Ring Deposition in White Spruce

---

3.1 Abstract

White spruce (*Picea glauca*) trees are browsed extensively by snowshoe hares (*Lepus americanus*) during population cycle peaks. Browsing may contribute to missing ring occurrence in white spruce if the trees are sufficiently suppressed. Our objectives were to determine whether browsing severity affected ring width and caused missing rings during the year that browsing occurred. In the early spring of 2000, we used clipping experiments with two severity categories (15 trees per treatment) to simulate hare browsing in both a 20- and 59-year-old stand. At the end of one growing season, ground-level disks from clipped trees were visually crossdated by comparison to unclipped control trees (15 trees per stand) using the skeleton plot method. Trees from the more severe clipping treatment in the 20-year-old stand had significantly thinner growth rings in 2000 than control trees, while the ring widths did not differ in less severely clipped trees (ring width not measured in the 59-year-old stand). In the younger stand, both clipping treatments caused a significant number of trees to fail to deposit the year 2000 growth ring (29% and 50% of crossdated trees for low and high severity clipping, respectively). In the older stand, a significant number of trees in the more severe clipping treatment failed to deposit a ring in 2000 (27% of trees). We are less confident in the accuracy of crossdating in the older stand because trees were very suppressed. Several alternative aging techniques are suggested for suppressed trees. Our results suggest that repetitive hare browsing can lead to considerable age underestimation in white spruce, and influence successional development of mixedwoods.

---

[2] This chapter is my own written version of work that Paul Fuellbrant assisted me in, and submitted in December 2000 for an honor's thesis project. I designed this project, participated in data collection, and co-supervised him along with Ellen Macdonald.

3.2 Introduction

Age estimation of white spruce in boreal mixedwood stands of Alberta is complicated by the occurrence of missing rings in most trees in 38- to 59-year-old stands (Peters *et al.* 2002; see Chapter 4). The frequency of missing rings increases with time since fire, and is most pronounced in suppressed trees (Peters *et al.* 2002). There are many factors that may cause suppression in white spruce (Berry 1982; Quiring and McKinnon 1999; Wang and Huang 2000), but none of them have been investigated as sources of aging error. Browsing by snowshoe hares causes suppression in white spruce seedlings (Quiring and McKinnon 1999) and may affect age estimation in older trees.

One of the main factors leading to suppression in tree species is low light availability (Berry 1982). Suppression leads to a reduction in radial growth (Kobe and Coates 1997), but may also cause missing rings (locally absent rings) in subcanopy trees (Lorimer *et al.* 1999). Extended periods of reduced growth increase the likelihood that annual growth rings will fail to reach ground level as stands age (Villalba and Veblen 1997). Snowshoe hare browsing does not stimulate growth in white spruce (Smith *et al.* 1988); therefore, browsed spruce may be unable to grow above understory vegetation that attenuates light in addition to canopy influences (Lieffers and Stadt 1994). Peters *et al.* (2002) found that the majority of white spruce sampled in northeastern Alberta remain in a suppressed state for several decades, and required an average of 34 years to exceed 1.3 m in height.

White spruce is not a species preferred by snowshoe hares (Smith *et al.* 1988); however, it is browsed extensively during cycle peaks that occur every 9 to 11 years (Sinclair *et al.* 1993; Krebs *et al.* 1986; Boutin *et al.* 1995). During one hare cycle in Kluane, Yukon, at least 51% of the available terminal leaders were snipped by hares between the buildup and crash of the hare population (1979-1982) (Sinclair *et al.* 1993). Hares browse spruce primarily during the winter, at heights up to 1.2 m or 2 m, depending on the snow pack depth (Pease *et al.* 1979; Smith *et al.* 1988; Parker 1984; Oldemeyer 1983). Hare browsing leaves a distinctive angular cut, and may include browsing of both the terminal leader and lateral branches (Pease *et al.* 1979; Sinclair *et al.* 1993). Sinclair *et al.* (1993) found that individual trees may be browsed during 6 separate cycles (spanning 50 years). The repetitive browsing of spruce over several cycles may contribute to more missing rings over time, or lead to the high prevalence of missing rings in spruce observed by Peters *et al.* (2002). Hare browsing also has implications to mixedwood succession, potentially lengthening the time for understory spruce to replace deciduous tree species.

We used clipping experiments to simulate hare browsing in a 20 and 59-year-old stand. We used two clipping intensities and a control that we assessed at the end of the first growing season. Clipped trees were visually crossdated with control trees to assess the presence of the most recent growth ring. Our objectives were to determine whether browsing severity affects ring width and ring deposition during the year that browsing occurs. A further objective was to determine whether stand age affected the response of white spruce to browsing, and thus provide an explanation for increased aging error with stand age.

3.3 Methods

3.3.1 Experimental design and treatments

In order to determine how browsing affected ring deposition in trees from stands of different ages, a 20-year-old stand (YOS) (1980 Conklin Trail Fire) and a 59 YOS (1941 Piche Lake Fire) were selected (see Fig. 4.2). The 1980 fire was 4 km North of Conklin, while the 1941 fire was approximately 100 km southwest of Conklin. The two study stands were also sampled to address objectives in Chapter 4; consequently, fire and stand selection criteria described in Chapter 4, section 4.4.1 applied to stands described here. One stand from each fire (stand 8, 1980 fire; and stand 1, 1941 fire) was selected for this part of the study because of the abundance of white spruce saplings between 0.5 and 1.3 m tall. This ensured that trees would not be entirely buried by snow, and would remain within the browse height of snowshoe hares (Pease *et al.* 1979; Oldemeyer 1983; Parker 1984; Smith *et al.* 1988). In each stand, 45 trees with no evidence of prior browsing or damage (i.e. breakage of leader or branches) were marked with a numbered metal tag. Tags were loosely attached to the stem, thereby ensuring that growth would not be restricted. Selected trees were at least one meter away from any conspecific in order to prevent indirect effects of shading from influencing the growth response of study trees to the imposed treatment.

At each site, we randomly assigned each of the 45 trees to one of two treatment categories, or the unclipped control group. Clipping treatments were conducted on May 6, 2000, a date that we assumed preceded ring deposition for the current year (i.e. recent frosts would have prevented growth). This date also ensured that trees would not be subsequently browsed, since woody vegetation is browsed primarily in the winter (Smith *et al.* 1988). In the first treatment, we clipped off the top 20 cm of the tree with tree-pruning shears (20 cm treatment, Fig. 3.1a,b). Frequently this removed several years of height growth. The clip was a single diagonal cut that removed the terminal leader as well as any smaller branches attached to the leader. These branches are typically the first to be browsed by snowshoe hares (Pease *et al.* 1979). We saw many black spruce and white spruce within the 20 YOS that had been browsed similarly by snowshoe hare (Fig. 3.1c) .

The second clipping treatment was more severe than the 20 cm treatment (Fig. 3.1d, e). We intended to remove the leader and all branches that were smaller than 3 mm in diameter (3 mm treatment) because white spruce branches of this size and smaller are most commonly browsed by snowshoe hares (Pease *et al.* 1979; Smith *et al.* 1988). However, upon examining trees in the field, we found that this treatment would remove all of the branches on the smaller trees and potentially kill them. It was important that all treatment trees survive until the end of the growing season in order to determine whether clipping affected ring deposition. Thus, we modified the treatment in several ways: 1) Leaders were clipped at the point that the diameter exceeded 3 mm (usually a portion of the previous years growth). 2) On each branch coming off the stem of the sapling, the diameter of the main branch immediately before the first lateral branch was measured (Fig. 3.2). If the main branch at the bifurcation was larger than 3 mm, we left the whole branch intact. If the main branch was smaller than 3 mm, we clipped the main branch before the bifurcation. We assumed that branches less than 30 cm above ground are covered by snow in most winters. These branches were not clipped because hares only browse branches above the snow (Pease *et al.* 1979). Again, we saw many naturally browsed trees that looked similar to this treatment (Fig. 3.1f). We did not clip the remaining 15 trees which were assigned as control trees.

We left all trees undisturbed for the remainder of the growing season. We assumed that ring deposition had ceased by mid-September because of several hard frosts. On September 23, 2000 we removed a 2.5 cm long disk from trees at ground level, because this is the location at which age is typically obtained. The disks were then taken back to the lab and prepared according to the procedures in Chapter 2, section 2.4.2. The entire disk surface was prepared on all trees.

3.3.2 Crossdating procedures

For crossdating, the outer five rings of the trees were examined because we believed that careful observation of several features in these rings would confirm the presence or absence of the year 2000 ring (i.e. Wang *et al.* 2002). We crossdated the outer five rings using the skeleton plot method (Schweingruber 1989). The following features were used to crossdate trees: relative ring thickness (designated as thin, medium or thick), ring color (light, medium, or dark chocolate or reddish brown) and latewood:earlywood ratio (10:90, 25:75, or 50:50). Ring thickness, color and latewood to earlywood ratios were assigned to a numerical scale (i.e. thin ring = 1, medium ring = 2 and thick ring = 3). We distinguished earlywood from latewood by its larger cells and thinner cell walls (Phipps 1985). The number of traumatic resin ducts within each ring was quantified; however, they were not useful for crossdating. Although we looked for false rings and frost rings, neither were observed in the ring sequences examined.

We made the assumption that the year 2000 growth ring was deposited at ground level in many control trees in the young stand, because many trees in this fire (1980 Conklin Trail Fire) dated back to the year after the fire (i.e. if missing rings occurred above ground level in these trees a distinct 1981 cohort would not have occurred; see Chapter 4, Fig. 4.6h). Consequently, we assumed that the mean value of the ring features for the control trees would provide a sufficiently clear pattern for crossdating treatment trees that were more likely to be missing rings. Based on the numerical values assigned to the ring features, we calculated the mean value for each characteristic for each of the 5 outer rings in the control trees for both the 20 and 59 YOS (the master skeleton plot; Fig. 3.3). The values of all ring features were recorded on the master plot. Concordance between the master plots of the younger and older stand was checked to confirm that the older stand did not appear to have missing rings between 1996 - 2000. This was important because missing rings at ground level increase as stands age (see Chapter 2, section 2.6.2) and we needed to ensure that the master plot was suitable for crossdating clipped trees. We determined whether a year 2000 growth ring was deposited in the treated trees by comparing the skeleton plot of each clipped tree to the master skeleton plot from the same stand (i.e. each ring was checked to see if it was thicker/thinner, had more or less latewood, was lighter or darker etc.). If the treatment ring sequence matched the master skeleton plot, we concluded that the 2000 ring was deposited. If the ring sequence of the clipped tree did not match, and the outermost ring matched the 1999 ring of the master skeleton plot, we concluded that the 2000 ring was missing. In this way we determined the presence or absence of the year 2000 ring for each clipped tree in both stands.

In some instances, a sufficiently distinct pattern did not occur in the clipped tree to determine the presence or absence of the year 2000 ring. For these trees the standard error of the mean was determined for each ring feature of each ring in the control group, and for each stand respectively. For each ring on clipped trees, we then determined if the numerical value of the ring feature was within 2 standard errors of the control group mean for each ring. If more than 50% of a clipped tree's ring values were outside of this range, we concluded the 2000 ring was absent. This approach enabled us to see the patterns of ring thickness, latewood:earlywood ratio, and color more clearly, and to obtain the same crossdating results among observers. In the event of conflicting results from the different ring features, we prioritized the patterns shown for ring thickness followed by latewood thickness when making decisions. The color of latewood was used so that we could classify as many trees as possible with respect to the presence or absence of the 2000 ring.

After working through all the ring features on the older stand, we found that ring thickness was the only useful criteria in making the presence/absence determination for the year 2000 growth ring. For control trees in this stand, the second ring (1999) was either thinner (6 out of 15) than or equal in width to the first ring (9 out of 15), while none of the second rings were thicker than the first ring (Fig. 3.3b). Furthermore, all third (1998) rings were thicker than the second ring. Therefore, all trees showing a thicker second ring than the first ring were classified as missing the year 2000 growth ring.

On trees that deposited the year 2000 growth ring we measured the width of the outermost ring (according to the procedures in Chapter 2, section 2.4.2). Ring width measurements were made for the younger stand but not for the older stand. We had less confidence in our identification of the presence or absence of the year 2000 growth ring in the older stand because trees were very suppressed (outermost rings were very thin) and crossdating was very difficult. Large amounts of compression wood prevented comparisons of latewood:earlywood, relative ring thickness, and ring color. We therefore could not be as certain whether we were measuring a 1999 or a year 2000 growth ring in the older stand.

3.4 Data Analysis

We used binomial logistic regression (Campbell 1974; Damon and Harvey 1987) to determine whether the level of clipping significantly affected the frequency of ring deposition relative to unclipped control trees. We used a one-way ANOVA to determine whether the width of the year 2000 ring differed in control trees from treated trees in which the ring occurred. We used Tukey's "honestly significant difference" test for post hoc comparisons of treatment means and control means (Zar 1996). Statistical analyses were performed using the software program SPSS version 10.0 (SPSS 1999).

3.5 Results

In total, 86 out of 90 trees were classified as either possessing or lacking a year 2000 ring. The remaining 4 trees could not be classified because they lacked the distinct features necessary for crossdating. In the younger stand, 6 out of the 12 trees in the 20 cm treatment group that could be classified were missing the year 2000 ring, while 3 out of the 14 classified trees in the 3 mm treatment group were missing this ring (Table 3.1). Both clipping treatments had significantly fewer trees producing a year 2000 ring than the control; however, the two treatments did not differ significantly from each other in this respect (Table 3.1). Ring width and latewood:earlywood ratios were features that usually supported the same conclusion regarding the presence or absence of the year

2000 ring. The year 2000 ring (in trees that deposited this ring) was significantly narrower in the 3 mm treatment than in the control (Table 3.2). The 20 cm trees did not show this pattern and had rings that were approximately the same width as control trees (Table 3.2).

In the older stand, 3 out of 15 trees in the 20 cm treatment group were missing the year 2000 ring (Table 3.3); this was considerably fewer trees than in the 20 cm treatment in the younger stand. Four out of 15 trees in the 3 mm treatment group were missing the year 2000 ring (Table 3.3); this was a similar frequency to the younger stand. In the older stand, the number of trees producing a year 2000 ring was significantly lower in the 3 mm treatment than in the control, and nearly significantly lower in the 20 cm treatment than in the control (Table 3.3). The two treatments did not differ significantly from each other in this respect (Table 3.3).

3.6 Discussion

3.6.1 Browsing effects on ring deposition

The response of treatment trees in this study to clipping similar to that made by snowshoe hares, suggests that browsing by hares can affect ring deposition in the year that it occurs. Missing rings occurred in a significant number of trees in both treatments and both age classes. Missing rings occur frequently in old suppressed trees (Lorimer *et al.* 1999); however, we even found them in young vigorous trees in the 20-year-old stand. These findings are important because trees are more likely to fail to deposit rings in the second year after browsing since annual growth is usually a reflection of the previous years growth (Messier, pers. com.). A higher percentage of the 3 mm treatment trees in younger stands may thus have missing rings in the second year.

Previous studies on other tree species show that the degree of defoliation by insects affects ring width (Ghent 1958; O'Neill 1963; Morin and Laprise 1997). Interestingly, more 20 cm trees were missing rings than 3 mm trees, but when a ring was produced in 20 cm trees, it did not differ in width from control trees. This suggests that the loss of the terminal leader (frequently several years of height growth) has a more pronounced effect on ring deposition at ground level than severe defoliation throughout the tree (i.e. the 3 mm treatment).

In general, early season herbivory slows cell division and development (Quiring and McKinnon 1999), and may lead to missing rings in balsam fir and black spruce during spruce budworm outbreaks (Simard and Payette 2001). Growth of understory spruce in mixedwoods is already suppressed because light levels in summer are frequently below the light compensation point (where photosynthetic gains exceed respiratory losses) (Constable and Lieffers 1996). Constable and Lieffers (1996) suggested that trees may rely heavily on photosynthetic gains during leaf-off periods (in the spring or fall) for growth. Trees were clipped in our experiment prior to spring leaf-out. The loss of spring photosynthesis plus reduced leaf area may have contributed to the inability of some trees to produce a growth ring. We propose that light limitation, coupled with severe browsing could contribute to the widespread occurrence of missing rings in white spruce.

Surprisingly, more trees were missing the year 2000 growth ring in the younger stand than the older stand, despite being less suppressed. Tree rings were much narrower in the older stand (pers. obs.*)*, and although trees were not aged, cursory examination of the disk indicated that many trees would date back close to the fire origin date. Trees that are more suppressed in older stands would be expected to have a higher frequency of missing rings (Lorimer *et al.* 1999). We suspect that methodological limitations likely resulted in an under-estimation of missing rings in the older stand; rings were too narrow and had too much compression wood to categorize latewood to earlywood ratios and ring color. All of these features in combination were helpful in crossdating trees in the younger stand. It was fortunate that master skeleton plots for the older stand were similar to the younger stand, because missing rings between 1996 and 2000 would have rendered the master plot unsuitable for crossdating clipped trees. Nonetheless, visual crossdating normally relies on several marker years (unusual years of growth) from long ring sequences; therefore, results from the older stand should be regarded cautiously. Our quantification of features that are usually used in a qualitative sense permitted comparison of short ring sequences when features were clear, but these features were not clear enough in the older stand to date rings with confidence.

Although white spruce is a less palatable species to snowshoe hare than several other boreal shrubs, it is browsed heavily during cycle peaks (Pease *et al.* 1979; Swihart and Yahner 1983; Oldemeyer 1983; Smith *et al.* 1988, Sinclair *et al.* 1993). Hare browsing can affect a large proportion of spruce, as evidenced by the browsing of at least 50% of available white spruce trees during a cycle peak in the Yukon (Sinclair *et al.* 1993). Browsed trees showed multiple browse events spanning a 50 year period (Sinclair *et al.* 1993). Extended suppression periods of white spruce in the understory of mixedwoods would increase the percent of trees that may be missing rings, as well as the amount of aging error that would accumulate from browsing over several hare population peaks. A study on hare cycles in the Yukon found that hare browsing caused dark marks in tree rings, and that these marks were useful for dating historic cycles (Sinclair *et al.* 1993). Surprisingly, we did not observe dark marks in clipped trees or in any hare-browsed trees that were aged in other chapters (i.e. Chapters 2, 4, and 5). We are not aware of the reason for this; however, sites examined by Sinclair *et al.* (1993) lacked a deciduous canopy whereas our sites had thick aspen canopies that possibly reduced mean annual ring width, and the expression of dark marks (qualitative ring features are difficult to discern in suppressed trees). Dark marks in clipped trees would have been a very useful feature to help confirm missing rings caused by clipping.

Several factors may contribute to the likelihood of snowshoe hare browsing in stands of different ages. Hares prefer stands that have been recently burned because the amount of overhead cover is greater due to high sapling densities, and fire-killed snags (Grange 1965). Browsing frequency of spruce in younger stands may be lower than in older stands because juvenile spruce (less than 2 m in height) produce more camphor than older trees (taller than 2 m) (Sinclair *et al.* 1988). Camphor is a plant secondary compound that deters herbivory (Sinclair *et al.* 1988). While there were no height differences between clipped trees in the younger versus the older stand, camphor production may differ between stands because of different tree ages.

3.6.2 Implications of browsing to forest dynamics

Multiple browse events may lead to considerable age underestimation in trees from mixedwoods. The majority of understory spruce spend at least 3.5 decades within the height range that hares browse (Peters *et al.* 2002), while some are there for longer than six decades (pers. obs.). Our results suggest that hare browsing may have significant implications for the estimation of key regeneration periods for white spruce. Variability in browsing, and hence the numbers of missing rings among trees, may help explain discrepancies in the apparent regeneration periods of white spruce following fire (Peters *et al.* 2002). Furthermore, hare browsing may contribute to the uneven size structure of mixedwood stands, and the time period required for understory spruce to replace aspen in the canopy.

Hare browsing may have been a factor preventing Peters *et al.* (2002) from being able to crossdate the most suppressed trees in a 38-year-old fire. Browsed trees would have different ring width patterns than the large trees used in the master chronology (Chapter 2, section 2.4.2), because the latter grew quickly, and therefore would not be susceptible to browsing for more than one or two hare cycles. Hare browsing may cause a strong ring width signal over time that could be used to more accurately age suppressed trees in mixedwoods. Growth would decline in browsed trees during hare cycle peaks, and missing rings may also occur in these trees. Browsed trees would likely recover and obtain maximum growth in years leading up to the next cycle peak. On trees that show external evidence of several browse cycles (Dale pers. com.), time intervals between growth declines may be shorter than the hare cycle (roughly every 10 years), and tree ring chronologies could be corrected with records of snowshoe hare cycles for that region. Lorimer *et al.* (1999) used a similar technique in stands that were partially thinned on a known date, to quantify missing rings in trees showing variable release dates.

3.6.3 Considerations for future work

If time had permitted, we would have included several additional aspects to this study. First, we would have treated more trees and left a portion of them for two years in order to check for a missing ring in the second year (2001). We also would have constructed skeleton plots for the entire ring sequence at ground level for both control and treatment trees in both age classes. Longer ring sequences would have been better for crossdating trees and confirming our results. Furthermore, we would have taken multiple disks from the entire height of each treatment tree in order to crossdate them internally, and identify the heights at which missing rings ceased basipetal development. We also would have included age and height of clipped trees in statistical analyses as explanatory covariates for missing ring occurrence. We suspect that missing rings would be negatively associated with increased height among trees of the same age, and positively associated with age among trees of similar height.

3.7 Conclusions and Management Implications

Simulated browsing of white spruce at levels comparable to natural browsing by snowshoe hare has significant implications for age estimation in white spruce. Our clipping experiments suggest that hares may cause reduced ring width and a missing ring in the year of browsing, even in vigorous trees in young stands. Clipping appeared to cause similar frequencies of missing rings in suppressed trees in older stands. Narrow rings in the older stand limited the use of additional features for visual crossdating; consequently, we were unable to confirm findings obtained from ring width plots. Hare browsing during cycle peaks may contribute to increased aging error as stands age and thus help explain previous findings that spruce establishes continuously over time. Hare browsing appears to lengthen successional development of mixedwood sites from aspen to white spruce by reducing growth of understory white spruce.

Our findings further support management implications in Chapter 2. Trees are considerably older than ground-level ring counts indicate, and consequently are growing slower than previously estimated. These findings suggest that harvest rotations need to be lengthened so that forest resources are not depleted. These results also have implications for the artificial regeneration of white spruce. If understory planting and treeplanting of spruce in cutblocks were minimized during the two years of peak hare cycles, it could help reduce growth setbacks caused by browsing. Brushing operations after planting may also help reduce browsing by reducing protective cover for hares during cycle peaks, and may be warranted until trees reach 2 m in height.

Table 3.1: Frequency of ring deposition in white spruce following simulated hare browsing in a 20-year-old stand. Trees were clipped in the spring of 2000, and ring deposition was assessed in the fall. The top 20 cm of growth were clipped in the 20 cm treatment, while branches less than 3 mm were clipped in the 3 mm treatment (see Fig. 3.1). Control trees were not clipped and were assumed to contain the year 2000 growth ring. Fewer trees were included in the sample than the number clipped (15 per treatment) because we could not determine whether the year 2000 ring was deposited in several treatment trees. Logistic regression comparisons are between each treatment and the control, and between the two treatments.

Treatment	Trees in sample	Trees with year 2000 growth ring	Statistical comparison	Coefficient of variation	*p*
20 cm	12	6	20 cm treatment vs. control	0.548	0.002
3 mm	14	11	3 mm treatment vs. control	0.365	0.026
control	15	15			
			20 cm treatment vs. 3 mm treatment	0.263	0.064

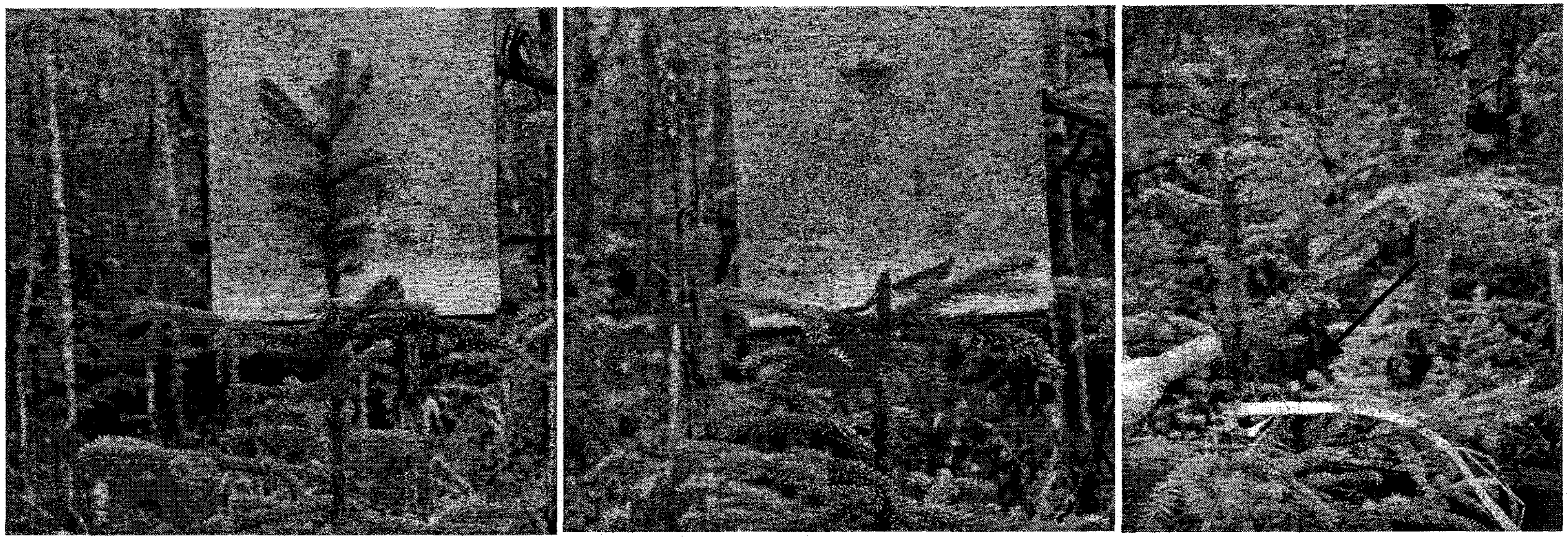
Table 3.2: Mean width of the year 2000 growth ring in browsed and unbrowsed white spruce trees from a 20-year-old stand. Trees were clipped in the spring of 2000 to simulate hare browsing, and ring deposition was assessed in the fall. The top 20 cm of growth were clipped in the 20 cm treatment, while branches less than 3 mm in diameter were clipped in the 3 mm treatment (see Fig. 3.1). Standard error of the mean is shown. Results of a one-way ANOVA and Tukey's "honestly significant difference" test are shown.

Treatment	Mean width (microns)
20 cm	$0.044^{a} \pm 0.009$
3 mm	$0.015^{b} \pm 0.003$
Control	$0.041^{a} \pm 0.005$

Note: superscripts with different letters denote comparisons that differed significantly ($p < 0.05$), while the comparisons with the same letter did not differ significantly.

Table 3.3: Frequency of ring deposition in white spruce following simulated hare browsing in a 59-year-old stand. Trees were clipped in the spring of 2000, and ring deposition was assessed in the fall. The top 20 cm of growth were clipped in the 20 cm treatment, while branches less than 3 mm in diameter were clipped in the 3 mm treatment (see Fig. 3.1). Control trees were not clipped and were compared with the control in the 20-year-old stand for the presence of the year 2000 growth ring. Logistic regression comparisons are between each treatment and the control, and between the two treatments.

Treatment	Trees in sample	Trees with year 2000 growth ring	Statistical comparison	Coefficient of variation	*p*
20 cm	15	12	20 cm treatment vs. control	0.291	0.068
3 mm	15	11	3 mm treatment vs. control	0.341	0.032
control	15	15			
			20 cm treatment vs. 3 mm treatment	0.009	0.666



a) 20 cm treatment - before clipping

b) 20 cm treatment - after clipping

c) a hare browsed tree

Figure 3.1(a-c): The 20 cm clipping treatment before clipping (a) and after the top 20 cm were clipped (b). A tree that was naturally browsed by a snowshoe hare in the same stand is shown for comparative purposes (c). Note that the browsed portion of (c) is being held above the browse mark (indicated by the white arrow).

d) 3 mm treatment - before clipping

e) 3 mm treatment - after clipping

f) hare browsed trees

Figure 3.1(d-f): The 3 mm clipping treatment before clipping (d) and after branches less than 3 mm in diameter were removed (e). A tree that was similarly browsed by a snowshoe hare in the same stand is shown for comparative purposes (left side of clipboard) (f). Note also the two trees that were completely defoliated by hares at the right side of the clipboard (f).

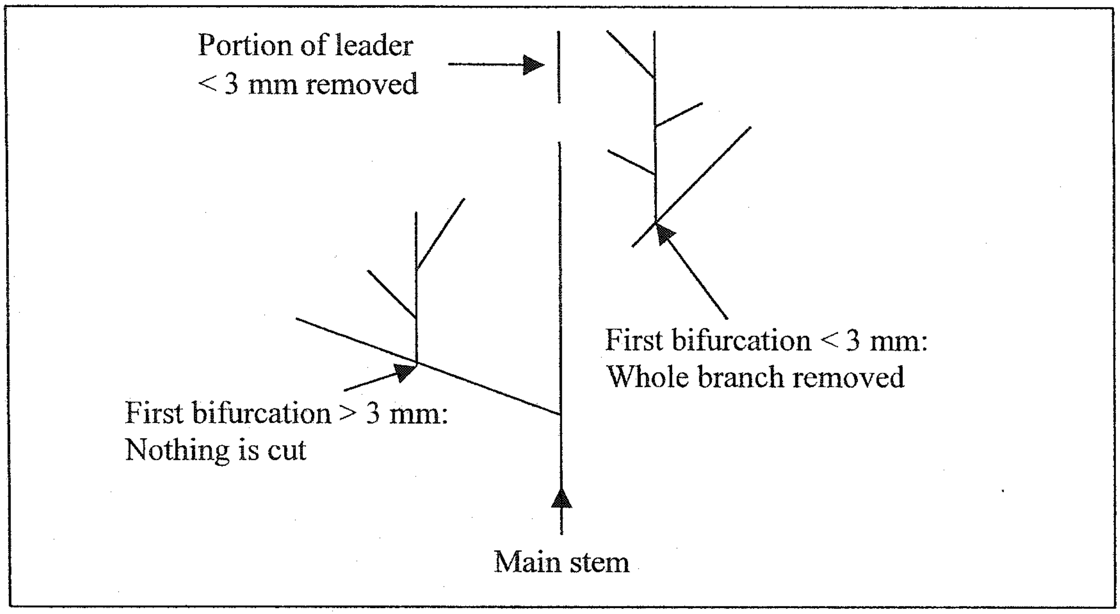


Figure 3.2. Depiction of stem characteristics of white spruce that were used to determine the appropriate clipping locations for the 3 mm treatment. Branches less than 3 mm in diameter were clipped as shown above.

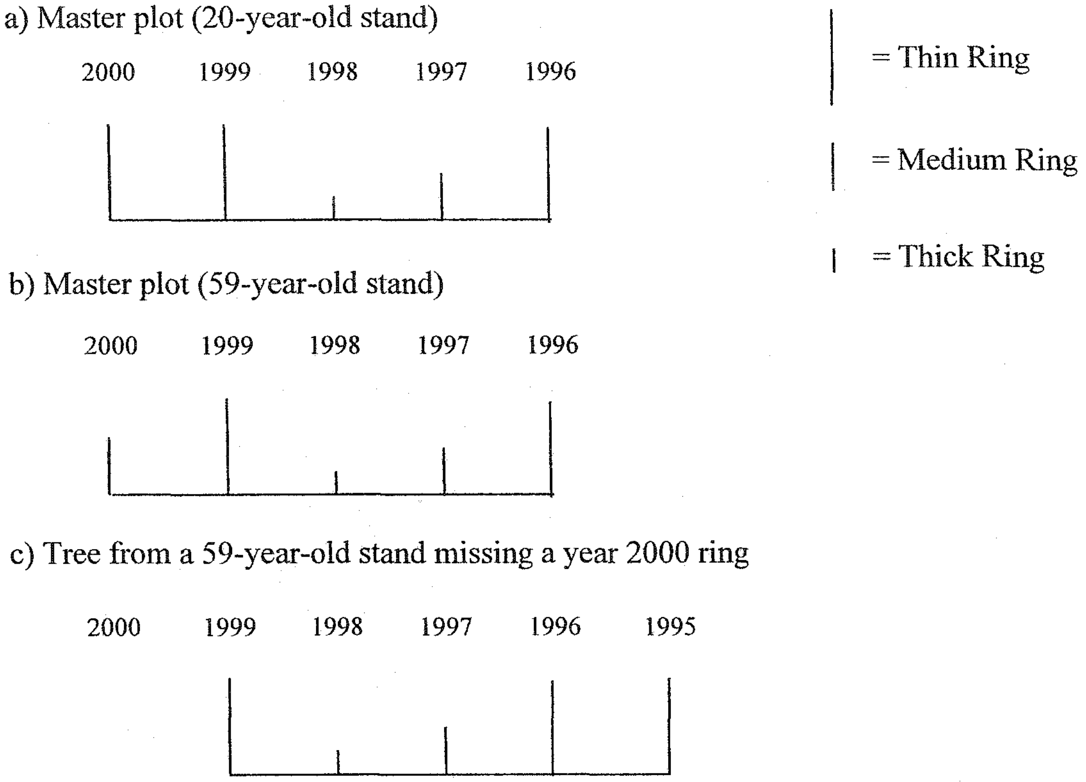


Figure 3.3: Master skeleton plot based on the ring width of 15 control trees from the 20-year-old stand (a) and from the 59-year-old stand (b). The skeleton plot for each treatment tree was compared with the master skeleton plot from the same stand. Plot (c) is an example of a tree whose five outermost rings did not match the master plot from the 59-year-old stand.

3.8 Literature Cited

Berry, A.B. 1982. Response of suppressed conifer seedlings to release from an aspen-pine overstory. For. Chron. **58**: 91-92.

Boutin, S., Krebs, C.J., Boonstra, R., Dale, M.R.T., Hannon, S.J., Martin, K., Sinclair, A.R., Smith, J.N., Turkington, R., Blower, M., Byrom, A., Doyle, F.I., Doyle, C., Hik, D., Hofer, L., Hubbs, A., Karels, T., Murray, D.L., Nams, V., O'Donoghue, M., Rohner, C., and Schweiger, S. 1995. Population changes of the vertebrate community during a snowshoe hares cycle in Canada's boreal forest. Oikos **74**: 69-80.

Campbell, R.C. 1974. Statistics for biologists: 2nd edition. Cambridge University Press, New York, NY.

Constable, A.J., and Lieffers, V.J. 1996. Seasonal patterns of light transmission through boreal mixedwood canopies. Can. J. For. Res. **26**: 1008-1114.

Damon, R.A. Jr., and Harvey, W.R. 1987. Experimental design, ANOVA, and regression. Harper & Row Publishers, New York, NY.

Ghent, A.H. 1958. Studies of regeneration in forest stands devastated by the spruce budworm. For. Sci. **4**: 135-146.

Grange, W.B. 1965. Fire and tree growth relationships to snowshoe rabbits. Annu. Proc. Tall Timbers Fire Ecol. Conf. **4**: 111-125.

Krebs, C.J., Gilbert, B.S., Boutin, S., Boonstra, R., Sinclair, A.R.E., and Smith, J.N.M. 1986. Population biology of snowshoe hares. I. Demography of food-supplemented populations in the southern Yukon, 1976-84. J. Anim. Ecol. **55**: 963-982.

Kobe, R.K., and Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can. J. For. Res. **27**: 227-236.

Lieffers, V.J. and Stadt, K.J. 1994. Growth of understory *Picea glauca, Calamagrostis canadensis,* and *Epilobium angustifolium* in relation to overstory light transmission. Can. J. For. Res. **24**: 1193-1198.

Lorimer, C.G., Dahir, S.E., and Singer, M. 1999. Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. Plant Ecol. **143**: 189-202.

Morin, H., and Laprise, D. 1997. Seedling bank dynamics in boreal balsam fir forests. Can. J. For. Res. **27**: 1442-1451.

Oldemeyer, J.L. 1983. Browse production and its use by moose and snowshoe hares at the Kenai moose research center, Alaska. J. Wildl. Manage. **47**: 486-496.

O'Neil, L.C. 1963. The suppression of growth rings in jack pine in relation to defoliation by the Swaine jack-pine sawfly. Can. J. Bot. **41**: 227-235.

Parker, G.R. 1984. Use of spruce plantations by snowshoe hares in New Brunswick. For. Chron. **60**: 164-166.

Pease, J.L., Vowles, R.H., and Keith, L.B. 1979. Interaction of snowshoe hares and woody vegetation. J. Wildl. Manage. **43**: 43-60.

Peters, V.S., Macdonald, S.E., and Dale, M.R.T. 2002. Aging discrepancies of white spruce affect the interpretation of static age structures in boreal mixedwoods. Can. J. For. Res. **32**: 1-6.

Phipps, R.L. 1985. Collecting, preparing, crossdating,.and measuring tree increment cores. U.S. Geol. Survey, Water Resources Investigations, Lakewood, CO, Rep. 85-4148.

Quiring, D.T., and McKinnon, M.L. 1999. Why does early-season herbivory affect subsequent budburst? Ecol. **80**: 1724-1735.

Schweingruber, F.H. 1989. Tree rings: basics and applications of dendrochronology. Kluwer Academic Publishers Group, Norwell, MA.

Simard, M. and Payette, S. 2001. Black spruce decline triggered by spruce budworm at the southern limit of lichen woodland in eastern Canada. Can. J. For. Res. 31: 2160-2172.

Sinclair, A.R., Gosline, J.M., Holdsworth, G., Krebs, C.J., Boutin, S., Smith, J.N., Boonstra, R, and Dale, M.R.T. 1993. Can the solar cycle and climate synchronize the snowshoe hares cycle in Canada? Evidence from tree rings and ice cores. Amer. Nat. **141**: 173-198.

Sinclair, A.R., Jogia, M.H., and Andersen, R.J. 1988. Camphor from juvenile white spruce as an antifeedant for snowshoe hares. J. Chem. Ecol. **14**: 1505-1514.

Smith, J.N., Krebs, C.J., Sinclair, A.R., and Boonstra, R. 1988. Population biology of snowshoe hares. II. Interactions with winter food plants. J. Anim. Ecol. **57**: 269-286.

SPSS 1999. SPSS for windows release version 10.0. Chicago, IL.

Swihart, R.K., and Yahner, R.H. 1983. Browse preferences of jackrabbits and cottontails for species used in shelterbelt plantings. J. For. **81**: 92-94.

Villalba, R., and Veblen, T.T. 1997. Improving estimates of total tree ages based on increment core samples. Ecoscience **4**: 534-542.

Wang, G. and Huang, S. 2000. Height growth pattern of white spruce in natural subregions in Alberta, Canada, For. Ecol. Manage. **134**: 271-279.

Wang, L., Payette, S., and Begin, K. 2002. Relationships between anatomical and densiometric characteristics of black spruce and summer temperature at treeline in northern Quebec. Can. J. For. Res. **32**: 477-486.

Zar, J.H. 1996. Biostatistical analysis. 3rd ed. Prentice-Hall, Inc. Upper Saddle River, New Jersey, USA.

CHAPTER 4

Keystone Processes Affect White Spruce Regeneration: The Masting Cycle and Fire History Connection

---

4.1 Abstract

Despite the frequent inference that mast years contribute to recruitment, there is little empirical evidence that the masting phenomenon is important to plant population dynamics. Using the mast-seeding tree species, white spruce (*Picea glauca*), we determined whether the timing of fire relative to mast years has a long-lasting effect on the density and timing of regeneration. We studied fires that occurred during mast years, as well as years with low cone production between 1941 and 1994. In addition, the effect of the length of delay between fire and mast year on density and age structure was tested on fires occurring in a mast year, and one, two, and three years before a mast year. Trees were carefully aged by crossdating the below-ground portion of trees with skeleton plots and by ring width analysis with Cofecha. Over the 59 year period that we studied, significantly more regeneration occurred on mast year fires than on fires that occurred in years of low cone production. Significantly more regeneration occurred on mast year fires than on those with a one, two, or three year delay before a mast year. Further declines in density occurred between one and two year delay fires, but not between two and three year delay fires. The first post-fire mast cohort comprised a significantly smaller proportion of regeneration if the mast year occurred later after the fire. We found that standard aging techniques underestimate the true age of spruce by as much as 27 years in 59-year-old stands; in other studies, aging errors may have obscured the long lasting importance of the first mast cohort on white spruce density and successional development. These results demonstrate that masting is a keystone process that interacts with natural disturbance regimes to shape stand composition in boreal mixedwoods.

4.2 Introduction

Masting is a common reproductive strategy amongst North American conifer genera (Eis *et al.* 1965; Koenig and Knops 1998). Masting is characterized by the widespread and synchronous production of large seed crops at varying time frequencies (Silvertown 1980; Koenig and Knops 1998). Numerous studies have investigated the causes of masting, but causal mechanisms have been difficult to demonstrate (Silvertown 1980; McKone *et al.* 1998; Shibata *et al.* 1998; Silvertown and Dodd 1999; Keely and Bond 1999; Koenig and Knops 2000). Only a few studies have investigated whether masting permits greater numbers of germinants in mast years than non-mast years (Taylor and Aarssen 1989; Ida and Nakagoshi 1996; Sato 2000). Masting appears to have evolved as a mechanism to enhance reproductive success (i.e. cross-pollination), and to satiate seed predators in mast years, thereby increasing the likelihood of recruitment (Janzen 1971; Silvertown 1980; Crawley and Long 1995). Despite the frequent inference that mast years contribute to recruitment (Sork 1983; Keely and Bond 1999), there is little empirical evidence that mast year cohorts contribute more than non-mast years to tree regeneration or forest succession, whether some mast years contribute a larger cohort than others, and whether disturbance timing in relation to mast years affects their importance in these respects.

White spruce (*Picea glauca*) possesses all the characteristics of a "true masting species" (Silvertown 1980). Synchronous seed production of white spruce occurs throughout Alberta (Kemp and Keith 1970), and is correlated over distances up to 2500 km, most strongly in mast years (Koenig and Knops 1998). Mast years are followed by years of virtual cone production failure (Nienstaedt and Zasada 1990). Mast frequency ranges from 2 to 6 years throughout the boreal plain, but is more intermittent at higher elevations and more northerly latitudes because hard frosts damage potential cone crops more frequently (Rowe 1955; Coates *et al.* 1994). In addition to the obligate seed predator, the red squirrel (*Tamiasciurus hudsonicus*), deer mice (*Peromyscus maniculatus*), red-backed voles (*Clethrionomys gapperi*), insects and birds can consume most of the seeds in years with low to moderate cone crops (Alden 1985; Coates *et al.* 1994; Peters 2000). Red squirrel populations peak in mast years and drop in the year after a mast year (Smith 1968; Kemp and Keith 1970; Rusch and Reeder 1978). The peak appears to be induced by feeding on reproductive buds during the winter preceding the maturation of cones (Kemp and Keith 1970), while the crash coincides with high juvenile mortality during the following year (Rusch and Reeder 1978).

In mast years, most trees within a stand are producing cones, and many trees are producing large numbers of cones (Coates *et al.* 1994). Dispersed seed within a mature white spruce stand can range between 2.5 and 4000 seeds / m^2, while cone production can range from 0 (pers. obs.) to 12,000 cones / tree (Waldron 1965; Nienstaedt and Zasada 1990). Seed production can vary considerably between high seed years, as indicated by a 13-year study in Alaska by Zasada (in Nienstaedt and Zasada 1990). Dispersed seed ranged between 1000 and 4000 seeds / m^2 (Zasada in Nienstaedt and Zasada 1990) in four years that could potentially be considered mast years, depending on regional synchrony and cone production in the year after masting.

The disturbance regime of the boreal forest is characterized by frequent, high intensity, stand-replacing fires (Johnson 1992). White spruce appears rather poorly adapted to this disturbance regime; it depends on surviving seed sources to disperse seed into the burned area (Galipeau *et al.* 1997), rather than serotinous cones or asexual sprouting. Consequently, it is likely to be recruitment-limited, and local populations are likely to go extinct. In addition, seeds are typically viable for only one year after dispersal (Coates *et al.* 1994). The preferred establishment substrate of white spruce is mineral soil (Nienstadt and Zasada 1990; Coates *et al.* 1994, Purdy *et al.* 2002). Seedbed receptivity after fire ends after three to five years (Zasada 1969; Zasada 1985; Coates *et al.* 1994). Consequently, timing of fire relative to mast years may be critical to initial establishment success.

Frequently portrayed as a late succession species in boreal mixedwoods, white spruce is typically found in the understory of broadleaf canopies comprised of trembling aspen (*Populus tremuloides*) or paper birch (*Betula papyrifera*), before emerging as a canopy dominant (Youngblood 1995). Immediate post-fire regeneration has not been regarded as critical to spruce stand development because studies have suggested that it can establish for many decades following fire, with substrates such as decayed logs facilitating this process (Kabzems and Lousier 1992; Lieffers *et al.* 1996; Galipeau *et al.*

1997). These findings suggest that the first mast cohort post-fire is only one of multiple regeneration events, and does not have an essential role in stand development.

We investigated the importance of fire timing relative to mast years over a 59 year post-fire period for white spruce regeneration in boreal mixedwoods (Alberta, Canada). Our objective was to determine whether the timing of fires relative to mast years affects the density and timing of white spruce regeneration, and whether any such density or age differences persist over time. A further objective was to determine the effect of the length of delay from fire to mast year on the density and age structure of regeneration. We hypothesized that more regeneration occurs on mast year fires than non-mast fires because more seed is available while seedbeds are most receptive ("mast year effect"). We further hypothesized that an initial mast cohort persists as the dominant cohort over time on mast year fires ("mast cohort effect"); however, this cohort is less dominant on non-mast year fires.

4.3 Study Area

The study area consisted of a 60,000 km^2 area of mixedwood forest in east-central Alberta, North of Lac la Biche (54°46'N 111°8'W), and Athabasca (54°43'N 113°17'W), situated within the Boreal Forest Natural Region (Alberta Environmental Protection 1999). Post-fire stands were dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), and white spruce, although paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), and black spruce (*Picea mariana* (Mill) BSP), were occasionally present. Soils on upland sites in this region are Gray Luvisols and Eutric Brunisols. Mean summer temperature is 13.5°C (May to August) while mean winter temperature is –13.2°C (November to February) (Strong and Leggat 1992). The mean annual precipitation is 397 mm, with most falling as rain in July (240 mm) (Strong and Leggat 1992).

4.4 Methods

4.4.1 Importance of mast seed years

We used a retrospective approach to test if a mast year effect on white spruce regeneration follows fire. Mast years between 1941 - 1996 within Alberta were identified from provincial cone collection records (Palamarek pers. com.), and red squirrel trapping records (Todd and Giesbrecht 1979; Neumann pers. com.) (Fig. 4.1). Records of the number of red squirrels trapped in Alberta are significantly correlated with provincial cone crops ($r^2 = 0.911, p < 0.01$) (Kemp and Keith 1970). Peak years in cone collection corresponded with peaks in squirrel trapping between 1979 - 1996 (years of overlapping records) (Fig. 4.1). Peaks in these records were identified as mast years, while the lowest year in the inter-mast period before or after the chosen mast year was selected as the non-mast year. Selected mast years were 1991, 1979, 1961 and 1941, while non-mast years were 1994, 1992, 1981, 1958 and 1942. Alberta-based forestry publications that rated cone crops of white spruce verified our identification of these years as mast and non-mast years (Crossley 1955; Quaite 1956; Lees 1963; Smith 1968; Kemp and Keith 1970, Rusch and Reeder 1978; Cerezke and Holmes 1986, Stewart *et al.* 2000). One fire was selected for most of the chosen years between 1979 and 1994 (except 1981), while two fires were selected for 1981, 1961, 1942, and 1941 (Fig. 4.2). Fires larger than 200 ha and that burned primarily between June 1st and August 15th, were selected from provincial fire databases (Table 4.1) (Delisle and Hall 1987; Department of Environmental Protection (DEP) 1996). At the time of sampling, fire dates were available on fires occurring between 1961 - 1994 .

Within each fire, we sampled a minimum of seven burned stands that were mixtures of primarily aspen and white spruce pre-fire. We selected stands for which canopy kill exceeded 95%, thus fire and stand selection criteria ensured that mineral soil microsites were probably available following fire. Sampled stands were adjacent to spruce seed sources containing trees which were seed producing at the time of fire. Seed sources that were 80 years-old or older at the time of the fire, according to forest inventories (Phase III and Alberta Vegetation Inventory) (DEP b; DEP c) were assumed to contain seed trees at the time of the fire. In fires originating in 1961 or earlier, we confirmed that white spruce trees were present in the canopy (i.e. seed producing, see Coates *et al.* 1994.) at the time of the fire with historical air photos. Stands were randomly selected from all suitable seed sources in the fire. Stands were located between 300 m to 5 km apart, and originated primarily from independent seed sources. Forest inventories (Phase III maps, and Alberta Vegetation Inventory), air photos (1:15840 –

1:31680, Black and White), and fire data were used to identify stands meeting these criteria prior to fieldwork (DEP 1996; DEP a; DEP b). We used geographic information systems (GIS) software ARCVIEW 3.0 for displaying fire and forest inventory data during stand selection.

We sampled during the summers of 1998 - 2000. We sampled along a transect that was oriented perpendicular to the unburned seed source, and that extended into the fire away from an unburned edge or residual. Three plots (2 x 2.5 m) were located at both 20 m and 100 m from the seed source. At each distance, the middle plot was located randomly on either the right or left side of the transect, while the two further plots were randomly located between 8 to 20 m from the transect (see Fig. 4.3). Spruce density and height of all spruce that were found, except germinants of the current year, were recorded in each plot at 20 and 100 m. Spruce densities were also recorded within a 3 m radius of the plot center at each plot (28.3 m^2 plot). Current year seedlings were only observed during the summer of 2000 in 1941 and 1942 fires. To determine whether current year seedling germinants on duff and moss substrates lived, the locations of 53 seedlings were marked in one stand in June 2000, and censused in September 2000, and early August 2001. In a minimum of three stands per fire, five live spruce trees (all sizes of post-fire establishment) that were located nearest to the plot center were collected for aging, for a total of 15 trees at each distance in the stand (see section 4.4.3 for aging methods).

Additional biotic and abiotic variables (see Table 4.2) were measured only within the middle plot at each distance (adjacent to the transect; see Fig. 4.3). The abiotic variables measured were slope, aspect, duff thickness, and soil texture. Percent cover estimates of vegetation were made to the nearest percent for the following strata: 1) ground cover (this stratum added up to 100%): lichens, bryophytes, liverworts, duff, conifer litter, exposed soil, trunk (live trees), downed wood on the ground, the percent of moss covered wood (out of total ground cover); 2) shrubs: ground shrubs (0 - 0.2 m), low shrubs (0.21 – 0.5 m), tall shrubs (0.51 – 2.0 m); 3) trees: for each species, percent cover was recorded between 0 – 0.5 m, and 0.51 – 2.0 m; 4) graminoids: live grasses and dead grasses (principally *Calamagrostis canadensis*; and 5) dead suspended wood: 0 – 0.5 m above the ground, 0.51 – 2 m from the ground; and 6) moss covered wood (percent of total ground cover with wood that was sufficiently decayed for spruce establishment).

For each tree species, we also recorded the number of live and dead individuals (post-fire regeneration) in the plot, and estimated its percent cover in the canopy using a convex spherical densiometer. Shrubs taller than 2 m were included in estimates of canopy cover. The basal area of each tree species was recorded with a number 10 Cruise Master prism (imperial units were ft^2 / acre). This estimate was made from the center of the 5 m^2 plot, but many trees recorded were outside the plot since such counts do not sample a fixed area. We estimated the proportion of total regeneration that each tree species represented (live individuals of all sizes) within a 3 m radius of the plot center.

We recorded the number of current seed trees (present at the time of sampling) and initial seed trees (present at the time of the fire) occurring in unburned patches within a 30, 60, and 100 m radius of the middle plot (at the 20 m distance on the transect). Thus, seed trees were counted within an arc that extended into the unburned patch. Current seed trees were those that occupied canopy or near canopy positions, while initial seed trees were trees that occupied these positions at the time of the fire. Based on observations that seed-producing trees typically had a breast height diameter (dbh) of 25 cm or greater (on fires up to 4 years old), and recent growth rates of tree rings from seed trees, we established diameter classes for estimating the number of initial seed trees present at the time of the fire. Trees were classified as initial seed trees if the dbh exceeded 30 cm in 1982 – 1979 origin stands, 35 cm in 1961 and 1958 origin stands, and 40 cm in 1941 and 1942 origin stands. We assumed that trees failing to meet these criteria were not seed producing at the time of the fire. Canopy trees that had blown down, but met the dbh requirement, were classified as initial seed trees. We counted seed trees that were within the burned area separately (fire survivors), and will henceforth refer to them as veteran trees. We recorded their abundance within a 30, 60, and 100 m radius of the middle plot, at both the 20 m and 100 m sites along the transect. The direction of burnt stands from seed sources was recorded with a compass. We estimated the basal area of white spruce trees in the unburned source plot using the prism mentioned earlier. This plot was situated 10 m away from the start of the transect, in the unburned forest. The height, dbh, and canopy position of the 5 nearest seed trees to this location were recorded. From these trees, the smallest, medium, and largest individual were cored at breast height to estimate age.

4.4.2 Effects of delay length on density

To test the influence of the length of delay between fire and the next mast year on white spruce density, we sampled fires with a 1, 2, and 3 year delay (1982, 1981, and 1980 respectively, where 1983 is the mast year). Using the fire selection criteria outlined in 4.4.1, two fires from each of these years were selected. 1983 was the only recent mast year for which replicate fires were available for each of the preceding three years. There were no 1983 (mast year) fires available to test if 0 year delay (YD) fires differed from 1 – 3YD fires; therefore, we used the 1979 mast year instead as the 0YD fire. One limitation to using 1979 for the 0YD fire in comparisons of regeneration density is that we do not know how similar seed production was between 1979 and 1983, and mast years can differ considerably in seed rain.

The sampling procedures outlined in section 4.4.1 were used. In addition, we estimated the proportion of live and dead (standing and fallen) pre-fire trees to species within a 5 m radius of the plot center. Trees were identified to species by examining shape, bark, or cones if present. We confined our analyses of pre-fire species data to fires between 1980 – 1982 (section 4.5.2), because species characteristics could not be accurately distinguished in several older fires in section 4.4.1.

4.4.3 Timing of regeneration on fires

Accurate ages of trees were required to determine the timing of regeneration. Aging errors in white spruce increase as stands age because greater burial of the root collar occurs below ground level (top of the humus soil layer) in older stands, and the number of missing rings at the root collar increases (see Chapter 2, section 2.6.1 and 2.6.2). We accounted for these errors by using more detailed crossdating techniques as stands aged. The procedures in Chapter 2, section 2.4.2 were used as follows: 1) trees from 1991, 1992, and 1994 fires were carefully aged the same as 7-year-old stands (YOS) (ring counting at the base of the hypocotyl (root collar age)), 2) trees from 1979 - 1982 fires were aged the same as 20 YOS (included below-ground crossdating (BGC) with skeleton plots), and 3) trees from 1961 to 1941 fires were aged according to 38 YOS (included BGC and visual crossdating above ground using a master chronology and the dendrochronology software program "Cofecha"). Trees from the 1981 Mariana Lake Fire were collected prior to our investigation of aging errors (see Chapter 2); consequently, BGC was not conducted, and only ground-level ring counting was conducted. Trees on 1941 and 1942 fires were crossdated with a master chronology that was constructed from stand 5 on the 1941 Piche Lake Fire. Stand 5 was selected because it possessed the same characteristics as the reference stand in Chapter 2, section 2.4.2. Ground-level ring counts are compared to crossdated ages on fires from 1982 to 1941.

To determine the age structure for stands originating in mast and non-mast years (section 4.4.1), we aged approximately 30 trees / stand (15 from each distance) from a minimum of two stands per fire according to the above procedures. To identify the age of the dominant regeneration cohort in fires with a one, two, or three year delay before a mast year (1982, 1981, and 1980 respectively), we used the above procedures to carefully age a minimum of 15 trees per stand in a minimum of three stands per fire age. In order to accurately age more stands with 1 – 3YD, trees from either the 20 m or 100 m plots were aged in each stand. Stands that were carefully aged were randomly selected from all stands sampled in each fire.

4.4.4 Cone production in northeastern Alberta

To assess the variation in cone production within the study area, cone crops of white spruce were monitored annually at 8 to 14 sites between 1998 - 2001. Surveyed sites spanned the N - S and E - W distribution of sampled fires, and were distributed along the principle highways (Hwy. 2, 55, 63, 813, 881). Surveyed sites were located at least 40 km from one another. Cone production was quantified on 10 canopy dominant white spruce from mixedwood stands. The length of the cone-bearing portion and the percent cover of cones (to the nearest percent) in this part of the tree were estimated on one side of the tree by an observer standing approximately 30 m from the tree. A cone production index was obtained from the multiplication of these two variables. To assess the range of interannual variation in cone production, coefficient of variation values (CV = SD / mean x 100) were calculated from the cone index for each site with three years of data. CV values are useful because they measure proportional variability independent of the mean (McArdle and Gaston in Herrera 1998). CV values are a widely used index for comparing the scale of mast-seeding in species showing interannual variation in seed production (Herrera *et al.* 1998), and may indicate the likelihood of mast years contributing proportionally more regeneration than non-mast years.

4.5 Data Analysis

4.5.1 Mast year effect

To test whether stands originating from mast year fires had significantly greater white spruce regeneration than stands originating from fires in years of low cone crop, all mast year fires and years of low cone production between 1941 and 1994 (non-mast year fires with moderate seed crops were excluded, i.e. 1980, 1982) were analyzed in a generalized linear model (GLM). Count data of all white spruce individuals from 2 x 2.5 m plots were initially modeled using a Poisson distribution. Error distributions were overdispersed; therefore, we used quasi-likelihood estimation with appropriate link and variance functions (McCullagh and Nelder 1989). Stands (rather than fires) were treated as the sampling unit because replicate fires were not available for many years, and because high variability in fire intensity occurs between stands. The large size of sampled fires and varying weather conditions in which stands burned (most fires burned for at least 3 weeks) contribute to burn variability within fires (Alexander and Degroot 1998; Johnson 1992). The variables tested while constructing the GLM are listed in Table 4.2. Variables included in the model were added following a stepwise procedure until the inclusion of additional variables did not yield a significantly better model ($p \leq 0.05$). All variables were tested for non-linear effects using generalized additive models and a smoothing spline. Variables with significant non-linear effects were modeled with a third order polynomial function model.

The above analysis was performed at: 1) the stand level, and 2) the plot level (Table 4.2):

1) The stand-level analysis included variables that had similar effects on all plots within: a) stands (seed trees, mast versus non-mast fire, time since fire, and wind direction), and b) 20 m and 100 m plots (proportion regeneration of other tree species, and the number of veteran trees within 30 m). Values of these predictor variables were used for each plot within its respective distance and stand.

2) The plot-level analysis included only the middle plot (adjacent to the transect) at each distance. This analysis included all of the above variables, as well as percent vegetation cover data (i.e. grass, herbs, shrubs, trees, canopy closure, ground cover).

Models included factors providing the most significant explanatory power for spruce regeneration. S-Plus 2000 Professional Release Version 2.1 was used for GLM analyses.

4.5.2 Effects of delay length on density

To test whether delay lengths of 1 - 3 years before the next mast year (1983 in this case) affected regeneration density, 1982, 1981, and 1980 fires were tested in another GLM analysis. In this analysis, the predictor variable fire type was replaced with delay length (1, 2, and 3 years), otherwise, the same procedures were followed as described in section 4.5.1 (i.e. stand and plot-level analyses were performed). The variables tested while constructing the GLM are listed in Table 4.3.

A general linear model (ANOVA) was then used to determine whether the density of spruce in the 1979 (mast year) fire differed from that in the 1980, 1981, and 1982 fires. Spruce densities from the 28.3 m^2 plot were used for this analysis rather than the 5 m^2 plots which were used in the above analyses. We thought the larger plots would provide a stronger test for density differences because a larger area was sampled. Delay length was tested as a fixed effect, while replicate stands were tested as random effects. Replicate stands were nested within delay length. The Type IV sums of squares method was used because the number of stands per delay length was not equal, and several plots were missing. Post hoc comparisons between delay lengths and the mast year fire were made using Tamhanes tests due to unequal varience between fires with different delay lengths (Zar 1996). SPSS version 10.0 was used for these tests.

4.5.3 Age structure tests

A number of statistical tests were used to determine if fire timing relative to mast year affects the age structure of regeneration. A one-tailed ANOVA was used to test whether the proportion of regeneration arising from the first mast year post-fire differed between fires with different delay lengths before the next mast year (1991 and 1979, 1982, 1981, and 1982; 0, 1, 2, 3YD respectively). For the 0YD fires, the one carefully aged (crossdated) stand from the 1979 fire was included in the analysis as well as 5 randomly selected stands from the 1991 fire; this made sample sizes more similar to fires with 1 – 3 year delays. We also used the carefully aged trees from the 1982, 1981, and 1980 fires (7, 4, and 6 stands respectively; section 4.4.3). Based on the tree ages, we calculated the proportion of regeneration originating from the first mast year post-fire in each stand ($n = 22$ stands). Proportion data were normalized with an arcsine transformation (Sokal and Rolph 1981). Tukey's "honestly significant difference" test was used for post-hoc tests.

Using the establishment year for all trees, we assigned a time-since-fire establishment date for each tree (i.e. 1, 2, 3 years post-fire etc.); this permitted standardization of age structures relative to fire age. Using a two-sided Kolmogorov Smirnov test (K-S; henceforth referred to as age structure tests), we then tested whether age structures differed between stands within each fire from 1980, 1981, and 1982. K-S tests are sensitive to the location, spread, and skewness of the data (Sokal and Rohlf 1981). Age structure tests were pairwise comparisons between two stands, and multiple pairwise comparisons were made between all aged stands from the same fire. Bonferroni corrections were applied in all K-S tests to maintain an alpha value of 0.05. These tests allowed us to determine whether variation in establishment timing occurred between stands burned in the same fire.

The ages of trees from all stands within a fire were then pooled to obtain an age structure for each fire. We then tested whether age structure differed between fires from 1979, 1980, 1981, and 1982 using a K-S test. Age structure tests were pairwise comparisons between two fires. Bonferroni corrections were applied in all K-S tests to maintain an alpha value of 0.05. These tests allowed us to determine whether significant variability occurred in establishment timing between fires when: 1) fires occur in different locations in the same year, and 2) a mast year occurred in different years post-fire.

Detailed age structure comparisons for the 1961 – 1941 fires are made in Chapter 5.

4.5.4 Cone surveys

We used a one-tailed ANOVA to determine whether the cone crop index differed between the years 1998, 1999, 2000, and 2001. Cone survey sites were used as the replicate. Post hoc comparisons between years were made using Tukey's "honestly significant difference" test.

4.6 Results

4.6.1 The mast year effect

Over the 59-year period studied, spruce densities were significantly higher in mast year fires (MYF, 1991, 1979, 1961, 1941) than years of low cone production (1994, 1992, 1981, 1958, 1942; $p < 0.001$; Table 4.4, Fig. 4.4). Spruce densities were higher on MYF at both distances for fires as recent as 1958, but not in 1941 and 1942 fires. Overall, spruce regeneration densities were about three times greater in MYF than non-mast year fires at 20 m from seed sources (3588 versus 910 stems / ha), and twice as great at 100 m from seed sources (2197 versus 1058 stems / ha) (Fig. 4.4). These densities excluded current year germinants that were found on leaf litter and moss in 1941 and 1942 fires because they had only 5.7% survivorship in their first growing season, and 0% overwinter survivorship.

In stand-level models, a total of 24.1% of the deviance in spruce density was explained by the model including fire occurrence in mast versus non-mast years, the direction of plots from the seed source, the number of initial seed trees (within 100 m of the 20 m plots), the proportion of black spruce regeneration, distance from seed source, and the number of veteran trees (within 30 m of the plots) (Table 4.4). A greater amount of variation was explained by seed trees and veteran trees at these distances; consequently, they were used in models rather than trees at other distances. Regeneration was greatest in burned stands situated downwind of seed sources relative to prevailing northwesterly winds (60 ° - 180°).

Plot-level models explained 33.6% of the deviance in white spruce regeneration, and verified the importance of all predictor variables from the stand-level analysis (Table 4.5). In addition, plot-level models identified that spruce density declined in plots with higher percent cover of live grass (principally *C. canadensis*). Percent cover of herbs, shrubs, tree species, and ground cover (mosses, litter, etc.) did not improve the model.

4.6.2 Regeneration versus delay length before a mast year

In the stand-level analysis of fires with a 1, 2, and 3YD before a mast year, several factors relating to seed availability were significant predictors of spruce regeneration. A total of 60.0% of the deviance in the generalized linear model (GLM) was explained by: the number of initial seed trees within 60 m of the 20 m plots, distance from seed source, direction from seed source, the proportion of black spruce regeneration, and the proportion of jack pine in the stand pre-fire ($p < 0.001$ in all cases; Table 4.6). In the GLM analysis, spruce densities did not differ significantly between fires of delay lengths ranging between 1 - 3 years, and delay length accounted for only 0.7% of the deviance ($p = 0.163$, Table 4.6, Fig 4.5). The abundance of seed trees within 60 m predicted a greater percentage of the deviance than total trees at other distances. Spruce densities were significantly higher downwind of seed sources, and at 20 m than 100 m.

In plot-level models, all of the variables in the stand-level model remained significant and provided the best explanatory power (69.5% of the deviance; Table 4.7). The percent dead grass cover was negatively related to white spruce density, and was the only plot-level variable that significantly improved the model fit ($p < 0.001$; Table 4.7); percent cover of herbs, shrubs, tree species, and ground cover (mosses, litter, etc.) did not improve the model. The abundance of seed trees adjacent to the edge did not provide as strong a predictive relationship as total trees within 60 or 100 m from the plots.

According to the ANOVA analysis of regeneration density in the 28.3 m^2 plots, the fire coinciding with the 1979 mast year had significantly higher white spruce density than fires with a 1, 2, or 3YD (1982, 1981, and 1980 respectively; $p < 0.02$ in all cases; Table 4.8; Fig. 4.5). Spruce density did not decline consistently with increasing delay length before a mast year. Fires with a 1YD had significantly more spruce than fires with a 2YD ($p = 0.022$, Table 4.8), but fires with a 2YD had significantly fewer spruce than 3YD fires ($p = 0.001$, Table 4.8). There were no significant differences between fires with 1YD and fires with a 3YD. For 0, 1, 2, and 3YD fires, mean abundance of initial seed trees within 60 m were very similar (15.6, 18.4, 14.8, and 19.6 respectively). For 0, 1, 2, and 3YD fires, the percent of stands downwind of seed sources were 40%, 18.8%, 37.5%, and 46.6% respectively. All stands were sampled at 20 m, while 80%, 100%, 75%, and 100% of stands were sampled at 100 m on 0, 1, 2, and 3YD fires.

4.6.3 Timing of regeneration

Age structures of trees in fires up to 20 years old demonstrated that the first mast year cohort was very important for white spruce regeneration. For these fires, the first mast year following fire was the most important cohort (largest) in both mast year fires (Figures 4.6a, b), in one fire with a 1YD (4.6c, d), and in one fire with a 2YD (4.6f). In fires with a 3YD, the first mast year cohort was smaller than regeneration in non-mast years (4.6g, h). These age structures were based on below-ground crossdating, which improved age estimation by between 1 - 10 years per tree (Table 4.9). The proportion of regeneration originating from the first mast year declined from 60.4% in mast year fires to 15.6% in fires with a 3YD (Fig. 4.7). Regeneration in the first mast year represented a significantly higher proportion of total white spruce density in mast year fires than in fires with delays (Fig. 4.7, Table 4.10; $p < 0.05$ in all cases). The mast cohort also represented a significantly higher proportion of spruce density in 1YD fires than in 3YD fires ($p = 0.028$). Mast years occurring four or more years following fire (e.g. 1987, 1991) did not account for more regeneration than preceding or subsequent non-mast years, and very little regeneration occurred between 7 - 20 years after fire (Fig. 4.6).

Significant differences in age structure were observed between fires of varying delay length, but not between fires with the same delay length (Table 4.11). The age structure in the mast year fire differed significantly from some of the 1 and 2YD fires, but surprisingly, not from fires with a 3YD before a mast year (Table 4.11). The similarity in age structure between the mast year and 3YD fires appeared attributable to the large 1981 cohort in 3YD fires, even though this was a non-mast year (Fig. 4.6). In contrast, limited regeneration occurred in 1 and 2YD fires (1981 and 1982) before the cohort arising from the 1983 mast year (Fig. 4.6).

Within individual fires, there were considerable differences in the amount of between stand variability in age structure. No significant differences were found between stands within each 1YD fire (Fig. 4.8a1 - a7). The 1984 cohort (originated from the 1983 mast year) was dominant in all four stands in the 1982 Rock Island Fire (4.8a1 - a4), but was dominant in only one out of three stands in the 1982 House River Fire (4.8a7). On the 2YD fire (1981 B), significant variation occurred between several stands (4.8b1 - b4). Only stand 6 showed a dominant mast cohort in 1984 (4.8b4). In 3YD fires, there was no significant variation among stands from the 1980 Winefred Lake Fire, and the 1981 non-mast year cohort was dominant in all stands (4.8c1 - c3). In contrast, the 1980 Conklin Trail Fire had significant variation among stands (4.8c4 - c6), and a dominant 1981 cohort occurred only in stand 7 (Fig. 4.8c6).

Overall, an initial mast cohort was less apparent in older fires. The initial mast cohort was dominant in the 1961 fire, and was important in the 1941 Piche Lake Fire (Fig. 4.9b). In both 1942 fires, regeneration appeared continuous throughout the first 10 years after fire. Despite crossdating, initial regeneration periods appeared considerably longer in fires from 1941 to 1961, than in more recent fires from 1980 to 1982 (Figures 4.9 and 4.8 respectively). Crossdating indicated that age underestimation increased significantly between 1979 and 1961 fires (Chapter 2, section 2.6.2). Fires between 1980 and 1982 showed similar aging errors to the 1979 fire, while fires between 1961 and 1941 had similar aging errors to the 1961 fire (Table 4.9).

4.6.4 Cone crops

Cone crops decreased each year following the 1998 mast year (Table 4.12). A significant difference in cone index existed between the 1998 mast year and each of the other years ($p < 0.034$ in all cases), and between 1999 and 2001 ($p = 0.031$; Table 13). The standard error of annual cone production was greater relative to the mean in non-mast years than in the 1998 mast year; therefore, between site variation was greater in non-mast years than mast years. Coefficient of variation values on sites with 3 years of data (n=13 sites) ranged between 39.1 - 155.5 with a mean of 93.9 (Table 13).

4.7 Discussion

4.7.1 The mast year effect

We found significantly higher densities of white spruce when fires coincided with mast years than when fires coincided with years of low cone crops (mast year effect). The mast year effect was most apparent in fires as recent as 1958 (Fig. 4.4); however, it did not appear as important in 1941 and 1942 fires. The duration of the mast year effect is surprising, because many stand age structures in previous studies suggest that gradual (2 or more years after fire) and / or delayed ingress (20 or more years after fire) accounts for the majority of white spruce regeneration that occurs in stands older than 60 years old (Youngblood 1995; Lieffers *et al.* 1996, Galipeau *et al.* 1997). The persistence of density differences between mast and non-mast fires suggests that an initial mast cohort (1 year after the fire) contributed more regeneration in mast year fires, and that this cohort was more important than regeneration in subsequent mast and non-mast years.

Only a few studies have demonstrated that higher recruitment actually occurs in mast years versus non-mast years (Wurtz and Zasada 2001, Zasada et al. 1978; Taylor and Aarssen 1989; Ida and Nakagoshi 1996; Salisbury in Crawley 1997; Sato 2000). In instances where several mast cohorts occurred, intraspecific competition within the cohort caused rapid self-thinning (Taylor and Aarssen 1989), and the oldest cohorts had extremely low densities (e.g. 1.3 oak saplings / ha) (Negi 1996). An initial mast cohort of white spruce is unlikely to self-thin rapidly because seedlings grow very slowly (Coates *et al.* 1994, Peters *et al.* 2002) and it is unlikely to occur in pure stands in mixedwoods. Some evidence of mortality of saplings was observed in stands from the 1961 and 1958 fires, but dead stems were common in 1941 mast year fires (see Chapter 5, Fig. 5.14). Greater mortality of initial regeneration in the 1941 mast year fires than in the 1942 non-mast fires suggests that self-thinning is greater in fires where regeneration is more dense, and helps explain why a mast year effect was not apparent in the oldest stands (see Chapter 5, section 5.6).

Statistical models identified several factors relating to substrate and seed availability that were important predictors of the density of white spruce regeneration. Higher spruce densities in fires coinciding with a mast year suggests that seedbeds were more suitable at this time, than when mast years occurred in years subsequent to the fire.

A few studies have reported a three to five year time window for regeneration after fire as a result of rapid seedbed deterioration (Zasada and Gregory 1969; Purdy *et al.* 2002). On harvested sites, mast years must usually occur within a few years of mineral soil exposure (through seedbed scarification) in order for dense recruitment to occur (Rowe 1955; Day 1964; Lees 1963), although Wurtz and Zasada (2001) also observed a case of dense regeneration on unscarified sites. Our data showed that spruce density also increased significantly with seed tree abundance. The number of initial seed trees within 100 m of plots ranged between 2 and 200 trees. Variables such as tree species composition, canopy closure, and percent cover of herbs and shrubs reflect the influence of biotic interactions over time such as competition. Most of these variables were poor predictors of white spruce regeneration, which suggests that early post-fire regeneration is a key stage for white spruce establishment. The increase in white spruce regeneration on mineral soils with greater black spruce regeneration may generally indicate better site conditions for germination and survival.

Modeling the importance of variables predicting spruce regeneration helped identify factors that may have confounded the observation of a mast year effect. Higher regeneration densities at 100 m from seed sources in 1942 non-mast fires than in 1941 mast year fires may have been due to veteran tree densities that happened to be 3.33 times greater in non-mast fires. Veteran tree abundance was significantly related to increasing spruce density, and was a variable included in statistical models. Poor spruce recruitment as a result of inadequate seed sources has been reported frequently (Greene and Johnson 2000, Coates *et al.* 1994).

Spruce densities were twice as high at 20 m versus 100 m from the seed source, despite the fact that seed densities are typically at least four times higher at 20 m than at 100 m (Coates *et al.* 1994). A contributing factor may be reduced mineral soil exposure in 20 m plots due to closer proximity to the unburned fire edge (pers. obs.). Many young stands (up to 20 years of age) in both mast and non-mast fires had no regeneration despite an adjacent seed source. In these cases, we suspect that burn severity was inadequate to expose mineral soil and permit regeneration. Variation in burn intensity was not assessed, and may have contributed to the large amount of unexplained deviance in statistical models. Mast years for white spruce also vary considerably in seed rain

(Waldron 1965; Zasada in Nienstaedt and Zasada 1990), and differences between the mast years studied may have further limited the explained deviance.

4.7.2 Effect of delay length on regeneration

Several factors may have led to the differences in white spruce density between fires with different delay lengths. The significantly lower density of white spruce in one year delay (YD) fires than the mast year fire may indicate that seedbed receptivity had already declined. This interpretation may be reasonable because burned seedbeds have been shown to deteriorate rapidly (Purdy *et al.* 2002); however, a confounding factor is that spruce regeneration originated from different mast years on the 0YD fire and the 1YD fire (1979 and 1983 were the respective mast years). Hence, seed production in these two mast years may have differed and contributed to density differences in spruce regeneration. ANOVA models detected significant density differences among fires with 1 - 3 year delays ($p = 0.008$, Table 4.8), even though generalized linear models did not ($p = 0.163$; Table 4.7). We regard the ANOVA model as more accurate than the generalized linear model because a larger sampled area was used in the ANOVA analysis (28.3 m^2 versus 5 m^2 plots, respectively). Still fewer spruce were found in fires with a 2YD than fires with a 1YD, suggesting further seedbed declines. Spruce density did not decline consistently with increasing delay length before a mast year (i.e. 3YD had significantly more spruce than 2YD). This suggests large cohorts occurred in some of the non-mast fires. Waldron (1965) found that seed rain was quite variable in years that he rated as light and moderate seed crops, with a range of 2.5 to 374 seeds / m^2 in pure white spruce stands. The forestry literature indicates that in harvested cutblocks, regeneration can occur at moderate densities in non-mast years (Rowe 1955; Day 1964; Lees 1963).

A few additional factors may have contributed to density differences between fires with different delay lengths. The percent of stands that were downwind of seed sources differed considerably between 0, 1, and 2YD fires (40%, 18.6%, and 37.5% respectively). This is important because Stewart et al. (1998) found that white spruce regeneration was greater in stands downwind of seed sources than in stands that were not downwind (relative to prevailing winds blowing from the West, northwest and southwest). Our data supports this; consequently, 1YD may have had higher densities than what we observed, if sampling had been more similar with respect to seed source location. This suggests that a smaller decline in density may occur between 0YD and 1YD fires, and a greater decline may occur between 1YD and 2YD fires. Weather conditions were not assessed and could also have influenced germination and survivorship differently in fires with different delay lengths. Nonetheless, our results and the literature strongly suggest that spruce regeneration declines rapidly with increasing time since fire (Zasada and Gregory 1969; Purdy *et al.* 2002).

Fire is regarded as a proximal trigger for seed production in some masting species (Kelly 1994). The environmental prediction hypothesis for masting proposes that plants are capable of predicting the best year for seedling establishment (Smith *et al.* in Kelly 1994). The supporting evidence for this hypothesis comes from monocot species that flower after fire despite depleted carbohydrate reserves (Gill in Kelly 1994; Payton and Brasch in Kelly 1994). White spruce cone induction is related to hot, dry weather at the time of bud differentiation (Eis 1967). If white spruce cone production was also induced by fire, it would affect the likelihood of observing delay length effects on regeneration. Reproductive bud differentiation occurs in the last two weeks of July (Nienstaedt and Zasada 1990); consequently, white spruce could potentially respond to an early summer fire and produce a mast crop the following year. This would mean a minimum delay of 1 year would occur after fire before masting. Fires with a 1YD only had moderate spruce regeneration (despite fire initiation dates in mid-June), rather than the greatest regeneration required by the environmental prediction hypothesis. Thus, fire induced masting would not be as advantageous as required by this hypothesis.

4.7.3 Mast cohorts and population dynamics

Crossdating verified that the first mast year post-fire accounted for the majority of regeneration in mast year fires as recent as 1979, and that the first mast year post-fire was the largest cohort in a 1961 mast year fire. A long lasting mast cohort effect (38 years) has not previously been demonstrated (in the age structure) for a polycarpic masting species. A larger mast cohort would probably have been observed in 1961 and 1941 mast year fires if aging errors did not increase in older stands and if all trees in these stands could be crossdated accurately (Peters *et al.* 2002). Right-skewed tails in age distributions after the first mast year are more likely an artifact of aging limitations (Peters *et al.* 2002; Desrochers and Gagnon 1997) and regeneration from seeds shed in non-mast years, than delayed germination from the mast year. White spruce shows extremely low seed viability beyond one year in the field (Coates *et al.* 1994), however a few studies suggest that a little delayed germination occurs in the second year (Stewart 2000; Stewart *et al.* 2000). If delayed germination was important, the first mast year could have contributed an even higher proportion of the total spruce regeneration.

The importance of the first mast cohort declined with increasing delay length. The first mast cohort post-fire (1984) was also the most important cohort in fires with a 1YD, but it was less important in fires with a 2YD (1981 fires). Still, this cohort was the largest in the 1981 B fire, and may have been larger in the 1981 Mariana Lake Fire than depicted because trees were not crossdated with skeleton plots, which would have yielded significantly higher estimates of age (Peters *et al.* 2002). Mast years occurring three or more years after fire did not contribute a large cohort in any fire during the time period examined. The rapid decline in mast cohort importance with increasing delay length further suggests that seedbed suitability declined with time since fire. This helps explain the mast year effect, because mast years occurring later after a fire had smaller cohorts than preceding non-mast years in many stands.

Age structure comparisons of fires with varying delays between fire and the first mast year demonstrate that both seed limitation and seedbed deterioration affect age structure. Differences in timing of regeneration between the 1979 mast fire, and fires with 1 and 2YD (1982 and 1981), show that seed crop availability has an important influence on age structure. If substrate deterioration was the main control of age structure we would have expected all age structures to resemble the 1979 mast year fire (i.e. domination by the cohort regenerating in the first year after fire), especially because regeneration was observed in non-mast years in several fires (Fig. 4.6g, h).

One reason why the mast year effect is so strong is that a higher proportion of mast year germinants may also survive in fires that coincide with mast years because of reduced plant competition immediately post-fire. *Calamagrostis canadensis* is a common grass species in mixedwoods that increases in cover following harvesting (Landhausser and Lieffers 1997). If the grass rapidly increases in cover after fire, it may prevent spruce regeneration within a few years of fire. *Calamagrostis canadensis* has a detrimental effect on white spruce survival and growth (Eis 1981), which may explain the negative relationship we found between *C. canadensis* and spruce density.

4.7.4 Mast cohorts and seed predator escape

The occurrence of a distinct mast year cohort of white spruce in recent fires, suggests that masting does permit significantly more seeds to escape predation at the pre- and post-dispersal stages, and seedling establishment stages. Previous studies on pre and post-dispersal seed predation indicate that white spruce seed crops can potentially be decimated by a combination of seed predators in non-mast years, but that seeds do escape to germinate in mast years on cutblocks (Alden 1985; Coates 1994; Peters 2000). Seed rain data indicate that varying levels of seed are dispersed in non-mast years (Waldron 1965; Nienstaedt and Zasada 1990; Stewart *et al.* 2000). Peters (2000) found that post-dispersal seed predators prevented higher seed densities from resulting in significantly higher numbers of recruits in mixedwood cutblocks. This suggested that post-dispersal seed predators ceased foraging at low seed densities, and thereby exhibited optimal foraging behavior. Optimal foraging behavior would reduce the likelihood that a mast year effect would occur on fires. The mast years studied must therefore have satiated seed predators because significantly more regeneration occurred on mast year fires than non-mast year fires. Sato (2000) found that microtine abundance was reduced by fire. Lower populations of seed predators within burned areas may enhance the mast year effect because proportionally more seeds would escape seed predators in mast year burns.

Regeneration in non-mast years (i.e. 1980 fires; Fig. 4.6g, h) demonstrates that white spruce does not rely solely on mast years for regeneration. Moderate regeneration in non-mast years has been observed in cutblocks when substrate and environmental conditions were favorable (Noble and Ronco 1978). Regeneration was not consistent in non-mast years on fires with varying delay lengths. Fifty-three percent of stands exhibited no regeneration in some of the non-mast years leading up to the first mast year, even though the first few years after fire are when seedbeds are most receptive (Fig. 4.8). The 1982 cohort from the 1981 seed crop was the most frequent non-mast cohort missing during the receptive period (Fig. 4.8b1 - 4, c5, c6); however, 1981 was also the year with the lowest cone harvest between 1979 - 1991 (Fig. 4.1). Reports of complete cone failure within individual stands of white spruce (no cones produced on any trees) are rare in the literature (e.g. Waldron 1965), and we observed complete failure only once in 1 out of 14 stands that we monitored over a 5 year period. Assuming some cones were produced in 1981 in stands lacking a 1982 cohort, our results suggest that seed predators may have prevented regeneration during some non-mast years in some stands. These results are interesting because several researchers have suggested that species in fire-prone systems may not show the same degree of seed loss to seed predators as communities lacking stand replacing disturbances (Silvertown 1980; Kelly and Sullivan 1997).

Silvertown (1980) identifies "true" masting species by the presence of a specific seed predator, whose populations fluctuate in synchrony with seed production, thereby necessitating greater variation in seed between mast and non-mast years to satiate and starve predators. Herrera *et al.* (1998) used coefficient of variation values (CV, variation in seed production between years) to identify the scale of interannual variability among masting species. CV values reported for white spruce range between 124.8 – 137, which exceeds the mean level of interannual variation reported for 144 tree species (115.2; Herrara *et al.* 1998). CV values for white spruce in the study area between 1998 - 2001 were a little lower (93.9). Our estimates are likely conservative because we assessed a shorter time interval than the other studies on white spruce, which leads to underestimates of CV (Pimm and Redfearn in Herrara *et al.* 1998). Furthermore, more viable seed is produced per cone in mast years than non-mast years (Coates *et al.* 1994). Thus, our use of cone abundance rather than seed abundance likely underestimated CV. It would be interesting to determine whether the strength of the mast year effect in masting species is dependent on the interannual variation in seed production. The short time window post-fire for dense regeneration may augment the mast year effect more than in systems that are not fire-prone. Furthermore, most other masting species have less specific microsite requirements, permitting frequent recruitment (Taylor and Aarssen 1989; Ida and Nakagoshi 1996; Sato 2000); this would reduce reliance on a single mast cohort for successful regeneration.

4.7.5 Mixedwood dynamics

The absence of dense regeneration on most fires (i.e. non-mast fires) may greatly reduce the prevalence of white spruce in the mixedwood landscape. Important fire years that coincided with mast years have probably been critical in determining existing white spruce populations in boreal mixedwoods of Alberta. While regeneration on decayed logs permits gradual ingress (see Chapter 5, section 5.7.1), later regeneration may fail to reach reproductive maturity prior to a stand-replacing fire (Gutsell and Johnson 2002). Sites with little regeneration immediately after fire will likely have too few seed trees to replace pre-fire spruce after fire. Fire and masting history could therefore contribute to temporal stochasticity in mixedwoods over several fire cycles, creating a shifting mosaic in forest composition.

The development of spruce understories in boreal mixedwoods is an important process that shapes successional changes in understory plant community structure, and habitat suitability for numerous wildlife species (De Grandpre *et al.* 1993; Stelfox 1995). We propose that masting cycle and fire relationships are keystone processes that affect the timing of these changes, and the extent to which they occur in mixedwood stands.

4.8 Conclusions

Annual variability in seed production is a critical aspect influencing white spruce regeneration in fire dominated landscapes. A mast year in the year of fire is more important than subsequent mast years, and accounted for the long lasting mast year effect. White spruce depends on recently burned mineral seedbeds for successful establishment. Initial establishment consistently lasted for five to seven years after fire in young stands, regardless of fire timing relative to mast years. Crossdating limitations on suppressed trees in middle aged stands, prevented age structures from showing the short duration of initial regeneration that is apparent in younger stands. The proportion of regeneration originating from the first mast year declined with increasing delay length, and indicated that seedbed receptivity declined with time. Non-mast years frequently do not contribute to regeneration despite moderate seed production, but in cases where they did, it occurred at substantially lower densities than mast years. Regeneration densities were greatly influenced by seed source strength, direction, and distance from source. The dynamic interaction of key fire years and masting cycles affects mixedwood successional trajectories, thereby creating temporal variability in forest composition that may be best characterized as a shifting mosaic.

Table 4.1: Characteristics and location of fires studied (Delisle and Hall 1987). The fire names provided are names I gave to study fires, while fire ID is the reference number used in provincial data inventories.

Year - Name	Size (ha)	Cause L = Lightning U = Unknown M = Man	Start Date	Location□ Twp-range-Mer	Fire ID
1994 Anzac Fire	2160	L	Jun-04	85-6,7-4	DA1-6-94■
1992 Rock Island Lake Fire●	65	L	Jun-09	76-23,24-4	DL3-7-92■
1991 Peerless Lake Fire	551	L	May-30	89-5-5	DS5-7-91■
1982 House River Fire	36762	L	Jun-12	75-15,16, 74-16-4	1639
1982 Rock Island Lake Fire	1402	L	Jun-13	75-23-4	1637
1981 Marianna Lake Fire	4119	L	Jul-03	79-13,12-4	1584
1981 B Fire	14209	L	Jul-03	80-12,13-4	1583
1980 Winefred Lake Fire	137313	M	May-02	73-4,74-3, 75-3-4	1537
1980 Conklin Trail Fire	1255	M	Apr-27	77-7-4	1531
1979 Winefred Lake Fire	389	L	Jun-26	75-4/76-3-4	1495
1961 House River Fire	2845	L	Jun-04	80-16-4	1223
1961 Goodwin Lake Fire	389	L	Jun-06	74-12-4	1224
1958 Lawrence Lake Fire	414	M	NA	69-24-4	1143
1942 Logan Lake Fire	2774	M	May-16	71-10-4	329
1942 Wabasca Fire	1558	M	May-06	78-22-4	344
1941 Piche Lake Fire	26871	M	Apr-30	70-11, 71-10,11-4	168
1941 Conklin Trail Fire	4355	U	Apr-26	71-13-4	187

■ Fire names according to the Alberta fire incidence database. These years were not mapped by Delisle and Hall (1987).

● No larger fires were found for this year, consequently the 1994 fire was sampled as well.

□ Cartographic grid system for Canada identifying locations by township, range, and meridian

Table 4.2 Variables tested in generalized linear models predicting spruce regeneration in mast and non-mast fires (section 4.5.1). Variables tested in stand-level models (Table 4.4) and plot-level models (Table 4.5) are identified with an "x". See note at bottom for tree species abbreviations.

Variables	Description	Stand Level	Plot Level
Time since fire	4-59 years	x	x
Fire type	2 categories: mast & nonmast	x	x
Distance	2 categories: 20 m & 100 m	x	x
Direction from seed source	six 60° intervals	x	x
Sin of direction●	trigonometry conversion	x	x
Downwind of seed source or not	2 categories (downwind: 60°-150°, not downwind: all other degrees)	x	x
Initial seed trees	within radii of:		
	30, 60, and 100 m	xxx	xxx
Current seed trees	30, 60, and 100 m	xxx	xxx
Veteran trees	30, 60, and 100 m	xxx	xxx
Mast & nonmast(Stand)*	105 stands	x	
Proportion regeneration of:	based on stem count		
Pm, Aw, Pbal, Jp, Bp, Fb		xxxxxx	xxxxxx
Canopy closure: all species	based on densiometer		x
Proportion canopy closure:	based on densiometer		
Pm, Pb, Pt, Pbal, Bp, Fb			xxxxxx
Proportion canopy closure:	based on percent cover		
Salix (all species)			x
Prunus virginiana			x
Amelanchier alnifolia			x
Alnus (all species)			x
Average Height	trees within 5 m^2 plot		
Sw, Sb, Aw, Pbal, Jp, Bp, Fb			xxxxxxx
Percent cover:	0-0.5 m from ground		
Sb, Jp, Aw, Pbal, Bp, Fb			xxxxxx
Percent cover:	0.5-2.0. m from ground		
Sb, Jp, Aw, Pbal, Bp, Fb			xxxxxx

Continued on next page

Table 4.2 Continued from previous page

Percent cover ground shrubs	0-0.2 m from ground	x
Percent cover low shrubs	0.2-0.5 m from ground	x
Percent cover tall shrubs	0.5-2.0 m from ground	x
Dead post-fire recruits of:	based on stem count	
Sb, Jp, Aw, Pbal, Bp, Fb		xxxxxx
Percent downed wood	on ground	x
Percent suspended wood	0-0.5 m from ground	x
Percent suspended wood	0.5-2 m from ground	x
Moss covered log		x
Percent grass	2 categories: live & dead	
Percent ground cover:		
duff, conifer litter, soil,		xxx
moss, trunk, liverwort		xxx
lichen, snag		xx

Note: Tree species abbreviations were: white spruce (Sw), black spruce (Sb), trembling aspen (Aw), balsam poplar (Pbal), jack pine (Jp), paper birch (Bp), and balsam fir (Fb).

• Sine of the direction from seed source (in degrees) along which the transect was oriented

Table 4.3 Variables tested in generalized linear models predicting spruce regeneration in relation to 1, 2, and 3 year delays before a mast year (1982, 1981, and 1980 respectively; section 4.5.2). Variables tested in stand-level and plot-level models are identified. All variables in table 4.2, except fire type and time since fire, were also tested in this analysis, however they are not listed here. The results from the stand and plot-level analyses are presented in Tables 4.6 and 4.7 respectively.

Variables	Description	Stand Level	Plot Level
Delay length	3 categories (1, 2, and 3 years)	x	x
Prefire species composition:	based on the proportion of fallen and standing stems		
black spruce		x	x
jack pine		x	x
trembling aspen		x	x
balsam poplar		x	x
balsam fir		x	x

Table 4.4 Results of a generalized linear model at the stand level. The model tests whether spruce regeneration densities differed on mast and non-mast fires (fire type) that occurred between 1941 and 1994, and shows which other variables from Table 4.2 were significant predictors of density. Variables are listed in the order of most significant to least significant, using a stepwise procedure. *p* indicates the significance of the deviance (analagous to variance) explained by each variable. *df* = degrees of freedom of the error. A polynomial function was used to model non-linear effects for initial seed trees in unburned seed sources that were within 100 m of the 20 m plots. ●Spruce seed trees in the burn that were within 30 m of the 20 m or 100 m plots.

Variable	*df*	% Deviance	*p*
Null	577		
Fire type	576	7.1	< 0.001
Direction	570	6.1	< 0.001
Initial seed trees within 100 m	567	5.0	< 0.001
Proportion black spruce regeneration	566	2.9	< 0.001
Distance (20 vs. 100 m)	565	2.0	< 0.001
Veteran trees within 30 m●	564	1.0	< 0.001
Total		**24.1**	

Table 4.5 Results of a generalized linear model at the plot level. The model tests whether spruce regeneration densities differed on mast and non-mast fires (fire type) that occurred between 1941 and 1994, and shows which other variables from Table 4.2 were significant predictors of density. Variables are listed in the order of most significant to least significant, using a stepwise procedure. *p* indicates the significance of the deviance (analagous to variance) explained by each variable. *df* = degrees of freedom of the error. A polynomial function was used to model non-linear effects for initial seed trees in unburned seed sources that were within 100 m of the 20 m plots. ●Spruce seed trees in the burn that were within 30 m of the 20 m or 100 m plots.

Variable	*df*	% Deviance	*p*
Null	222		
Fire type	221	7.9	< 0.001
Initial seed trees within 100 m	218	5.6	< 0.001
Proportion black spruce regeneration	217	5.1	< 0.001
Distance	216	4.9	< 0.001
Direction	210	4.6	< 0.001
Live grass cover	209	4.5	< 0.001
Veteran trees within 30 m●	208	1.0	< 0.001
Total		**33.6**	

Table 4.6 Results of a generalized linear model at the stand level. The model tests whether spruce densities differed on fires with a 1, 2, and 3 year delay before a mast year (1982, 1981, and 1980 respectively), and shows which variables from Table 4.3 were significant predictors of density. Variables are listed in the order of most significant to least significant, using a stepwise procedure. *p* indicates the significance of the deviance (analagous to variance) explained by each variable. *df* = degrees of freedom of the error. A polynomial function was used to model non-linear effects for variables with a ●. The seed trees modelled occurred within 60 m of the 20 m plots. ■ Delay length was not significant, and only explained 0.7 % of the deviance. Consequently its deviance was excluded in the total deviance.

Variable	*df*	% Deviance	*p*
Null	250		
Initial seed trees within 60 m●	247	30.9	< 0.001
Distance (20 vs. 100 m)	246	11.3	< 0.001
Direction	240	7.3	< 0.001
Proportion black spruce regeneration●	237	6.3	< 0.001
Proportion of jack pine prefire●	234	4.2	< 0.001
Delay length■	232		0.163
Total		**60.0**	

Table 4.7 Results of a generalized linear model at the plot level. The model tests whether spruce densities differed on fires with a 1, 2, and 3 year delay before a mast year (1982, 1981, and 1980 respectively), and shows which variables from Table 4.3 were significant predictors of density. Variables are listed in the order of most significant to least significant, using a stepwise procedure. *p* indicates the significance of the deviance (analagous to variance) explained by each variable. *df* = degrees of freedom of the error. A polynomial function was used to model non-linear effects for variables with a ●. The seed trees modelled occurred within 60 m of the 20 m plots. ■ Delay length was not significant, and only explained 1.6 % of the deviance. Consequently its deviance was excluded in the total deviance.

Variable	*df*	% Deviance	*p*
Null	94		
Proportion of black spruce regeneration	93	20.3	< 0.001
Initial seed trees within 60 m	92	18.7	< 0.001
Distance (20 vs. 100 m)	91	12.5	< 0.001
Dead grass cover	90	5.3	< 0.001
Proportion of jack pine prefire●	87	5.2	0.010
Direction	81	7.5	0.011
Delay length■	79		0.166
Total		**69.5**	

Table 4.8 Results of an analysis of variance testing whether spruce densities differed on fires with a 0, 1, 2, and 3 year delay before a mast year (1979, 1982, 1981, and 1980 respectively). Counts of live spruce were from 29.6 m^2 plots. Six plots were located within each stand (3 plots at 20 and 100 m respectively), and a total of 10 - 16 stands were sampled per delay length.

Source of variation	$df_{num.}$, $df_{denom.}$	*MS*	*F*	*p*
Delay	3, 51	2.902	4.402	0.008
Stand within Delay	50, 245	0.711	8.622	< 0.001
Error	51			
Total	299			

● Stand was nested within delay length

Table 4.9: Age underestimation between ground-level ring counts and crossdating at the root collar. Below-ground crossdating was conducted on trees from all fires, while above-ground crossdating was performed on fires occurring in 1961, 1941, and 1942 (see section 4.4.3).

Fire	Number of trees	Number of stands	Mean error (years)	Range of underestimation (years)
1982 House River Fire	40	3	2.8	0-7
1982 Rock Island Fire	58	4	2.6	0-6
1981 B Fire	51	4	2.5	0-10
1980 Winefred Lake Fire	54	3	2.6	0-9
1980 Conklin Trail Fire	54	3	3.1	0-8
1979 Winefred Lake Fire	29	1	2.4	0-6
1961 House Rive Fire	55	2	6.7	1-16
1958 Lawrence Lake Fire	55	2	4.4●	0-16●
1941 Piche Lake Fire	28	1	5.6	0-15
1941 Conklin Trail Fire	28	1	7.1	1-27
1942 Logan Lake Fire	30	1	5.4	1-12
1942 Wabasca Lake Fire	29	1	5.9	1-17

Note: Trees from the 1981 Mariana Lake Fire were not crossdated and are therefore omitted from this table.

●Trees were not crossdated above ground so estimates of aging errors are conservative

Table 4.10 Results of an analysis of variance testing whether the proportion of trees establishing from the first mast cohort post-fire differed between fires with varying delay length. Fires with a 0 year delay before the first mast year (coincided with the mast year) occurred in 1991 and 1979, while 1, 2, and 3 year delay fires occurred in 1982, 1981, and 1980 respectively. Between 4 to 7 stands were aged for each delay length treatment. See Figure 4.7 for post-hoc comparisons between delay length fires.

Source of variation	*df*	*MS*	*F*	*p*
Delay	3	0.319	15.437	< 0.001
Error	19	0.021		
Total	23			

Table 4.11 Pairwise comparison of age distributions between fires of varying delays before the first mast year. Significance tests indicate whether establishment timing differs relative to time since fire. Values are z statistics from two-sided Kolmogorov-Smirnov tests. Bolded values show the between fire comparisons with the same delay length.

Treatment	Fire	1982 Rock Island (RI)	1982 House River (HR)	1981 B	1980 Winefred Lake (WL)	1980 Conklin Trail (CT)
1 Year Delay	1982 RI					
	1982 HR	**0.90**				
2 Year Delay	1981 B	2.19*	1.21			
3 Year Delay	1980 WL	2.27**	1.80*	3.12**		
	1980 CT	1.81*	1.41	2.02*	**0.03**	
0 Year Delay	1979 WL	1.90*	1.57	2.63**	0.21	1.22

* Significant difference ($p \leq 0.05$)

** Significant difference ($p \leq 0.01$)

Table 4.12 Cone indices from 14 sites sampled annually between 1998-2001. Sites were located at least 40 km apart, and distributed throughout northeastern Alberta. Cone indices were calculated as the length of the cone bearing portion of the tree in feet, multiplied by the percent cover of cones. Mean cone index is given for each site based on 10 trees. Bolded values indicate which sites had their highest cone crop in 1998 (a mast year). Coefficient of variation values are presented for sites with three or more years of data.

Site	Year				Coefficient of Variation●
	1998	1999	2000	2001	
1		452.0	0.6	32.8	155.6
2		262.8	141.3	138.9	39.1
3	**522.2**	93.8	295.9	2.1	101.1
4		380.0	154.5		
5		396.5	45.0	110.3	101.6
6		57.7	92.0	0.4	92.5
7	155.1	79.0	47.5	197.0	57.3
8	**257.5**	77.0	81.6	42.5	84.4
9	**382.0**	96.4	4.9	21.1	138.9
10	**517.5**	164.1	241.2	10.5	91.0
11	**525.0**	143.5	204.8	33.9	93.0
12	**383.5**	247.6	123.3	17.3	81.9
13	**246.1**	70.4	81.1	0.1	104.8
14		122.9	48.5	24.0	79.1
Average■	373.6^{a}	188.8^{b}	111.6^{bc}	48.5^{c}	93.9
Std. error	50.6	36.2	23.5	17.0	

● Coefficient of variation = (standard deviation / mean) X 100

■ Different superscipts denote years where the average cone index differed significantly. A Dunnett's T3 test was used for post hoc comparisons (see Table 4.13 for ANOVA).

Table 4.13 Results of an analysis of variance testing whether the cone index differed between years. The number of sites surveyed annually ranged between 8 and 14.

Source of variation	*df*	*MS*	*F*	*p*
Year	3	187592	16.594	< 0.001
Error	43	11305		
Total	46			

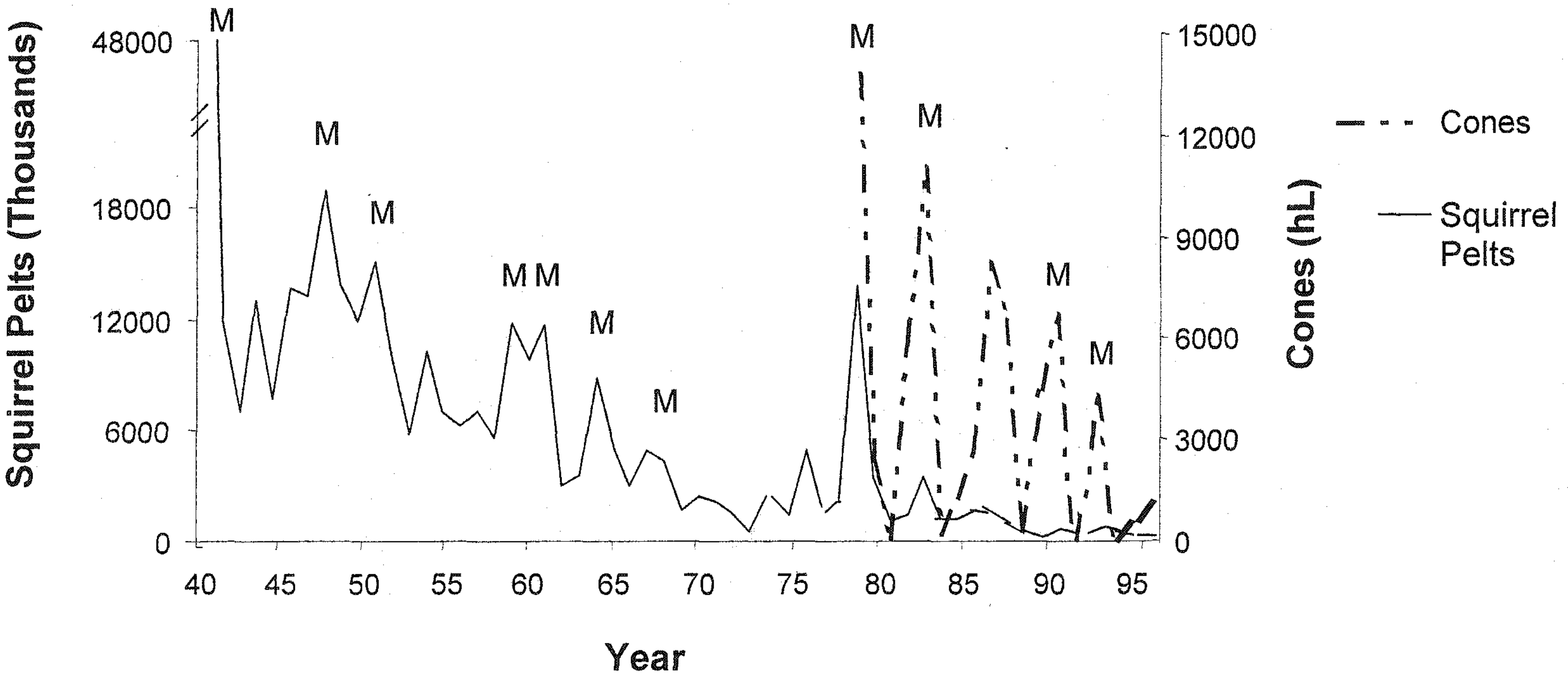


Figure 4.1: Masting history of white spruce in Alberta between 1941 and 1996. Seed shortages between 1979 and 1996 necessitated cone collections whenever cone crops occurred. Provincial red squirrel trapping records between 1941 and 1996 were compiled by the Alberta Fur Trappers Association. Years reported as mast years in forestry publications and journal articles are indicated by an M.

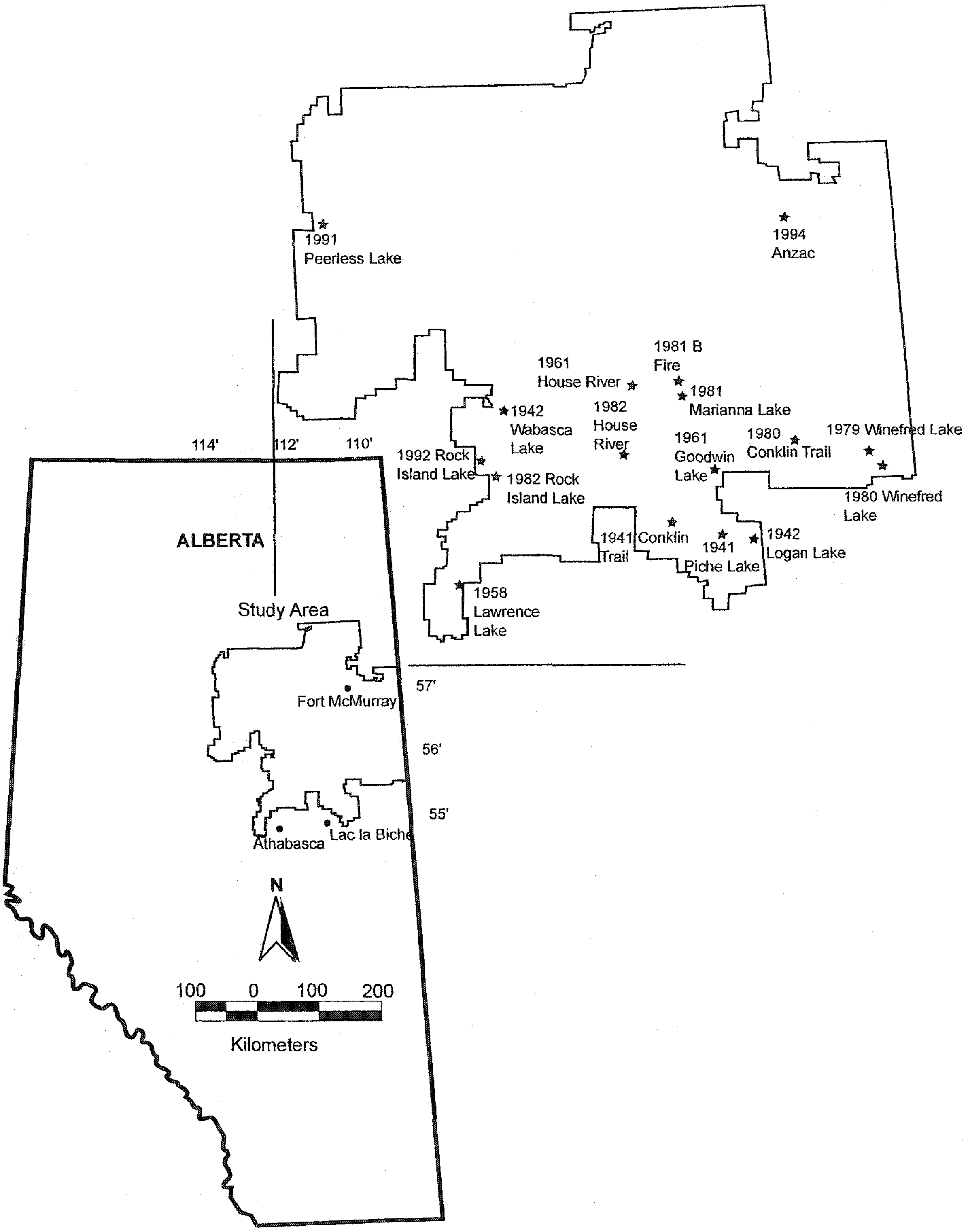


Figure 4.2. Map of study area in northeastern Alberta showing the location of study fires. All fires were located within the forest managment area of Alberta Pacific Forest Industries. Fire names are according to those described in Table 4.1.

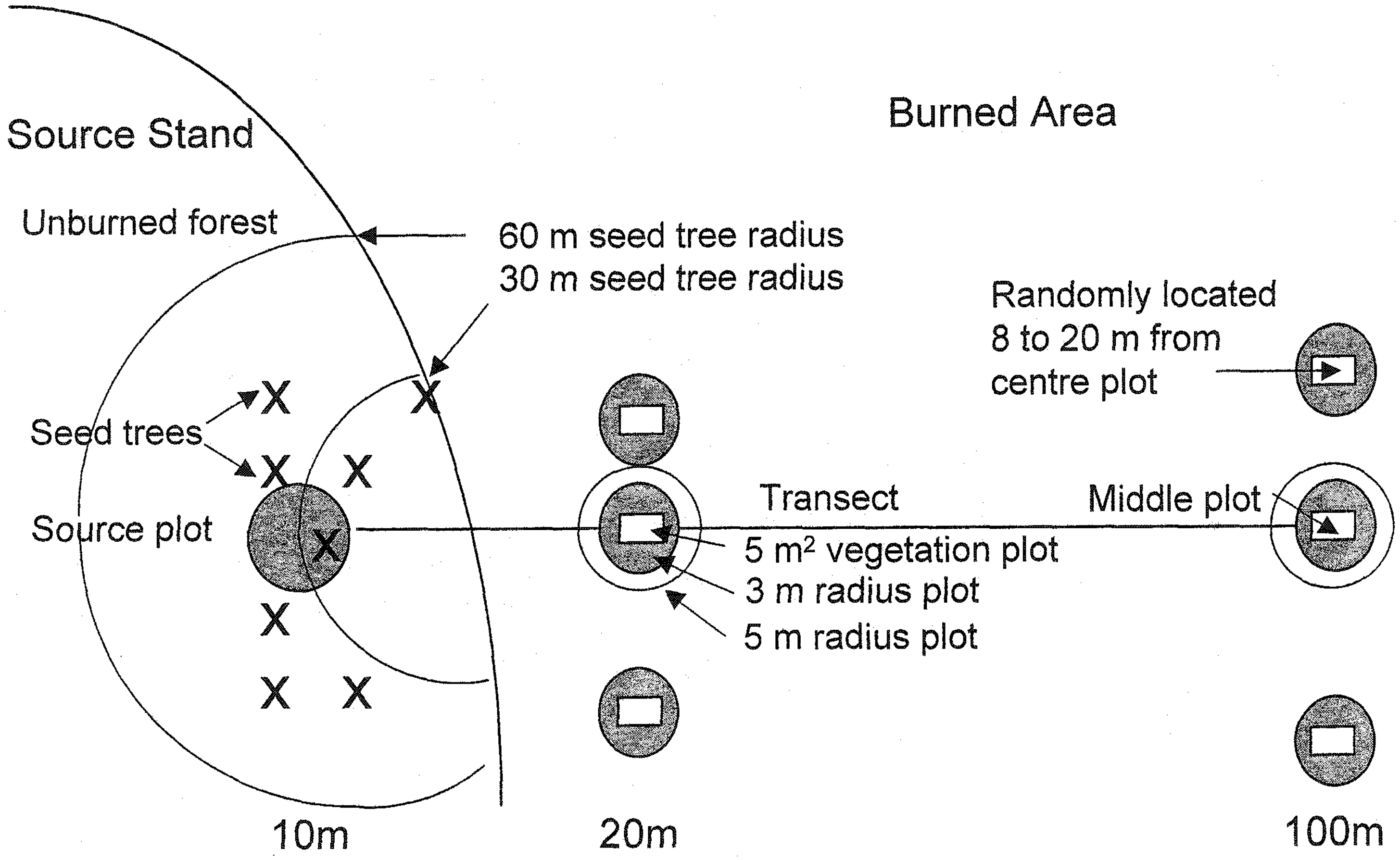
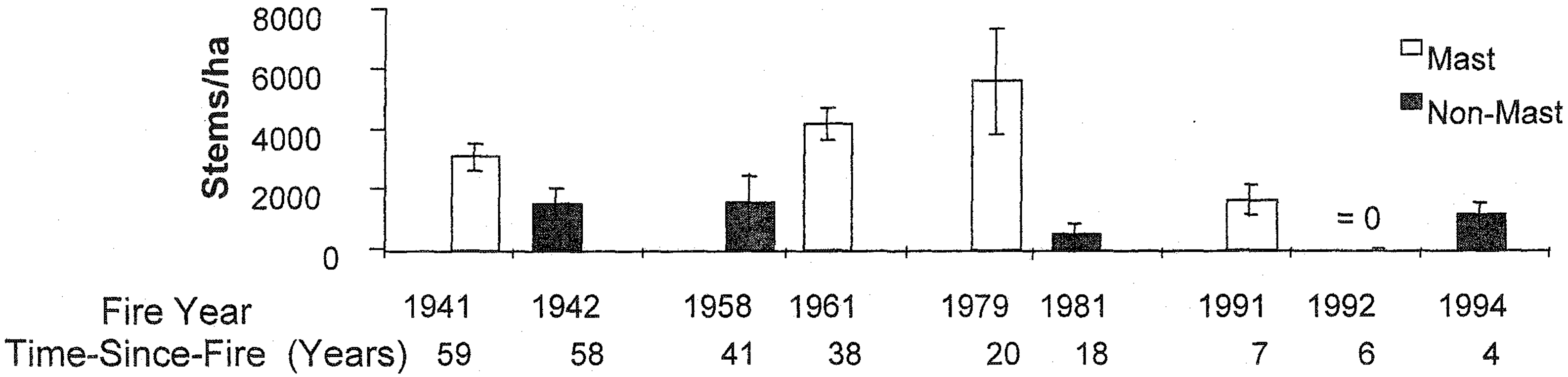


Figure 4.3. Sampling design for each stand. Percent cover of vegetation, and abiotic variables were measured in the middle plot (5 m^2) at each distance, while the proportion of regeneration of tree species was assessed in the 3 m radius middle plot at each distance. White spruce density was recorded in each 5 m^2 and 3 m radius plot at each distance. The proportion of pre-fire tree species was estimated in the 5 m radius plot. The number of seed trees were estimated within the 30 and 60 m arcs.

a) 20 m from seed source



b) 100 m from seed source

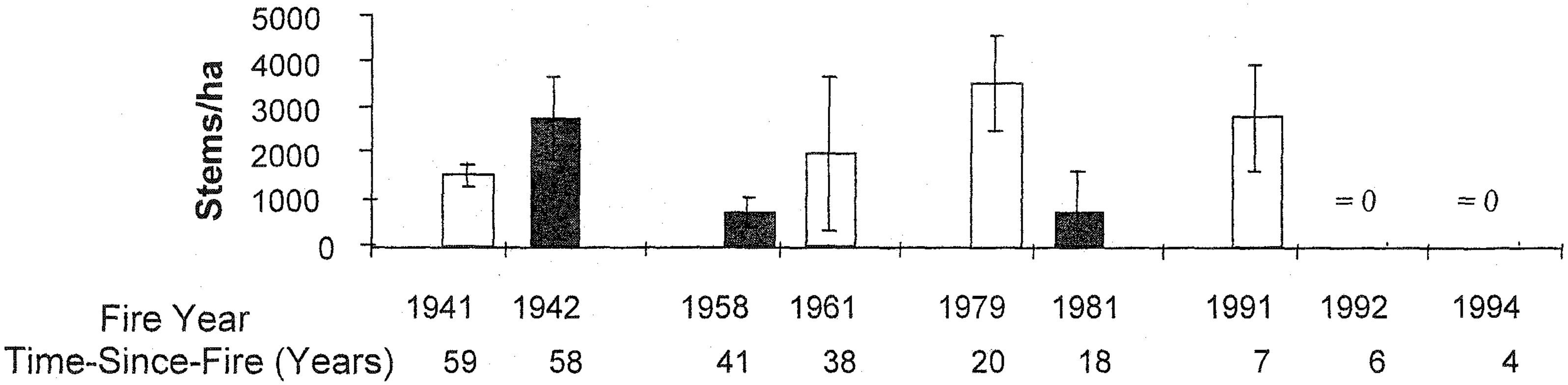


Figure 4.4: Average white spruce densities at 20 m (a) and 100 m (b) from seed sources in burned stands. Non-mast year fires occurred in years of low cone crop, and occurred one or more years prior to a mast year, while mast year fires coincided with a mast year. 1992 was a non-mast burn with no spruce regeneration in sampled stands, while 1994 was a non-mast burn with no regeneration in sampled stands at 100 m. Means were obtained from 2 fires for the years 1941, 1942, 1961, and 1981, and from one fire for 1958, 1979, 1992, and 1994. A minimum of 7 stands were sampled per fire. Spruce density was significantly greater on mast than non-mast fires and significantly greater at 20 m than at 100 m (Generalized Linear Models, $p < 0.001$ in both cases).

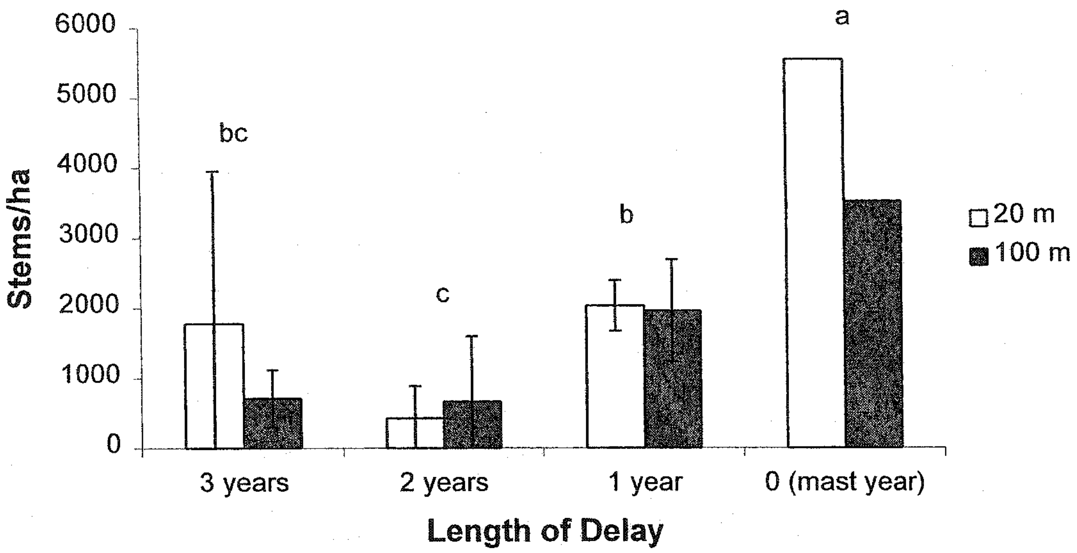


Figure 4.5: White spruce densities relative to length of delay period following fire before a 1983 mast year (+/- 1 standard deviation). Fires with a 1, 2, and 3 year delay were 1982, 1981, 1980 respectively (*n* = 2 fires per year). Densities on a 1979 mast year burn are shown for comparison. Mast year burns had significantly more spruce than fires with 1, 2, and 3 year delay length (Tamhanes tests, $p = 0.019$, < 0.001, and < 0.001), while fires with one year delays differed significantly from two year delay fires (Tamhanes test, $p = 0.022$). Fires with 3 year delays differed significantly from 2 year delay fires (Tamhanes tests, $p = 0.001$). Densities at both distances were grouped together in the statistical analysis.

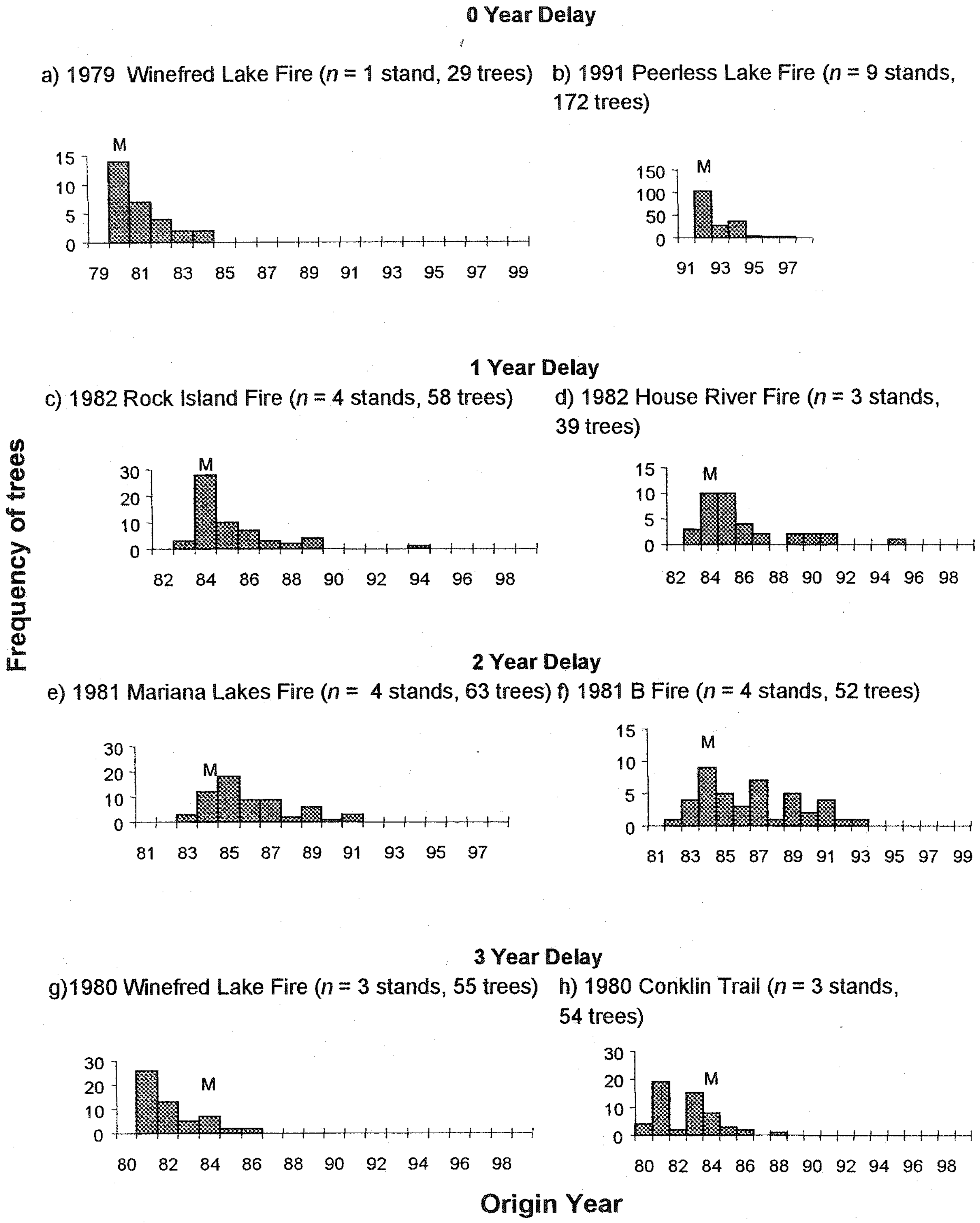


Figure 4.6: White spruce regeneration timing relative to delay period before a mast year in burns with **No delay** a) 1979 fire, b) 1991 fire; **One year delay** c) 1982 Rock Island Fire, d) 1982 House River Fire; **Two year delay** e) 1981 Mariana Lake Fire, f) 1981 B fire; and **Three year delay** g) 1980 Winefred Lake Fire h) 1980 Conklin Trail Fire. 1979 and 1991 were the first mast years to occur following fire for 1a and 1b. 1983 was the first mast year to occur following fire for 1c-1h. The first mast year cohort (M), is shown in all figures, 1 year after the mast year. Mast years also occurred in 1987, 1991, 1993, and 1998 (not shown). All trees were crossdated below ground with skeleton plots, except trees from the 1981 Mariana Lake Fire which were aged at ground level.

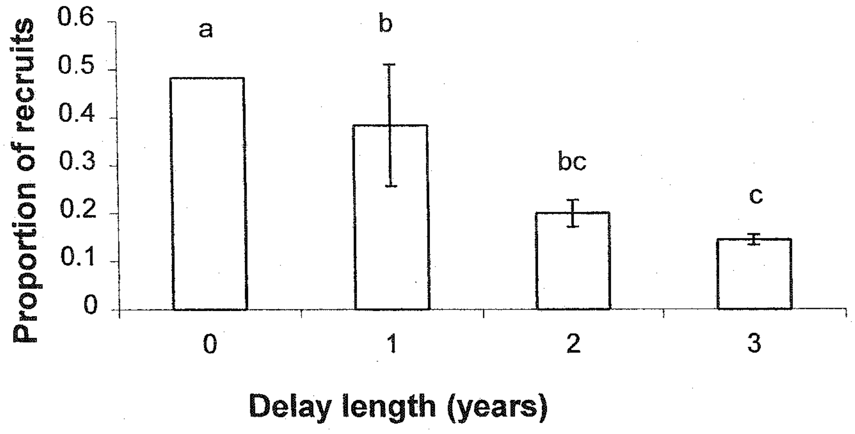
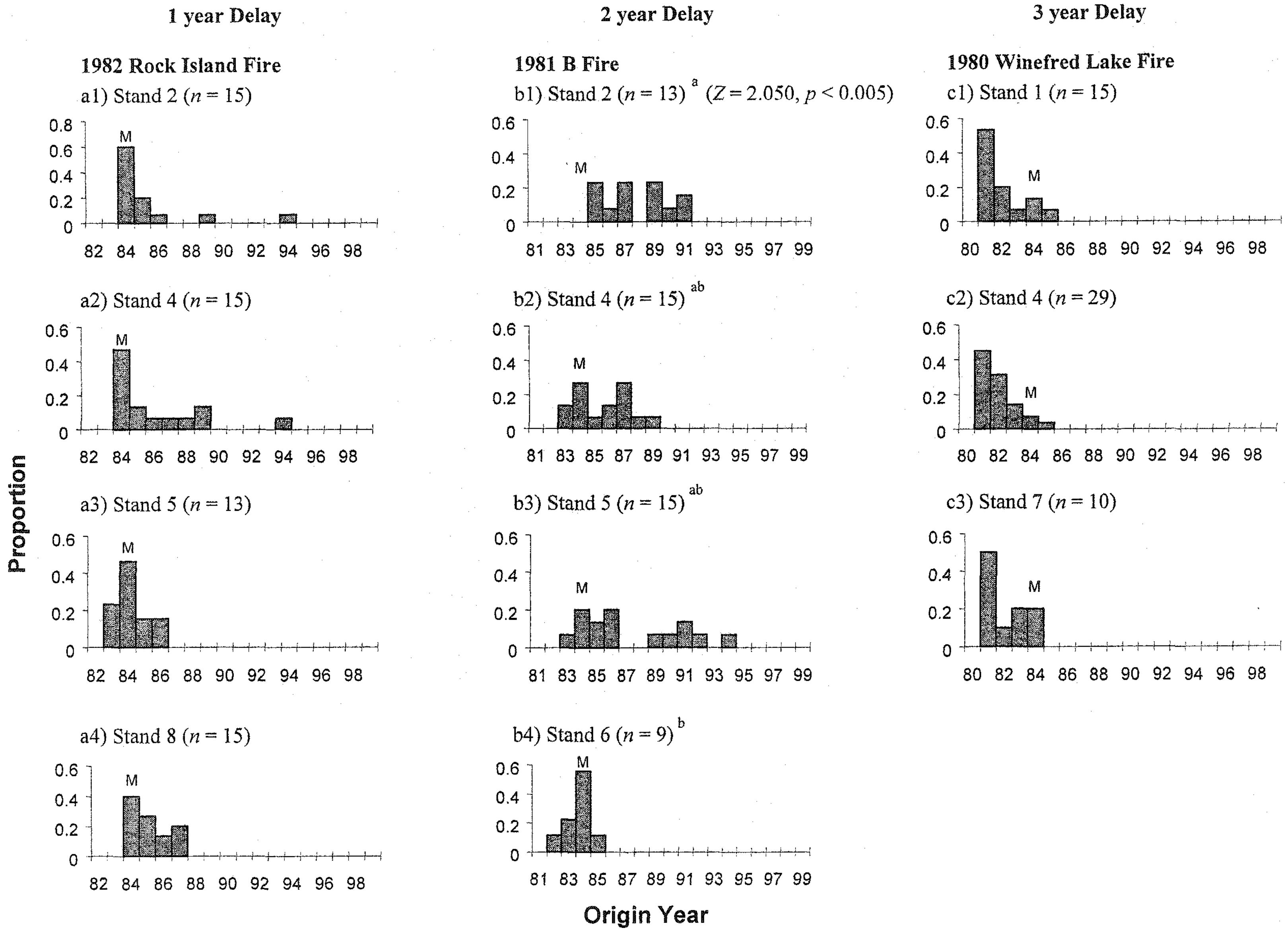
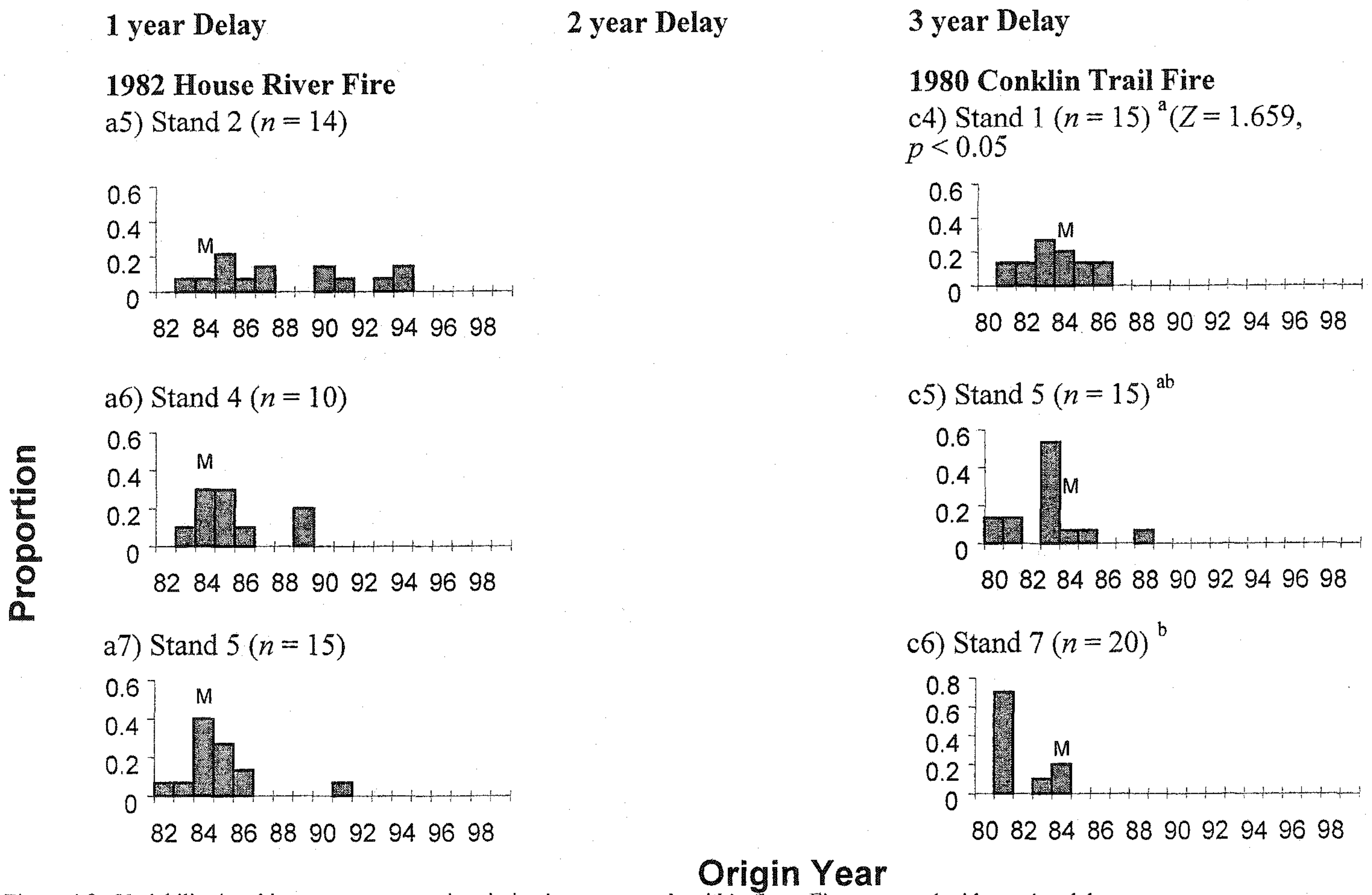


Figure 4.7: Proportion of trees establishing from the first mast year cohort for fires differing in delay length before a mast year. Fires with a 0 year delay were 1979 and 1991. The 1, 2, and 3 year delay fires occurred in 1982, 1981, and 1980, and the mast cohort shown originated from seed produced in 1983 ($n = 2$ fires for each year, standard error bars are shown). Mast burns had significantly higher proportions than fires with 1, 2, and 3 year delay lengths (YD) (Tukey tests, $p = 0.022$, < 0.001, and < 0.001 respectively), while fires with a 1 YD differed significantly from fires with 3 year delays (Tukey test, $p = 0.022$), but did not differ significantly from fires with 2 year delays (Tukey test, $p = 0.088$).


1 year Delay
2 year Delay
3 year Delay
1982 Rock Island Fire
1981 B Fire
1980 Winefred Lake Fire
a1) Stand 2 (n = 15)
b1) Stand 2 (n = 13) a (Z = 2.050, p < 0.005)
c1) Stand 1 (n = 15)
a2) Stand 4 (n = 15)
b2) Stand 4 (n = 15) ab
c2) Stand 4 (n = 29)
a3) Stand 5 (n = 13)
b3) Stand 5 (n = 15) ab
c3) Stand 7 (n = 10)
a4) Stand 8 (n = 15)
b4) Stand 6 (n = 9) b
M
Proportion
Origin Year
0
0.2
0.4
0.6
0.8
82 84 86 88 90 92 94 96 98
81 83 85 87 89 91 93 95 97 99
80 82 84 86 88 90 92 94 96 98



1 year Delay

2 year Delay

3 year Delay

1982 House River Fire

a5) Stand 2 ($n = 14$)

a6) Stand 4 ($n = 10$)

a7) Stand 5 ($n = 15$)

1980 Conklin Trail Fire

c4) Stand 1 ($n = 15$) ^{a}($Z = 1.659$, $p < 0.05$

c5) Stand 5 ($n = 15$) ^{ab}

c6) Stand 7 ($n = 20$) ^{b}

Figure 4.8: Variability in white spruce regeneration timing between stands within fires. Fires occurred with varying delay periods before a mast year: One year delay: 1982 Rock Island Fire (a1-a4); 1982 House River Fire (a5-a7); Two year delay: 1981 B fire (b1-b4); and Three year delay: 1980 Winefred Lake Fire (c1-v3); 1980 Conklin Trail Fire (c4-c6). 1983 was the first mast year to occur following fire for all stands. The first mast year cohort (M), is shown in all figures, establishing 1 year after the mast year. *Stands within fires that have significantly different age distributions have superscripts denoting* differences. Only 1 pairwise comparison was different for two of the fires; consequently, Z-statistics are reported for these pairs (two-sided K-S tests were used and p is Bonferroni corrected).

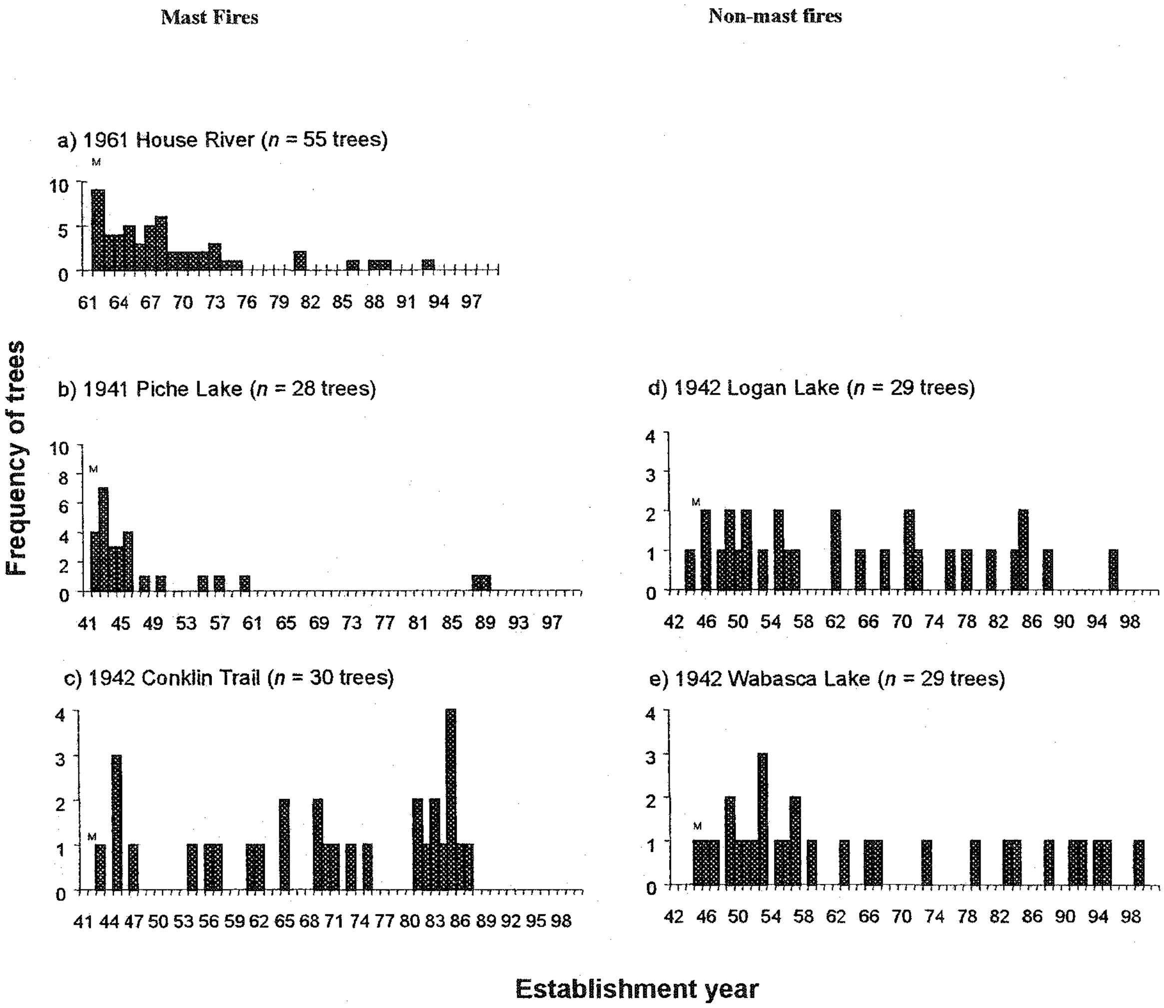


Figure 4.9: Comparison of white spruce regeneration timing on mast (a-c) and non-mast fires (d-e) as inferred from crossdated age structure (both above and below ground crossdating). Two stands were aged on the 1961 fire (a), while one stand was aged on each 1941 (b-c) and 1942 fire (d-e). The location of the cohort expected from the first mast year post-fire is marked with an M [a) 1962, b-c) 1942, and d-e) 1945].

4.9 Literature cited

Alberta Environmental Protection. 1999. Natural regions and sub-regions of Alberta. AB. Nat. Heritage Inf. Centre, Edmonton, AB.

Alberta Sustainable Resource Development. Historical Spatial Wildfire Data. AB. For. Prot. Branch. http://envweb.env.gov.ab.ca/env/forests/fpd/.

Alden, J. 1985. Biology and Management of White Spruce Seed Crops for Reforestation in Subarctic Taiga Forests. Fairbanks, Alaska, Inst. North. For., Agric. For. Exp. Sta., School of Agric. Land Resource Mgmt., University of Alaska-Fairbanks.

Alexander, M.E., and Degroot, W.J. 1988. Fire behavior in jack pine stands as related to the Canadian Forest Fire Weather Index (FWI) System. Can. For. Ser., North. For. Centre, Edmonton, AB.

ArcView GIS 3.0. Environmental Systems Research Institute. United States of America

Cerezke, H.F., Holmes, R.E. 1986. Control studies with carbofuran on seed and cone insects of white spruce. North. For. Res. Centre, Edmonton, AB., Inf. Rep. NOR-X-280.

Coates, D.K., Haeussler, S., Lindeburgh, S., Pojar, R., and Stock, A.J. 1994. Ecology and Silviculture of Interior Spruce in British Columbia. For. Canada, B.C. Min. For., B.C. Canada, FRDA Rep. 220.

Crawley, M. 1997. Plant Ecology. 2nd ed. Blackwell Science Ltd. Oxford, U.K.

Crawley, M.J., and Long, C.R. 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robar* L. J. Ecol. 83: 683-696.

Crossley, D. 1955. Survival of white spruce reproduction resulting from various methods of forest soil scarification. Canada, Dept. North. Affairs and Nat. Resources, For. Branch, Tech. Note No. 10.

Day, R.J. 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains, Can. Dept. For., For. Res. Branch Pub. 1037.

De Grandpre, L., Daniel, G., and Bergeron, Y. 1993. Changes in the understory of Canadian southern boreal forest after fire. J. Veg. Sci. 4: 803-810.

Delisle, G.P. , and Hall, R.J. 1987. Forest fire history maps of Alberta, 1931 to 1983. Can. For. Serv., North. For. Centre, Edmonton, AB.

Department of Environmental Protection. 1996. Fire Incidence Database. AB Land and For. Serv., For. Prot. Div., Edmonton, AB.

____ a. Alberta Vegetation Inventory Maps. AB Land and For. Serv., Land Inf. Serv. Div., Resource Inf. Branch, Edmonton, AB.

____ b. Alberta Phase III Forest Inventory Maps. AB Land and For. Serv., For. Pro. Div., Edmonton, AB.

Desrochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? Can. J. For. Res. **27**: 1263-1267.

Dobbs, R.C. 1976. White spruce seed dispersal in central British Columbia. For. Chron. **52**: 225-228.

Eis, S., Garman, E.H., and Ebell, L.F. 1965. Relation between cone production and diameter increment of douglas fir (*Pseudotsuga menziesii* (Mirb) Franco), grand fir (*Abies grandis* (Dougl.) Lindl.), and western white pine (*Pinus monticola* Doug.). Can. J. Bot. **43**: 1553-1559.

Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. **27**: 139-147.

Greene, D.F., and Johnson, E.A. 2000. Tree recruitment from burn edges. Can. J. For. Res. **30**: 1264-1274.

Gutsell, S.L., and Johnson, E. A. 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. J. Ecol. **90**: 153-166.

Herrera, C.M., Jordano, P., Javier, G., and Traveset, A. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. Amer. Nat. **152**: 576-594.

Ida, H., and Nakagoshi. 1996. Gnawing damage by rodents to the seedlings of *Fagus crenata* and *Quercus mongolica* var. *grosseserrata* in a temperate Sasa grassland-deciduous forest series in southwestern Japan. Ecol. Res. **11**: 97-103.

Janzen, D.H. 1971. Seed predation by animals. Annu. Rev. Ecol. Syst. **2**: 465-492.

Johnson, E.A. 1992. Fire and Vegetation Dynamics: Studies from the North American boreal forest. Cambridge University Press, Cambridge, Great Britain.

Kabzems, R.D., and Lousier, J.D. 1992. Regeneration, growth and development of *Picea glauca* under *Populus* spp. canopy in the Boreal White and Black Spruce Zone, For. Canada, B.C. Min. For., Victoria, BC., FRDA Rep. 176.

Keely, J., and Bond, W. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. Amer. Nat. **154**: 383-391.

Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends Ecol. Evol. **9**: 465-470.

Kelly, D., and Sullivan, J.J. 1997. Quantifying the benefits of mast seeding on predator satiation and wind pollination in *Chionochloa pallens* (Poaceae). Oikos **78**: 143-150.

Kemp, G.A., and Keith, L.B. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology **51**: 763-779.

Koenig, W.D., and Knops, J.M.H. 1998. Scale of mast-seeding and tree-ring growth. Nature **396** (Nov.): 225-226.

______ and Knops, J., M. H. 2000. Patterns of annual seed production by northern hemisphere trees: A Global Perspective. Amer. Nat. **155**: 59-69.

Landhausser, S., and Lieffer, V.J. 1998. Growth of *Populus tremuloides* in association with *Calamagrostis canadensis*. Can. J. For. Res. **28**: 396-401.

Lees, J.C. 1963. Partial cutting with scarification in Alberta spruce-aspen stands. For. Res. Branch., Dept. For., Ottawa, ONT., Pub. No. 1001.

Lieffers, V.J., Stadt, K.J., and Navratil, S. 1996. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. **26**: 1002-1007.

McCullagh, P. and Nelder, J.A. 1983. Generalized linear models. Chapman and Hall, London, Great Britain.

McKone, M.J., Kelly, D., and Lee, W.G. 1998. Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. Global Change Biol. **4**: 591-596.

Negi, A.S., Negi, G.C.S., Singh, S.P. 1996. Establishment and growth *of Quercus floribunda* seedlings after a mast year. J. Veg. Sci. **7**: 559-564.

Neumann, F. pers. com. Director, Alberta Trappers Assoc., Westlock, AB.

Nienstaedt, H., and Zasada, J.C. 1990. *Picea glauca*. Pages 165-185 *In:* R.M.Burns and B.H. Honkala, (eds.). Silvics of North America. Vol. 1, Conifers. U.S. Dept. Agric. For. Serv., Agric. Handbook 654.

Noble, D.L., and Ronco, F.J. 1978. Seedfall and establishment of Engelmann spruce and subalpine fir in clearcut openings in Colorado, USDA For. Serv., Rocky Mountain For. Range Exp. Sta., Res. Paper RM-200.

Palamarek, D. pers. com. Seed Officer, AB Tree Improvement and Seed Centre, Smoky Lake, AB.

Peters, S.H. 2000. The impact of small mammals on natural regeneration of white spruce after logging. Dept. Biol. Sci., Edmonton, University of Alberta. Masters Thesis.

Peters, V.S., Macdonald, S.E., and Dale, M.R.T. 2002. Aging discrepancies of white spruce affect the interpretation of static age structure in boreal mixedwoods. Can. J. For. Res. **32**: 1-6.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fenn. **36**: 289-306.

Quaite, J. 1956. Survival of white spruce seedlings resulting from scarification in a partially cut mixedwood stand. For. Res. Div., Calgary, AB., Technical Note No. 44.

Rowe, J.S. 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Dept. North. Affairs. Nat. Res, For. Res. Div., Ottawa, ONT., Tech. Note 3.

Rusch, D.A., and Reeder, W.G. 1978. Population ecology of Alberta red squirrels. Ecology **59**(2): 400-420.

Sato, T. 2000. Effects of rodent gnawing on the survival of current-year seedlings of *Quercus crispula*. Ecological Research **15**: 335-344.

Shibata, M., Tanaka, H., and Nakashizuka, T. 1998. Causes and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. Ecology **79**:

54-64.

Silvertown, J. 1980. The evolutionary ecology of mast seeding in trees. Biol. J. Linn. Soc. **14**: 235-250.

Silvertown, J., and Dodd, M. 1999. The demographic cost of reproduction and its consequences in balsam fir (*Abies balsamea*). Amer. Nat. **29**: 322-332.

Smith, M.C. 1968. Red squirrel responses to spruce cone failure in interior Alaska. J. Wildl. Manage. **32**: 305-317.

Sokal, R.R., and Rohlf, F.J. 1981. Biometry. 2nd ed. W.H. Freeman and Company, New York.

Sork, V.L. 1983. Mast-fruiting in hickories and availability of nuts. Amer. Midl. Nat. **109**: 81-88.

SPSS 1999. SPSS for windows release version 10.0. Chicago, IL.

S-Plus 2000 Professional Release 2. MathSoft, Inc., Seattle, WA.

Stelfox, J.B., Ed. 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta., AB Env. Centre, Can. For. Serv., Edmonton, AB.

Stewart, J. 2000. White spruce regeneration in mixedwood forests of the EMEND Project in the northwest boreal region of Alberta. Can. For. Serv. Res., Edmonton, AB., MDFP, 15/99.

Stewart, J.D., Landhausser, S.M., Stadt, K.J., and Lieffers, V.J. 2000. Regeneration of white spruce under aspen canopies seeding, planting and site preparation. W. J. App. For. **15**: 177-182.

Stewart, J. D., Hogg, E. H., Hurdle, P. A., Stadt, K. J., Tollestrup, P., Lieffers, V. J. 1998. Dispersal of white spruce seed in mature aspen stands. Can. J. Bot. 76: 181-181.

Strong, W.L., and Leggat, K.R. 1992. Ecoregions of Alberta. AB For., Lands and Wild., Land Inf. Serv. Div., Edmonton, AB, T/245.

Taylor, K., and Aarssen, L. 1989. Neighbor effects in mast year seedlings of *Acer saccharum*. Amer. J. Bot. **76**: 546-554.

Todd, A., and Giesbrecht, L. 1979. A review of Alberta fur production and management, 1920-1921 to 1977-78. Ab Energy and Nat. Resources, Fish and Wildl. Div.

Waldron, R.M. 1965. Cone production and seedfall in a mature white spruce stand.

For. Chron. **41**: 316-329.

Wurtz, T.L., and Zasada, J.C. 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. Can. J. For. Res. **31**: 999-1011.

Youngblood, A.P. 1995. Development patterns in young conifer-hardwood forests of interior Alaska. J. Veg. Sci. **6**: 229-236.

Zar, J.H. 1996. Biostatistical Analysis. 3rd ed. Prentice-Hall, Inc. Upper Saddle River, New Jersey, USA.

Zasada, J.C. 1985. Production, dispersal, and germination of white spruce and paper birch and first year seedling establishment after the Rosie Creek fire. University of Alaska, Fairbanks, Misc. Publ. 85.

Zasada, J.C., and Gregory, R.A. 1969. Regeneration of white spruce with reference to interior Alaska: a literature review, USDA For. Ser., Pac NW For. Exp. Sta., Gen. Tech. Rep. PNW-79.

Zasada, J.C., Foote, M.J., Deneke, F. J., and Parkerson, R. H. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination, and seedling survival. USDA For. Serv., Pac. NW For. Exp. Sta., Gen. Tech. Rep. PNW-65.

CHAPTER 5

The Importance of Initial Versus Delayed Regeneration of White Spruce in Boreal Mixedwood Succession

---

5.1 Abstract

It appears that succession in mixedwood forests may follow different pathways because white spruce may establish immediately after fire on burned substrates, or after some delay, largely on decayed logs. The relative importance of immediate versus delayed regeneration to stand age structure (reflecting successional pathway) has not been determined. Over a 59-year period of fire recovery, we determined: 1) if and when a delayed regeneration period occurred, 2) whether burn timing relative to mast years, proximity of seed source, and prevailing wind direction affect whether a stand will be dominated by initial versus delayed white spruce regeneration, 3) the substrates which are most important for white spruce regeneration, and 4) whether factors indicative of competition affected age structure. Delayed regeneration exhibited significant periodicity, peaking between 38 - 44 years post-fire. During this time period, 55.7% of delayed regeneration occurred on logs. Of the 20 stands that we studied, stands dominated by initial regeneration occurred as frequently as stands with even mixtures of initial and delayed regeneration, and stands dominated by delayed regeneration (7, 7, and 6, respectively). Stand age structure was not affected by timing of fire relative to mast years, nor by distance from seed source, but did vary significantly between fires and relative to prevailing winds. There was little evidence for density-dependent effects on succession at the stand level; however, size and proximity of initial regeneration affected the density of delayed regeneration at the plot level. It is now apparent that different successional pathways can arise from similar post-fire conditions. These findings clarify the influence of fire history and seed availability on mixedwood succession.

5.2 **Introduction**

The succession of trees in boreal forests is generally characterized by initial floristic composition models due to the prevalence of serotiny in coniferous trees and suckering from root sprouts by broadleaf species as regeneration strategies after fire (Egler 1954; Connell and Slatyer 1977; Bergeron 2000). The reproductive strategy of white spruce is a stark contrast to most boreal tree species because it depends on surviving seed sources to disperse seed into burned areas (Galipeau *et al.* 1997). Consequently, it is more apt to be recruitment-limited after fire (Greene and Johnson 2000), and gradual ingress into stands is considered important to white spruce occurrence in mixedwoods (Youngblood 1995; Lieffers *et al.* 1996a).

Immediate regeneration has not been regarded as critical to the eventual transition from dominance by broadleaf species in the canopy to white spruce, because white spruce also establishes over time on decayed logs (Kabzems and Lousier 1992; Simard *et al.* 1998). White spruce grows as well on logs as on other substrates (Lieffers *et al.* 1996b); therefore, trees recruiting later on logs may eventually reach the canopy in the absence of fire. After fire, white spruce establishment occurs over a three to five year period ("initial regeneration"), particularly following mast seed years (Day 1964; Zasada and Gregory 1969; Purdy *et al.* 2002; see Chapter 4). A delay may occur in regeneration between when the forest floor microsites become unfavorable, light attenuation and competition with other plant species lessens, and a good supply of suitably decayed logs is available. Most snags in mixedwoods are down within 20 years of fire, after which they must decay sufficiently before they are suitable for spruce to establish ("delayed regeneration") (Lee 1998). Following fire, the timing of delayed regeneration and its importance to spruce age structures and thus successional pathways in boreal mixedwoods is not well documented.

Although variation in the age structure of white spruce in boreal mixedwoods is well documented, succession in this system has not been recognized as following two fundamentally different pathways that have been defined in the ecological literature. Several authors suggest that when intense fires occur and mature seed sources are within the effective dispersal distance of white spruce, regeneration will be immediate, and spruce will be even-aged (Rowe 1955; Kabzems and Lousier 1992; Lieffers *et al.* 1996b).

In contrast, the absence of any one of these factors may contribute to regeneration delays leading to multi-aged stands (Kabzems and Lousier 1992; Lieffers *et al.* 1996b). These successional pathways are different because even-aged stands are described by Egler's (1954) initial floristic model (suitable conditions exist for establishment immediately after disturbance), while stands dominated by delayed regeneration may indicate that the relay floristics model is a more important pathway (burned seedbeds are not suitable after fire and logs must decay before most regeneration occurs). These two models also differ in the influence that successional mechanisms such as tolerance to low resource levels (i.e. initial floristics), and inhibition and facilitation (relay floristics) have on affecting species composition changes (Connell and Slatyer 1977). Non- equilibrium theory (Glenn-Lewin and van der Maarel 1992; Olson 1958; Horn 1981; Pickett *et al.* 1987), may be a more encompassing picture of succession in mixedwoods that contain white spruce and several deciduous species because different species may frequently dominate late seral stages.

Even-aged stands may occur more often if fires coincide with mast years. Fires occurring in non-mast years have significantly less immediate regeneration after fire than mast year burns due to rapid deterioration of the seedbed (see Chapter 4, section 4.6.1), and may therefore be regeneration limited during initial establishment phases. Seed dispersal declines rapidly downwind of a seed source; consequently, few trees may regenerate farther than 100 meters away in years with average seed rain (Zasada and Lovig 1983; Nienstaedt and Zasada 1990; Dobbs 1976). Delayed regeneration may be proportionally greater on non-mast burns and sites with weak seed sources than mast burns and sites with strong seed sources because there is less competition with initial regeneration (i.e. greater survivorship of later cohorts). No previous study has measured the frequency of stands originating primarily from immediate regeneration, both immediate and delayed regeneration (multi-aged stands), or from delayed regeneration, relative to seed availability and substrate conditions at the time of the fire.

Several key limitations in retrospective studies have prevented the rigorous testing of whether conditions at the time of fire determine successional pathway. First, conditions at the time of the fire have not been known (i.e. timing relative to mast years, or availability of seed source) in historic fires. Secondly, insufficient numbers of trees or stands have been studied to perform tests on the importance of substrate versus seed availability on age structure. Finally, substantial age underestimation from ground-level ring counts and variation in aging error with tree age have limited the identification of key regeneration periods (see Chapter 2, section 2.7.2). Successional dynamics may not be accurately inferred from static age structures when assumptions about aging methodology are inaccurate (i.e. ground level equals root collar, and ring count equals age (Desrochers and Gagnon 1997; Gutsell and Johnson 2002).

Our principle objective was to determine the importance of initial versus delayed regeneration of white spruce in succession of boreal mixedwood forests in Alberta. The timing and duration of the initial regeneration period was addressed previously in Chapters 2 and 4. Here we address the relative importance of initial versus delayed regeneration by answering the following questions: 1) Does a delayed regeneration pulse occur and, if so, when? 2) Does the frequency of stands dominated by initial versus delayed regeneration vary in relation to factors that affect the density of immediate regeneration (specifically: burns occurring in mast versus non-mast year, proximity to seed source, and location of seed sources relative to prevailing wind direction? 3) How important is regeneration on logs versus substrates that are available immediately after fire to mixedwood development? and 4) Do density-dependent factors affect age structure at the plot level (5 m^2)? The stand history attributes addressed by these questions may lead to fundamentally different successional pathways in boreal mixedwoods, and have important implications for forest managers.

5.3 Study Area

See chapter 4, section 4.3 for a detailed description of the study area.

5.4 Methods

5.4.1 Timing of delayed regeneration

Results of tree aging in Chapter 4, demonstrated that an initial regeneration pulse lasting approximately 5 - 7 years post-fire characterized the age structure of stands up to 20 years old (based on 283 trees from 19 stands, on 6 fires that occurred between 1979 - 1982). Since a delayed regeneration pulse did not occur in the first 20 years after fire, herein only trees that established 21 or more years after fire were classified as delayed regeneration. In order to determine if there was a later period of regeneration (delayed regeneration), two stands were randomly selected per fire on fires occurring in mast years in 1961 and 1941, and non-mast years in 1958 and 1942. One fire from each of 1961 and 1958 (38 and 41 years old) was sampled, while two fires from both 1942 and 1941 (58 and 59 years old) were sampled; thus, a total of 12 stands were assessed. All fires and stands were selected according to the procedures outlined in Chapter 4, section 4.1. Fire initiation dates were not available for 58 and 59-year-old fires at the time of sampling; however, subsequent updates to fire database records show that the these fires started between April 30th - May 16th (Tymstra, pers. com.). Stands were sampled according to the procedures in Chapter 4 section, 4.4.1 in order to identify which trees would be collected and aged. At both the 20 and 100 m site in each stand, 15 live white spruce trees were cut at ground level, and the below-ground stumps were excavated and collected (360 trees in total from the 12 stands). The rooting substrate was recorded for each tree (in case delayed regeneration occurred on substrates other than logs) (see section 5.4.3). A ground-level disk was aged according to the procedures in Chapter 2, section 2.4.2. If this ring count indicated a minimum establishment date of 21 or more years after fire, trees were crossdated both above and below ground according to the procedures in Chapter 2, section 2.4.2. A total of 134 trees met this criterion after crossdating; these trees were used to determine the timing of delayed regeneration. Trees that established within 20 years of the fire were classified as initial regeneration, and were used to address objectives in subsequent sections (see section 5.4.2). We used frequency histograms of tree establishment dates over time to determine the temporal pattern of delayed regeneration after fire.

The timing of delayed regeneration may be dependent on the level of competition from other plant species, light attenuation, and substrate availability. We measured the mean percent cover of shrubs, herbs, grass, and canopy closure on fires between 4 and 59 years old to determine whether delayed regeneration coincided with periods of reduced understory or overstory cover. The percent of moss-covered logs (sufficiently decayed for establishment) was also measured over this time period to determine if substrate availability coincided with delayed regeneration. The fires and sampling procedures described in Chapter 4, sections 4.4.1 and 4.4.2 were used.

5.4.2 Initial versus delayed regeneration

Due to the high variability reported in the timing of spruce establishment in developing mixedwood stands, we needed a large number of stands to test which factors at the time of the fire could lead to stands dominated by initial regeneration, or delayed regeneration, or both. In addition to the trees collected from two stands on each 58 and 59-year-old fire (4 fires in total), 3 additional stands were sampled for each of the 58 and 59-year-old fires, according to the procedures in section 5.4.1. Hence a total of 15 excavated stumps were collected at two sites in each stand (20 and 100 m from the seed source), from five stands per fire (4 fires, 20 stands in total). Henceforth, the word "stand" will only be used in contexts where sites within a stand are not distinguished (i.e. analyses in which the data from both sites within a stand are pooled), while "sites" will distinguish specific locations within stands.

Due to the large number of stumps collected, we needed a method to distinguish initial regeneration from delayed regeneration without the time-consuming process of crossdating every tree. Our method had the following four steps (see Figure 5.1). 1) Ground-level disks were sanded to 400 grit and the rings were counted according to the procedures in section 5.4.1. 2) Aging errors were measured in one stand from each of the 58 and 59-year-old fires (30 trees per stand, from 4 stands total) using the crossdating methods in chapter 4, section 4.4.3 (Appendix 5.1). 3) The mean aging error below ground was added to the ground-level ring count (Appendix 5.2). 4) Trees that originated within 20 years of the fire based on this age, were classified as initial regeneration. Twenty years was used as the cut-off for initial regeneration because previous work in 10 fires up to 20 years old showed that an initial regeneration period occurred shortly after fire, but that virtually no regeneration occurred between 11 – 20 years after fire. Crossdating of the trees used to measure aging error in 58 and 59-year-old stands (see point 2) verified that most trees with ground-level disks up to 20 years old could be dated back to within 10 years of the fire. If the ground-level ring count plus the aging error indicated that trees originated more than 20 years after fire, they were classified as delayed regeneration. 5) The length of the buried trunk was measured in the lab, and trees for which it was more than 15 cm, were crossdated below ground using skeleton plots according to the procedures in Chapter 2, section 2.4.2. If, during the crossdating process trees turned out to have originated within 20 years of the fire, they were classified as initial regeneration, and no further crossdating was done. If, after crossdating the age indicated that regeneration occurred more than 20 years after fire, they were classified as delayed regeneration. A total of 577 trees were classified as either initial or delayed regeneration in the 58 and 59-year-old stands (YOS).

Burn intensity affects the likelihood of mineral soil exposure, and therefore the likelihood of initial regeneration. We used the basal area of live residual trees in 58 and 59 YOS (at the time of sampling) as an indication of burn intensity. We assumed that residuals that survived the fire, but died and fell prior to sampling, occurred in similar proportions to their immediate post-fire abundance. Basal area was measured in the 20 stands described above, according to the procedures in Chapter 4, section 4.4.1. Residual trees were easily distinguished from the post-fire cohort by much larger diameters, and greater canopy height. A Cruise Master prism that estimated ft^2 / acre (10 X multiplication factor) was used. These values were converted to m^2 / ha.

5.4.3 Regeneration substrates

The rooting substrate was recorded for all white spruce trees sampled in each of the 20 stands from 58 and 59-year-old fires that were aged in section 5.4.2 (577 trees). The rooting substrate of all trees in 3 m radius plots was recorded in an additional three stands for each of these four fires; however, none of these trees were aged (an additional 12 stands, 72 plots, and 217 trees). The rooting substrate of white spruce trees from all sampled stands in fires that were 19 to 41 years old (see Chapter 4, section 4.4.1 and 4.4.2) was also recorded in order to compare if the importance of rooting substrate changed with fire age ($n = 1332$ trees). Leaf litter was removed at the base of each tree to mineral soil to identify as well as possible the substrate the tree initiated on. The substrates identified for younger trees were logs, humus, mineral soil, leaf litter, and conifer litter, while for older trees we distinguished the substrates as logs, humus, and mineral soil. Logs were classified as above-ground logs and below-ground logs. Above-ground logs were recently fallen logs and decayed logs where the trunk outline remained visible. Above-ground logs were assumed to be fire-killed snags that had fallen (provided they showed evidence of fire, i.e. charcoal). Below-ground logs were covered by leaf litter and were not visible without excavation. We assumed that below-ground logs were downed wood prior to the fire, in fires that were up to 41 years old at the time of sampling. We could not distinguish whether below-ground logs in 58 and 59-year-old fires were downed wood prior to the fire, or a fire killed snag that had decayed considerably.

5.4.4 Density-dependent effects on age structure

Previous methods addressed the effects of seed and substrate availability on the dominance of initial versus delayed regeneration of white spruce. The density and size of initial regeneration may indicate the level of intraspecific competition within stands, and affect age structure by limiting delayed regeneration (i.e. due to shading, or occupying all regeneration niches), or by affecting mortality of later establishing conspecifics. Density-dependent effects on age structure were assessed at the site level (20 m and 100 m sites), and at the plot level. We used the 20 stands from the 58 and 59-year-old fires in section 5.4.2 for these tests, for which we had 577 trees classified as initial and delayed regeneration. These trees had been collected from the 3 nested plots at the 20 and 100 m sites in each stand (5 trees per nested plot [closest to the plot center], for a total of 15 trees per site; see Chapter 4, section 4.4.1). The location of these trees was recorded as within the 5 m^2 subplot (centered within the 3 m radius plot [28.3 m^2]), the 3 m radius plot, or outside the 3 m radius plot (see Chapter 4, section 4.4.1). In addition to identifying these trees as either initial (I) or delayed (D) regeneration, their height was also measured.

The density of initial and delayed regeneration at the site level was calculated from the average spruce density in the three 3 m radius plots, multiplied by the I:D ratio from the 15 collected trees at the site. Individual plot densities of initial and delayed regeneration were determined using three steps. 1) At the time of collection, the location of trees were identified as within the 5 m^2 subplot, outside the subplot but within the 3 m radius plot, or from outside the 3 m radius plot. 2) In 3 m radius plots containing less than 5 spruce, the actual density of trees that were either initial or delayed regeneration was known from the previously described aging work. 3) In 3 m radius plots containing more than 5 spruce, the ratio of I:D (from the 5 collected spruce) was used to estimate the density of initial and delayed regeneration based on the total number of trees in the 3 m plot. The mean height of trees classified as initial regeneration was determined for each plot from the collected trees, and was used in subsequent data analyses ($n = 115$ plots; height data were not recorded for the 5 other plots sampled). Vegetation and ground cover data were collected from one of the three 5 m^2 subplots (the middle one) ($n = 39$ subplots) according to the methods in Chapter 4, section 4.4.1.

To determine if spruce density affected self-thinning (i.e. dead spruce were usually found in dense clumps of taller, live spruce) over time, dead stems were recorded in 17 fires between 4 and 59 years old (fires are described in Chapter 4, sections 4.4.1 and 4.4.2). The sampling of dead stems was conducted in the same manner as live stems in Chapter 4 (recorded in both 5 m^2 subplots and the surrounding 3 m radius plot); however, dead stems were not aged. Plots were carefully searched for standing and fallen dead stems. All of the vegetation variables described in chapter 4, section 4.4.1 were recorded in these plots, and were used in analyses of stem mortality.

5.5 Data Analysis

5.5.1 Timing of delayed regeneration

To test whether delayed regeneration showed a regeneration peak over time, the establishment dates of the crossdated trees (from section 5.4.1) were tested against a uniform distribution, using two Kolmogorov-Smirnov (K-S) one sample tests. Out of the 134 trees, all 27 delayed trees from the 38 and 41-year-old fires (all 4 stands combined) were used in one K-S test, and the remaining 107 trees from the 58 and 59-year-old fires (all 8 stands combined) were used in another K-S test. The similarity of establishment delays between stands in 38 and 41-year-old fires were tested using a one-tailed ANOVA. The age of each delayed tree within a stand served as the sample unit within each stand. One 41-year-old stand was omitted from the one-tailed ANOVA of mean establishment delay because the sample size was small (3 stands were used). Post hoc comparisons between stands were made using Tukey's "honestly significant difference" test. The mean establishment delay for each stand is compared in the results; it was calculated by summing the establishment dates of delayed trees in the stand, and dividing by the number of delayed trees. A one-tailed ANOVA was also performed on stands from the 58 and 59-year-old fires to determine if the timing of delayed regeneration differed between stands. Two of the eight stands from these fires were omitted from this analysis because they had small sample sizes of delayed trees. SPSS version 10.0 was used for statistical analyses (SPSS 1999). Delayed regeneration from 38 and 41-year-old fires were omitted from all subsequent statistical analyses because these fires assessed a shorter time interval that did not span the full delayed establishment period (see Fig. 5.2).

5.5.2 Initial versus delayed regeneration

A Wilcoxan signed rank test was used to test whether initial regeneration was more abundant than delayed regeneration in the 20 aged stands (Zar 1996). Ratios of initial and delayed regeneration in stands from 58 and 59-year-old fires ($n = 20$ stands) were analyzed using the log-likelihood ratio statistic (G) (Bishop *et al.* 1975). The total variation in the ratio of initial to delayed regeneration occurring among sites was determined using the separate initial to delayed ratios from the 20 m and 100 m sites within stands (i.e. 2 sites per stand, therefore 40 sites in total [trees were not aged at one site; therefore, only 39 sites were used in the analysis]). G values were calculated for the factors: burn timing in mast versus non-mast year (Gm), fire replicate (Gf), distance (Gd) and direction from seed source (Gw), in order to determine whether they explained a significant amount of Gp. G values were then compared with the χ^2 distribution to determine significance. The position of stands was assigned as either downwind of seed source (relative to prevailing winds: $60 - 150^{\circ}$) or not downwind of seed source (all other directions). Friedman Tukey residuals were examined to determine which sites contributed the most variation to the G statistic.

Using the basal area of live residual trees (at the time of sampling) in 58 and 59 YOS as an indicator of burn intensity, we tested whether initial regeneration density (in 28.3 m^2 plots, $n = 116$) declined with increasing residual basal area in 58 and 59 YOS. The model used was:

$$Y_i = u + \beta_d d + \beta_c c + \epsilon$$

Where Y_i = initial regeneration, u = slope intercept, β_d = the coefficient of deciduous trees, d = basal area of residual deciduous trees, β_c = the coefficient of coniferous trees, c = basal area of coniferous trees, and ϵ = residual error. A quasi-likelihood function was used to model the data due to considerable overdispersion. Quasi-likelihood models are "distribution free", and therefore do not have assumptions about the variance to mean ratio (McCullagh and Nelder 1983).

5.5.3 Regeneration substrates

In statistical analyses, trees on both log substrate classes were pooled into a single log class, while trees rooted on mineral soil, humus, leaf litter, and conifer litter were pooled into a single mineral soil/humus class because the location of the root collar could not be determined in the field (see Chapter 2). A Wilcoxan signed rank test was used to test if regeneration was more abundant on mineral soil and humus versus logs using data from trees in all 32 stands described in section 5.4.3 (n = 64 sites). G tests were used as in section 5.5.2 to test whether the same factors affected the ratio of regeneration on logs versus mineral soil/humus (Gp_{log}, Gm_{log}, Gf_{log}, Gd_{log}, and Gw_{log}). The same 20 stands analyzed in section 5.5.2 were used (n = 40 sites).

5.5.4 Density-dependent effects on age structure

We used generalized linear models (GLM) in order to determine whether density-dependent factors appeared to affect age structure at the site level and plot level (see Table 5.1). Models were developed using S-Plus version 2000 (S-Plus 2000).

Delayed Regeneration

Site Level

a) Using the following model:

$$Y_d = u + \beta_i I + \epsilon$$

Where Y_d = delayed regeneration density, u = slope intercept, β_i = the coefficient of initial regeneration, I = the density of initial regeneration, and ϵ = residual error. In this model we tested whether the average density of delayed regeneration at each site was affected by the average density of initial regeneration (n = 39 sites). A quasi-likelihood function was used to model the data.

b) Using the above model we also tested whether the proportion of delayed regeneration (Y_p) at each site (out of 15 trees / site, $n = 39$ sites) was affected by the density of initial regeneration at each site. This test indicates whether delayed regeneration affects the age structure more on sites with low initial regeneration. A binomial distribution was used to model the data. Non-linear effects were tested for using a generalized additive model (GAM); however, they did not improve the model fit, and were therefore omitted.

Plot level

c) Using the following model:

$$Y_d = u + \beta_i d + \beta_h h + \beta_{ih}(dh) + \epsilon$$

Where Y_d = density of delayed regeneration, u = slope intercept, β_i = the coefficient of initial regeneration, d = density of initial regeneration, β_h = the coefficient for height, h = height of initial regeneration, β_{ih} = the coefficient for the interaction term, dh = the interaction between density and height of initial regeneration, and ϵ = residual error.

We tested whether the density and height of initial regeneration affected the density of delayed regeneration in all 58 and 59-year-old plots with aged trees ($n = 115$). A quasi-likelihood function was used to model the data due to considerable overdispersion. Non-linear effects were tested for using a generalized additive model (GAM); however, they did not improve the model fit, and were therefore omitted.

d) Using the above model and stand, we then used the subsample of plots where additional vegetation variables were collected ($n = 39$ plots, see section 5.4.4), to test whether the following variables helped explain the density of delayed regeneration: density of initial regeneration, height of initial regeneration, percent downed wood, percent moss covered logs, percent canopy by species, proportion regeneration of other tree species, and initial seed trees (see Chapter 4, section 4.4.1). Variables included in the model were added to the GLM following a stepwise procedure until the inclusion of additional variables did not yield a significantly better model ($p < 0.05$). A quasi likelihood distribution was used for modeling count data of delayed regeneration due to overdispersion.

Mortality (dead stems)

Site Level

e) The importance of delayed regeneration to age structure may be influenced by temporal and spatial variability in mortality of initial regeneration. GLMs were used to determine which variables best explained the density of spruce stems that had established post-fire and then died on 17 different fires (4 to 59 years old). The same variables and procedures used to predict live spruce in chapter 4, section 4.4.1 were used to predict dead stems.

Plot Level

f) Another GLM was used to assess plot level effects on mortality (height and density of initial regeneration) in the 58 and 59-year-old fires only. This model was constructed in the same manner as the model in section 5.5.4c), however the density of dead spruce in 5 m^2 plots was the response variable.

5.6 Results

5.6.1 Timing of delayed regeneration

Crossdated ages of trees from fires between 16 to 20 years old showed that regeneration rarely occurs between 7 - 20 years following fire (8.1% of regeneration; and only 4.2% between 11 - 20 years; see Chapter 4, Fig. 4.8). Seedlings in 38 and 41-year-old fires showed a slight peak in delayed regeneration, with an earlier mean delay (28 - 29.7 years) than in the 58 and 59-year-old fires (35.3 - 41.8 years; Figures 5.2 and 5.3). On 38 and 41-year-old fires, regeneration between 21 - 41 years after fire did not differ significantly from a uniform distribution ($Z = 0.986, p = 0.285, n = 27$). No significant differences were observed in the timing of delayed regeneration among stands from 38 and 41-year-old fires ($F = 0.233, p = 0.794$, df within groups = 23, df between groups = 2).

In the 58 and 59-year-old fires, regeneration between 21 - 59 years after fire departed significantly from a uniform distribution ($Z = 1.710, p = 0.006, n = 107$). In these fires, a distinct peak in regeneration occurred on logs between 38 and 44 years after fire during which 57.5% of all regeneration on logs established (Fig. 5.2b). Regeneration on logs was very rare prior to 24 years after fire, after which it occurred at a low, but apparently continuous rate between 24 and 37 years, and 45 and 56 years after fire. Seedlings on logs exhibited a delayed establishment peak more clearly than seedlings on humus and mineral soil (Figures 5.2b and 5.3). Six of the stands from 58 and 59-year-old fires showed a similar regeneration pulse. Mean delays did not vary significantly between stands from 58 and 59-year-old fires ($F = 2.302$, $p = 0.051$, df within groups = 94, df between groups = 5). Most shrub, herb, and grass cover values were lowest, while moss-covered wood and canopy cover were highest in fires with a similar age to when delayed regeneration peaked (38 and 41-year-old fires) (Tables 5.2 and 5.3).

5.6.2 Initial versus delayed regeneration

On average, initial regeneration comprised 53.5% of all trees in 58 and 59-year-old fires; at this time after fire, there was no significant difference in the number of initial versus delayed trees ($Z = -0.894$; $p = 0.371$; $n = 20$). In the thirty-nine 58 and 59-year-old sites sampled (1942 and 1941 respectively), significant variation occurred among sites in the ratio of initial to delayed regeneration (I:D ratio) ($Gp = 236.5$; $p < 0.001$; $df = 38$). This variation was not attributable to differences in I:D ratios between mast year (1941) versus non-mast year burns (1942) ($Gm = 0.84$; $p > 0.25$; $df = 37$; Fig. 5.4a). Significant variability occurred in the I:D ratios among the two "replicate" fires from the mast year (1941) and non-mast year (1942) ($Gf = 158.6$; $p < 0.001$; $df = 35$; Fig. 5.4b). I:D ratios did not differ significantly between sites 20 m and 100 m from seed sources (Gd = 1.95; $p > 0.5$; on 31 df; Fig. 5.4c). A significant difference was observed in I:D ratios between sites that were downwind of the prevailing Westerlies from those that were not. Sites situated downwind of seed sources had significantly lower proportions of initial regeneration than sites that were not downwind of seed sources ($Gw = 20.59$; $p < 0.005$; $df = 25$; Fig. 5.4d). Initial regeneration ranged from 0 to 100% in sites within mast year burns (Appendix 5.3). On non-mast fires, the percent initial regeneration had a slightly smaller range (0 to 86.7%). Considerable variability occurred between fires in the frequency of stands dominated by initial regeneration, delayed regeneration, or "even" mixtures of both initial and delayed regeneration (Fig. 5.5). Overall, 35% of stands were dominated by initial regeneration, 35% by "even" mixtures of initial and delayed regeneration, and 30% by delayed regeneration (Fig. 5.5).

The density of initial regeneration decreased significantly as the basal area of deciduous trees that survived the fire increased ($p < 0.001$; Table 5.4, Fig. 5.6).

5.6.3 Regeneration substrates

Regeneration on logs accounted for a significantly smaller proportion of total regeneration than trees on mineral soil and humus in 58 and 59-year-old fires ($Z = -3.486$; $p < 0.001$; $n = 64$) (Fig. 5.7). In 58 and 59-year-old sites, initial regeneration were found predominantly on mineral soil and humus, while delayed trees (establishing more than 20 years after fire), were distributed more evenly across substrates (Fig. 5.7). Log substrates were dominated by delayed regeneration (89.4%), particularly on above-ground logs (97.9%). On fires between 38 to 59 years old, seedlings were found predominantly on fire-killed logs, rather than on coarse woody debris pre-dating the fire. In 16 - 20 YOS , only 7.4 % of trees occurred on logs. Most of these trees were on logs that were down prior to fire because most log regeneration established before the fire (71.6%) (i.e. some spruce saplings survived the fire). No seedlings were found on downed stems of trees that had established after the fire, and subsequently died. Regeneration that was on logs increased with time since fire, despite a decrease in downed woody material between 20 - 59 years after fire (Table 5.2).

In 58 and 59 YOS , significant variation occurred among sites in the ratio of spruce on logs versus mineral soil and humus ($Gp_{log} = 210.4$; $p < 0.001$; 39 *df*). The proportion of spruce on logs was significantly greater on non-mast year burns than mast burns (Fig. 5.8; $Gm_{log} = 19.15$; $p < 0.001$; $df = 38$), and differed significantly between replicate fires ($Gf_{log} = 40.6$; $p < 0.001$; $df = 36$). The ratio of spruce on logs versus mineral soil and humus was not affected by distance from seed source ($Gd_{log} = 7.9$; $p > 0.5$; $df = 32$), while significantly higher than expected frequencies of trees on logs occurred downwind of seed sources (relative to prevailing Westerlies) ($Gw_{log} = 53.4$; $p < 0.001$; $df = 26$). Freeman-Tukey residuals indicated that sites situated on the upwind side of seed sources (relative to prevailing winds) frequently had fewer trees on logs than expected (8 of 10 significant residuals).

5.6.4 Density-dependent effects on delayed regeneration and stem mortality

Despite a density range of 0 - 6666 stems / ha of initial regeneration between sites in 58 and 59 YOS, the density of delayed regeneration did not decrease with increasing densities of initial regeneration at the site level (Table 5.5a; Fig. 5.9). However, sites with low initial densities had significantly higher proportions of delayed regeneration (Table 5.5b, Fig. 5.10; $p = 0.026$, $df = 39$).

The density of delayed regeneration at the sub-plot scale (5.0 m^2) was significantly reduced by increasing height of initial regeneration surrounding the subplot (in the 28.3 m^2 plot; Table 5.6a, Fig. 5.11) ($p < 0.001$, $df = 115$). The density of initial regeneration did not significantly improve the fit of the model ($F = 2.96$, $p = 0.088$, $df = 114$), although a trend was observed (Fig. 5.12). On the subset of plots where additional vegetation attributes were assessed, the density of delayed regeneration was significantly reduced by increasing height of initial regeneration, and increasing canopy closure ($p =$ 0.001 and 0.005 respectively; $df = 36$), although the latter trend was weak (Table 5.6b). The species comprising the canopy did not affect the density of delayed regeneration. Delayed regeneration densities varied substantially between fires, and with distance from seed source (Fig. 5.13).

The density of dead white spruce increased significantly with time since fire (Fig. 5.14), number of seed trees, and was significantly higher on mast year burns, and downwind of seed sources (relative to prevailing winds) ($p < 0.001$ in all cases; see Table 5.7). Only one dead spruce in total was found in 10 fires between 4 - 20 years of age ($n =$ 80 stands). In 58 and 59 YOS, the density of dead spruce in subplots (5 m^2) increased significantly in a non-linear fashion with increasing density of live initial regeneration in surrounding plots (28.3 m^2) ($p < 0.001$, $df = 112$; see Table 5.8). The height of initial regeneration did not affect the number of dead stems ($p = 0.775$, $df = 111$).

5.7 Discussion

5.7.1 The second window of establishment

A window of opportunity for delayed regeneration of white spruce in mixedwood stands occurred after fire on fire-killed logs. A substantial peak of regeneration was observed between 38 - 44 years after fire on decayed logs in 58 and 59-year-old fires. A peak in regeneration was not observed in 38 and 41-year-old fires; however, the time period assessed was shorter. Regeneration of white spruce on logs has been reported in several studies throughout the boreal forest (Rowe 1955; Nienstaedt and Zasada 1990; Lieffers *et al.* 1996b; Simard *et al.* 1998), but the length of delay was not-well documented. Delayed regeneration was not observed in this time period after fire in northern Saskatchewan; however, most stands assessed in that study were older and later regeneration had died (Gutsell and Johnson 2002). The delay period we observed coincided with the time when most snags had fallen (only 8% remain standing after 23 years; Lee 1998), and reached suitable decay classes for spruce establishment (Lee, pers. com.). Although fallen snags were most abundant in fires that were 16 - 20 years old, logs were not sufficiently decayed for seedling establishment. Logs in these fires had decay classes ranging between 1 and 3 according to the decomposition classes described by Mills (2001) (pers. obs.). In 38 and 41 YOS, seedlings were usually found on above-ground logs with a decay class of 4. Nurse logs were usually partially covered by a thin layer of moss (< 1 cm, pers. obs.), had no bark remaining, and were soft with small pieces of wood missing. In our oldest stands (58 and 59 years old), the amount of downed wood that was visible had decreased; most logs supporting seedlings were covered with a thick layer of moss or leaves and were in decay classes of 5 to 7. The window of opportunity for delayed regeneration may be short on logs because moss depth increases, logs are colonized by herbs, and further decay results in eventual burial by leaf litter. Moss layers exceeding 5 cm have been shown to prevent recruitment in other tree species (Harmon *et al.* 1986). In our oldest sites, the amount of downed wood, and moss covered logs were not significant predictors of the density of delayed regeneration (Tables 5.1 and 5.6b). This finding concurs with Lieffers *et al.* (1996b), and suggests that factors other than substrate availability may limit later regeneration.

The delayed regeneration pulse we observed may partly be due to the age class of sites assessed, and burn intensity. Assuming that at the time of the fire burned stands were the same age as adjacent unburned stands (at least 80 years old), fire-killed snags would have been large, and reached suitable decay classes for spruce establishment at a similar time among all the stands studied. No seedlings were found on fallen snags from self-thinning of aspen and birch regeneration in stands up to 59 years old. We suspect self-thinned logs were too small and were too rapidly covered with leaf litter to serve as regeneration microsites during the time frame examined. Recently-thinned logs in 59 YOS may be sufficiently large to serve as substrates, once decayed. If we had assessed stands that were considerably younger when they burned, we hypothesize that a distinct peak of delayed regeneration would not occur because the fire-killed trees would create smaller logs lacking suitable regeneration niches; ingress would thus be less abundant. The timing of delayed regeneration did not differ among stands with various basal areas of residual trees (0 to 12.6 m^2 / ha); however, stands with little canopy kill may exhibit more continuous establishment on logs as canopy trees die slowly over time and recruit into decay stages suitable for spruce establishment. The delay period we observed may occur frequently in aspen-dominated mixedwood sites in Alberta (with proximal seed sources at the time of fire) because the fires we sampled are representative of fires accounting for most of the area burned within the province (Eberhardt and Woodard 1987; Alberta Sustainable Resource Development 2001).

5.7.2 Substrate influences on delayed regeneration

Delayed regeneration on logs was more important than establishment on humus, even though logs occupied only 5.1% of the forest floor in 38 - 41 YOS. Transplant and seeding experiments in similar mixedwood stands in Alberta (43 – 73 years old) has indicated that establishment and overwinter survival (first year) is greater on logs than leaf litter (Delong *et al.* 1997). Although leaf litter is a poor substrate for white spruce regeneration (Zasada and Gregory 1969; Coates *et al.* 1994; Purdy *et al.* 2002), 25% of delayed regeneration was rooted in humus that originated from leaf litter. Sporadic recruitment on leaf litter was observed in 58 and 59 YOS during a wet summer in 2000. Few of these seedlings survived dry weather in late summer (5.7% alive in mid-September), and none survived the winter (see Chapter 4, section 4.5.1). Up to 70% overwinter survival has been observed in white spruce on leaf litter (Delong *et al.* 1997). These findings suggest that delayed regeneration on leaf litter may be confined to persistently moist sites (observed by Rowe 1955), or occurs sporadically in consecutive moist years. Overall, delayed regeneration occurred on logs substantially less than immediate regeneration on mineral soil and humus, thereby demonstrating the greater importance of immediate regeneration after fire on sites adjacent to seed sources.

Previous authors have suggested that white spruce establishes better on logs than leaf litter or moss due to better light and nutrients, reduced competition, less leaf litter accumulation, and better root growth (Lieffers *et al.* 1996b; Simard *et al.* 1998; Delong *et al.* 1997). The majority of delayed regeneration established when canopy closure was greatest but shrub, grass, and herb cover were at their lowest values (Table 5.3). White spruce establishment during this period may have been facilitated by reduced light attenuation and direct competition with understory vegetation (Lieffers *et al.* 1996b). Ingress declined by 58 and 59 years after fire, which coincided with reduced canopy cover, and increased understory cover (Table 5.3). Microclimate shifts with forest maturation such as increased humidity and more moderate temperatures may also have facilitated establishment on logs and leaf litter, because neither of these substrates was suitable in younger stands.

Galipeau *et al.* (1997) observed a second regeneration period for white spruce in eastern boreal forests. This period appeared attributable to seed production by initial regeneration, commencing as early as 40 years after fire. This was not the case in aspen-dominated mixedwoods in Alberta because none of the trees up to 59 years old were sexually mature, or had any shed cones beneath the trees. This time period to reach reproductive status is longer than the 30-year period reported by Nienstaedt and Zasada (1990). Most of the trees we examined had long periods of suppression (in ring width sequences) that likely delayed reproduction.

5.7.3 Post-fire influences on successional pathways

It is apparent that mixedwood stands do not follow the same successional pathway (a consistent ratio of initial to delayed regeneration) even under the same post-fire conditions with respect to mast year, seed source availability, distance from seed source, and direction from source. The ratio of initial to delayed regeneration varied considerably even when these factors were held constant. These findings suggest that further clarification is required to define the role of seed limitation on the successional pathway of mixedwood stands. Models of forest succession (e.g. JABOWA) have also indicated that the same initial conditions may lead to different development outcomes; consequently, succession is often recognized as being subject to stochasticity (Glenn-Lewin and van der Maarel in Glenn-Lewin *et al.* 1994). The greatest variation in ratios of initial to delayed regeneration occurred at the level of fire replicates, suggesting that burn intensity and substrate exposure were more critical factors in determining successional pathway. Fire intensity has been suggested by several authors as a determinant of spruce age structure (Rowe 1955; Kabzems and Lousier 1992; Lieffers *et al.* 1996a); however, this hypothesis has not been critically tested. Fires vary in timing, intensity, and size, and can have many direct and indirect effects on plant community recovery. Fire variability poses problems for chronosequence studies because differences in fires are assumed to be small compared to differences in regeneration patterns over time. Many of the factors investigated in this study are difficult to obtain for historic fires. If regeneration patterns are attributable to the specific characteristics of fires, generalizations about subsequent changes in species composition over time are unfounded. Allogenic factors are widely recognized as altering successional pathways (Glenn-Lewin and van der Maarel in Glenn-Lewin *et al.* 1994)

Fires of sufficient intensity to kill 100% of the canopy expose mineral soil, thereby creating microsites suitable for white spruce regeneration (Kabzems and Lousier 1992; Lutz in Zasada and Gregory 1969). Despite controlling for burn intensity by selecting stands with nearly complete crown kill (based on historic air photos), we suspect that variation in substrate exposure influenced the density of spruce regeneration immediately after fire on many sites. Significantly lower densities of initial regeneration occurred on sites where residual basal area of deciduous species was high. The high basal areas of residual aspen (fire survivors totaled 4.88 m^2 / ha) on the Conklin Trail fire suggest that less mineral soil was exposed than on other fires, and may explain the dominance of delayed regeneration. Mineral soil exposure can range between 0 and 100% among stands within the same stand replacing fire (Lutz in Zasada and Gregory 1969). This, in turn, leads to significant differences in the density of immediate establishment between stands within fires (Purdy *et al.* 2002). Several sites in mast burns with proximal seed sources and virtually no immediate regeneration experienced delayed regeneration that dominated the age structure 59 years after fire.

We expected to see age structures dominated by initial regeneration more frequently on mast year burns (MYB) than non-mast year burns (NMYB). Since immediate regeneration density is 3.84 times greater on MYB than on NMYB (based on fires between 1979 and 1994; Figures 4.4 and 4.5), a given density of delayed regeneration would be expected to comprise proportionally more of the total regeneration on non-mast burns. This was not the case on the Conklin Trail fire (MYB) which was dominated by delayed regeneration. Several confounding factors may have contributed to this: 1) none of the stands were downwind of seed sources; consequently, initial establishment densities were lower than expected; 2) as mentioned earlier, these stands had the most residual aspen surviving the fire, suggesting lower burn intensity, and thereby reducing the likelihood of a mast year effect on regeneration; and 3) season of burn.

Spring fires are typically less intense than summer fires, expose less mineral soil (Kabzems and Lousier 1992), and require higher rates of spread in order to crown in mixedwoods (Alexander *et al.* 1984). White spruce regeneration is highly variable on spring fires. Significant mineral soil exposure and spruce regeneration occurred on a spring fire in Alaska (late May) (Zasada 1985); however, Kabzems and Lousier (1992) found that fire occurrence in the spring rather than the summer reduced immediate post-fire regeneration, and suggested this would affect successional pathway. Our data do not support the idea that all spring fires follow a similar successional pathway. Both MYB (1941) started within 4 days of each other in April and likely burned under similar conditions for at least a month (they were only 15 km apart), yet they had very different successional pathways. Eighty percent of stands were dominated by initial regeneration on the 1941 Piche Lake fire, while 80% of stands were dominated by delayed regeneration on the 1941 Conklin Trail fire (Figure 5.5). Spring fires may limit initial regeneration density more on MYB than NMYB, because there is greater potential for higher regeneration on MYB. Seedbeds on NMYB have already deteriorated by the time a mast year occurs (see Chapter 4, section 4.7.2); consequently, an intense summer fire may provide only slightly more opportunities for regeneration than a spring fire.

Non-mast burns were variable in terms of the frequency of stands dominated by delayed regeneration (Fig. 5.5). This appeared to be attributable to greatly different densities of delayed regeneration. The Logan Lake fire had 334 stems / ha of delayed regeneration, while the Wabasca Lake fire had 3167 stems / ha. Counter-intuitively, higher densities of initial trees on the Wabasca Lake fire did not preclude it from also having substantially more delayed regeneration than the Logan Lake fire. These two fires had similar burn dates, log substrate availability, numbers of seed trees, frequency of stands downwind of seed sources (relative to prevailing winds), and similar crown kill, indicating that other factors controlled the density of delayed regeneration. The Wabasca Lake fire was 200 km northwest of the other fires, and may have had more suitable conditions for delayed establishment on logs, such as more precipitation or larger downed logs. Precipitation records are not available after 1947 for the town of Wabasca, so a comparison of the two areas could not be made (http://www.msc-smc.ec.gc.ca/climate/station_catalogue/index _e.cfm).

Proximity to seed sources has frequently been cited as a critical aspect shaping forest succession. The hypothesis rests on the principle that dispersal limitations affect regeneration density, and subsequent compositional shifts will be dictated by the rate of regeneration and tree growth. Palik and Pregitzer (1995) hypothesized that spatial variation occurs in age structure with distance from seed sources. In the eastern boreal forest, this phenomenon has been exhibited in multi-generation stands with advancing fronts of maturing seed dispersers (Galipeau *et al.* 1997). We did not find any supporting evidence for this in our western boreal mixedwood sites; none of the initial trees had produced cones by age 59, nor did the ratio of initial to delayed regeneration differ between 20 and 100 m distances from seed sources within individual stands, despite 20 fold differences in total density. It appears that variation in seed dispersal over this distance has no impact on age structure in stands in stands less than 60 years old; effects on age structure at greater distances are less probable because densities are lower. Significantly higher proportions of delayed regeneration occurred downwind of seed sources than upwind and this may be due to an ongoing supply of seed.

5.7.4 Density-dependent effects on age structure

Several factors could lead to the development of even-aged stands immediately after fire. After a regeneration episode, the absence of suitable microsites over time could lead to an even-aged stand. Alternatively, if initial establishment densities were very high and trees grew rapidly, later regeneration may not survive due to shading from conspecifics. Lieffers *et al.* (1996b) suggested that regeneration periods of white spruce post-fire would be short if establishment occurred at high densities because light reductions by the developing conifer understory would preclude further regeneration. Light limitation reduces growth and increases mortality rates of white spruce (Kobe and Coates 1997), and would therefore affect delayed regeneration more than initial regeneration.

Stand and fire level factors were less important influences on delayed regeneration than fine scale factors such as the density, proximity, and size of initial regeneration. We suspect that the patchy distribution of initial regeneration resulted in areas with little initial regeneration, which were thus suitable for delayed regeneration. Delayed regeneration did not occur in any 5 m^2 plots that had an initial regeneration tree over 6 meters tall that was within 3 meters of the plot center. Most initial regeneration was below this height (median = 3.32 m), and likely caused little mortality of delayed trees. The tremendous variation in height of initial regeneration (range 0.045 m – 18 m, mean = 4.62 m) probably made density-dependent effects on delayed regeneration quite variable in 58 and 59 YOS.

White spruce can tolerate extremely suppressed growth (see Chapter 2, section 2.7.1) and shows little self-thinning in fire-origin stands up to 41 years old. White spruce is a little less shade-tolerant than black spruce (Kobe and Coates 1997), which does not self-thin before 35 years of age (Carleton and Wannamaker1986). If white spruce starts to self-thin about this same time, then mortality of initial regeneration coincides with the peak of delayed regeneration on logs (between 35 and 45 years post-fire); thus, density-dependent effects would be reduced. Since most delayed trees were between 15 and 25 years old at the time of our sampling, it is unlikely that they had yet experienced self-thinning. Considerable mortality was commonly observed in dense patches of regeneration in 58 and 59 YOS (pers. obs.). Although dead spruce were not aged, it is likely that they were predominantly initial regeneration. This hypothesis is supported by generalized linear models that best predicted dead stem densities by variables that were significant predictors of live initial trees (masting, seed tree density, and direction from seed source, see Table 5.7 and Chapter 4, section 4.6.1). If initial regeneration experienced much higher mortality than delayed regeneration, it would help explain why few detectable influences of stand level attributes on age structure were observed. As trees grow over time, the density of initial regeneration may affect stand age structure more through greater competition with delayed regeneration. Hence, the observed ratios of initial to delayed regeneration may partly be a function of the age of stands we assessed, because delayed regeneration would experience mortality later. Gutsell and Johnson (2002) found no delayed cohorts of trees older than 50 years in older boreal forests in Saskatchewan (78 – 154 years); however, they assessed only 4 stands with white spruce in this age range, and regeneration on logs was not reported in their study.

5.7.5 Successional paradigms of mixedwoods

Mixedwood forests do not readily fall into the exclusive successional models proposed by Egler (1954) and Connell and Slatyer (1977). Initial floristics models (Egler 1954) appear suitable for only 35% of the sites studied over a 58 and 59 year post-fire period (sites with 60% or more immediate regeneration); however, only 15% of stands had more than 80% initial regeneration). This pattern contrasts with much of the boreal forest where the initial floristics model adequately describes regeneration dynamics of tree species (Bergeron 2000). Even for stand-replacing fires, burn intensity appeared highly variable between fires, within fires, and within stands. This variability limits the success of initial regeneration, and prevents one successional pathway from dominating severely burned stands. Initial establishment densities of spruce were so variable that when stands mature they may range from pure white spruce to pure deciduous species. The slow growth of the initial cohort of white spruce under deciduous species (see Chapter 2, section 2.7.1) demonstrates the importance of tolerance mechanisms for mixedwood succession (Connell and Slatyer 1977).

Inadequate exposure of mineral soil in many stands also underscores the importance of facilitative mechanisms for white spruce regeneration, and ultimately to mixedwood succession. This represents a fundamentally different successional pathway in mixedwoods and should be recognized as such. Ingress on decayed logs and humus occurred in most stands; however, their relative contribution to canopy composition is unclear because stands will experience more self-thinning as they mature. By 59 years after fire, delayed regeneration dominated 30% of sites (sites with 60% or more delayed regeneration). Even with a strong seed source, the density of delayed regeneration was usually insufficient to fill the canopy, even if all trees survive. Developing stands of pure white spruce average 1400 stems / ha at 60 years of age (Alberta Forestry Lands and Wildlife 1985) (67.5% of 58 and 59-year-old stands in our study had less than 1000 stems / ha of delayed regeneration. This suggests that deciduous species will continue to remain in the canopy long after most delayed regeneration reaches the canopy. White spruce rarely replaces deciduous species completely; consequently, mixedwood succession does not readily fit into the relay floristics model (Egler 1954; Connell and Slatyer 1977).

Many studies indicate that succession within a plant community can occur at different rates and have different dominant species in late seral stages (Olson 1958; Horn 1981; Pickett *et al.* 1987). A non-equilibrium picture of succession (Glenn Lewin and van der Maarel 1994) is applicable in mixedwoods because the time required for white spruce to achieve dominance will vary greatly depending on seed source availability (Lieffers *et al.* 1996a), and aspen stands may persist for hundreds of years without changing to spruce (Cummings *et al.* 2000). Cyclic succession also applies to mixedwoods because the dominant tree species may fail to regenerate, and differ in abundance between fire events (see Chapter 6, Fig. 6.5).

The successional models of Egler (1954) and Connell and Slatyer 1977) do not adequately describe the multiple pathways that succession follows, nor do they allow for several mechanisms to operate within a given successional pathway, sere, or species (Pickett *et al.* 1987). In their study of primary succession following deglaciation in Alaska, Chapin *et al.* (1994) concluded that no single factor or mechanism adequately explains primary succession. Both primary and secondary succession may follow multiple pathways of development and this has been shown in many studies spanning a variety of plant communities (Glenn-Lewin and van der Maarel 1994). Our study of secondary succession support these studies, and suggest that several successional mechanisms occur concurrently in mixedwoods: facilitation of delayed regeneration on decayed logs, competition between initial regeneration resulting in increased mortality mid-succession, and tolerance of many trees to suppressed growth. The concurrent operation of these mechanisms may help explain the wide variation we observed in age structure between stands with similar stand histories with respect to burn timing relative to mast years and seed availability. We suspect that competitive balances between and amongst tree species will change over time in the sites studied, and the ratios of initial and delayed regeneration that we observed may vary with time.

5.8 Conclusions

Age distributions in mixedwood sites demonstrate that several successional pathways are possible from similar post-fire conditions. The slow growth of white spruce, its high tolerance of suppression, and variable initial establishment densities all appear to contribute to this. Delayed regeneration exhibits a strong peak (second window of opportunity) that is attributable to increased establishment between 38 - 44 years after fire on down, fire-killed snags. On intense fires with strong seed sources, age structures indicated that succession was dominated as frequently by initial regeneration as delayed regeneration, and equal mixtures of initial and delayed regeneration were just as common. Under these conditions, delayed regeneration occurs in most stands, but does not usually occur in sufficient densities during the second window of opportunity to completely replace the deciduous canopy.

Table 5.1 A summary of variables tested in generalized linear models predicting initial regeneration density, delayed regeneration density, proportion delayed regeneration, and the density of dead stems in 58 and 59-year-old mixedwood stands. Variables tested in section 5.5.2 (Table 5.4) are identified with the letter x. Variables tested in site-level and plot-level analyses described in section 5.5.4 (a - f) are identified by the letters (a - f) that correspond with each of these analyses.

Independent Variables	Dependent Variable			
	Density of initial regeneration	Density of delayed regeneration	Proportion delayed regeneration	Density of dead stems
Site level analyses				
Initial regeneration (avg. stems/site)		a	b	
Decid. resid. (m^2/ha)	x			
Conif. resid (m^2/ha)	x			
Time since fire				e
Masting				e
Distance				e
Direction from seed source				e
Initial seed trees within 60 m				e
Plot level analyses				
Initial regeneration (stems/plot)		c,d●		f
Height of initial regeneration		c,d●		f
Canopy closure		d		
Downed wood		d		
Moss covered log		d		
Seed trees (within 60 m)		d		
Proportion regeneration (by tree species)		d		

●model c tested all 115 plots in 58 and 59-year-old stands, while model d tested 39 of these plots for which additional vegetation variables were available

Table 5.2: Regeneration of white spruce on logs relative to availability of wood and wood that appeared to be in suitable decay classes (moss covered wood). Fires occurred between 4 to 59 years prior to the time of sampling. The root collar of the sampled trees was situated in wood. Means are averages from at least 7 stands for a single fire in most years, except 16, 18, 58, and 59-year-old fires, which are means from two fires (at least 14 stands total).

Fire Year	Time-since-fire (years)	Percent of total ground cover		Proportion of total trees that were on logs	Number of trees assessed
		Wood on ground	Moss on wood●		
1994	4	3.1	1.7	■	■
1992	6	1.7	1.3	■	■
1991	7	8.2	3.2	■	■
1982	16	7.9	1.8	0.063	423
1981	17	7.6	1.1	0.100	80
1980	18	6.6	1.8	0.067	381
1979	19	8.9	2.4	0.066	30
1961	38	6.3	3.7	0.149	208
1958	41	3.8	3.9	0.695	210
1942	58	3.1	2.2	0.207	376
1941	59	2.5	3.5	0.425	418
Total					**2126**

● a subset of wood on the ground

■ Substrate was not recorded for these trees; however, we observed that the majority of seedlings were rooted on mineral soil and humus.

Table 5.3: Shrub, grass, and herb cover in relationship to canopy closure in mixedwood stands with different lengths of time since fire. Values reflect means from three fires per stand age (4 - 7 and 38 - 41-year-old fires respectively), 7 fires for 16 -20-year-old fires, and 4 fires for 58 and 59-year-old fires. A minimum of 7 stands were sampled per fire. Bolded values show the peak of canopy closure (38 - 41 years post-fire), and which cover attributes are the lowest during the same time interval.

Stand age (years)	Canopy closure	Percent shrub cover by height class			Percent grass cover			Herb cover
		0 - 0.2 m	0.2 -0.5 m	0.5 - 2.0 m	live	lying dead	standing dead	
4-7	25.0	8.5	11.9	8.3	6.3	10.9	5.4	21.3
16-19	51.9	6.2	6.2	5.0	1.5	5.3	1.2	10.4
38-41●	73.3	**0.8**	7.9	**4.0**	**0.9**	**1.2**	**0.9**	12.8
58-59	50.7	1.8	6.9	6.9	1.7	2.6	1.0	17.4

● this period coincides with delayed regeneration

Table 5.4 Results of a generalized linear model testing whether the initial regeneration density of white spruce in 58 and 59-year-old mixedwood stands was affected by the basal area of live deciduous and coniferous residual trees. For each variable, the percent of total deviance explained, the significance (p), and the direction of the effect on density is presented. Only basal area of live deciduous residuals was significant using a stepwise procedure and included in the final model (indicated by the letter x). *df* = degrees of freedom. A polynomical function was used to model non-linear effects for deciduous residuals.

Variable	*df*	% Deviance	Direction of the relationship	p	model
Null	116				
Deciduous residuals	113	9.9	negative	< 0.001	x
Coniferous residuals	112	0.6	positive	0.039	

Table 5.5 Results of a generalized linear model at the site level that tests whether a) the density of delayed regeneration and b) the proportion of delayed regeneration, decreased with increasing initial regeneration density. Percent of total deviance explained by initial regeneration as well as the significance (*p*) is presented. *df* = degrees of freedom.

Variable	*df*	% Deviance	*p*
a)			
Null	39		
Initial regen. density	38	2.1	0.978
b)			
Null	39		
Initial regen. density	38	28.8	0.026

Note: models a) and b) are described in sections 5.5.4a) and b) respectively

Table 5.6 Results of a generalized linear model testing whether the density of delayed regeneration in subplots (5 m^2) was affected by the density and height of adjacent initial regeneration surrounding the plot (28.3 m^2) in 58 and 59-year-old stands (a). A similar analysis was also done on the subset of these plots (b) where additional abiotic and biotic variables were collected to determine if they were significant predictors of delayed regeneration. For each variable, the percent of total deviance explained (in the order of most to least), the significance (*p*), and the direction of the effect on density is presented. Variables included in the model column (indicated by an x) were significant using a stepwise procedure, and included in the final model. *df* = degrees of freedom.

Variable	*df*	% Deviance	Direction of relationship	*p*	model
a)					
Null	115				
Height	114	21.1	negative	< 0.001	x
Initial regen. density	113	2.8	negative	0.009	
Height * Initial regen.	112	0.3	negative	0.411	
b)					
Null	38				
Height	37	21.1	negative	< 0.001	x
Canopy closure	36	11.6	negative	0.005	x
Initial regen.	35	4.5	negative	0.058	
% Moss covered log	34	0.3	positive	0.643	
% Log substrate	33	0.1	positive	0.804	

Note: models a) and b) are described in sections 5.5.4c) and d) respectively

* indicates an interaction term

Table 5.7 Results of a generalized linear model testing which variables best explain the density of dead spruce in mixedwood stands (see section 5.5.4e). Seventeen fires that occurred between 4 - 59 years prior to sampling were analyzed. For each variable, the percent of total deviance explained (in the order of most to least), the significance (*p*), and the direction of the effect on mortality is presented. Variables included in the model column (shown by the letter x) significantly improved the model using a stepwise procedure and were included in the final model. *df* = degrees of freedom. A polynomial funtion was used to model significant non-linear effects for variables with an (●)

Variable	*df*	% Deviance	Direction of relationship	*p*	model
Null	798				
Time since fire●	795	26.6	positive	< 0.001	x
Masting	794	14.9	positive	< 0.001	x
Initial seed trees-60 m●	791	11.3	positive	< 0.001	x
Direction from source■	785	7.9	□	< 0.001	x

■ six direction categories of 60 degrees each

□ higher mortality occurred downwind of seed sources (60 to 180 degrees)

Table 5.8 Results of a generalized linear model testing whether the density of dead spruce in subplots (5 m^2) was affected by the density and height of initial regeneration in surrounding plots (28.3 m^2) in 58 and 59-year-old mixedwood stands (see section 5.5.4f). For each variable, the percent of total deviance explained (in the order of most to least), the significance (*p*), and the direction of the effect on density is presented. Variables included in the model column (indicated by an x) significantly improved the model using a stepwise procedure and were included in the final model. *df* = degrees of freedom. A polynomial funtion was used to model significant non-linear effects of initial regeneration.

Variable	*df*	% Deviance	Direction of relationship	*p*	model
Null	115				
Initial regen. density	112	45.0	positive	< 0.001	x
Height	111	0.1	positive	0.755	
Initial regen. * Height	108	6.2	positive	0.183	

* interaction between terms

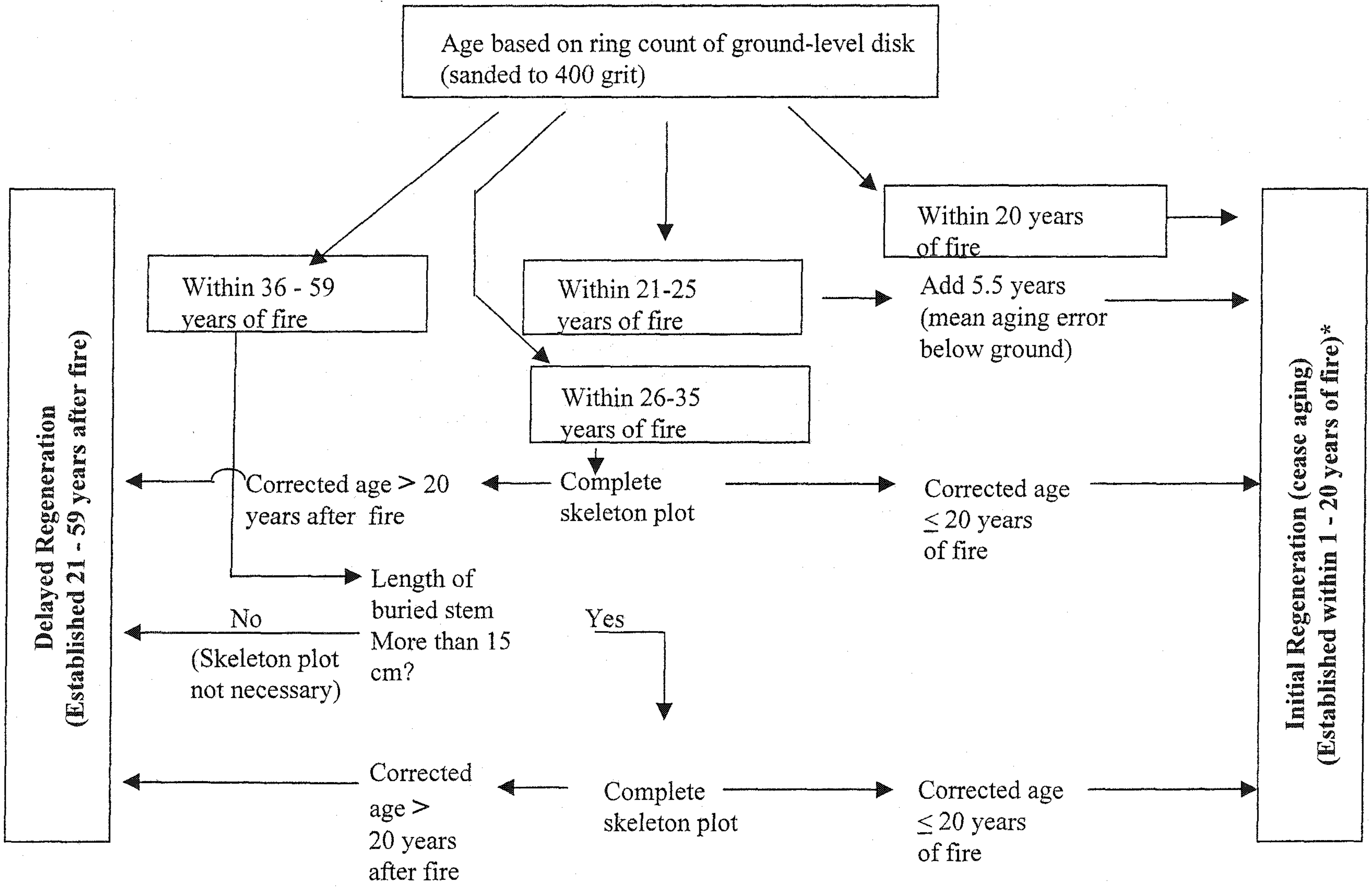
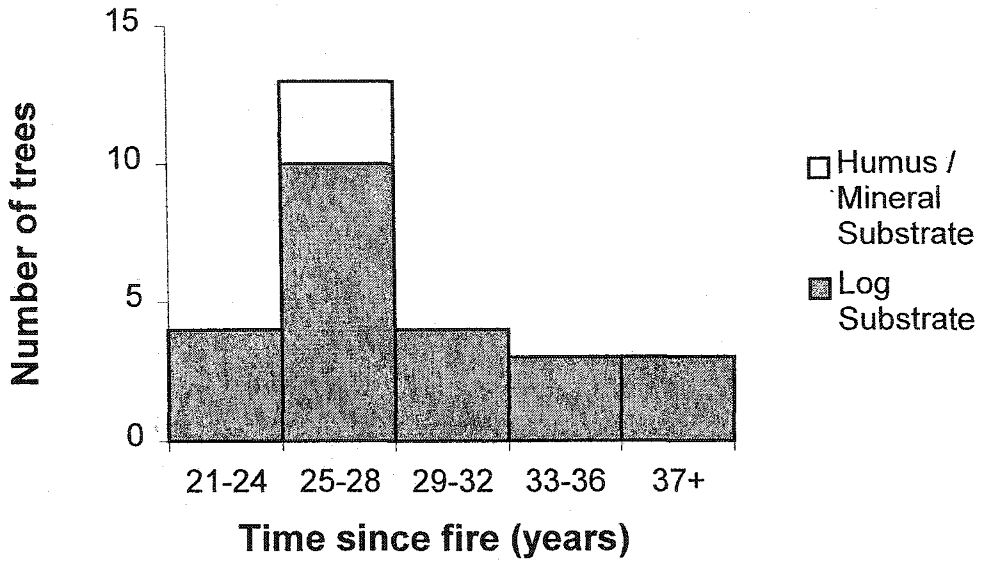


Figure 5.1: Sequential aging procedures and decisions made to distinguish initial regeneration from delayed regeneration on 58 and 59-year-old fires. This method did not require all the time consuming crossdating procedures for every tree, that were outlined in Chapter 2. * Trees dating to within 20 years of a fire based on a ring count at ground level are actually initial regeneration that established within a few years of the fire; careful crossdating demonstrated this repeatedly.

a) 38 and 41 year old stands combined



b) 58 and 59-year-old stands combined

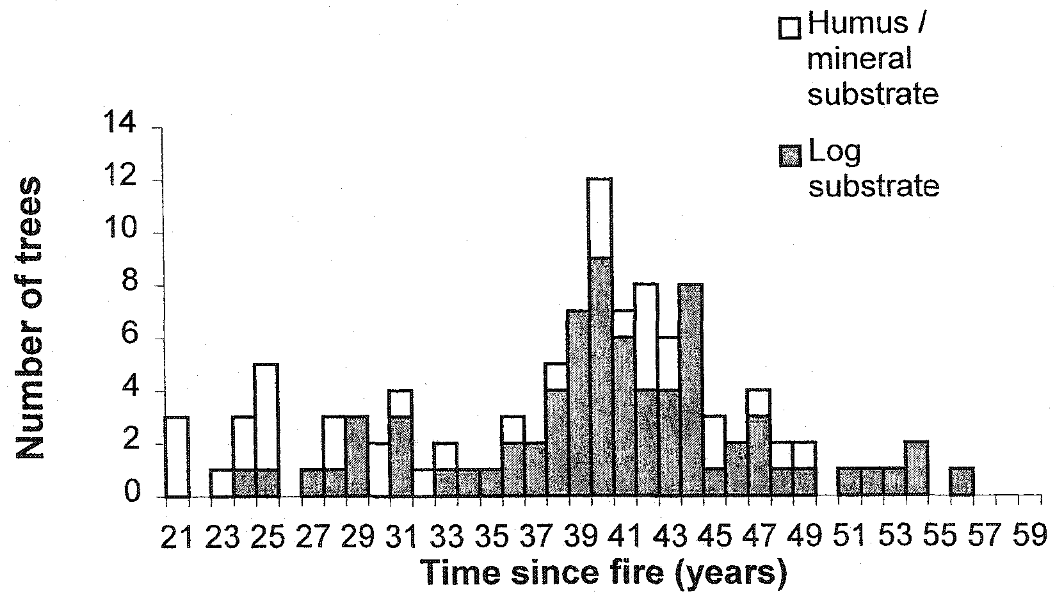


Figure 5.2: Timing of delayed regeneration on logs versus the forest floor. Trees that established within the first 20 years following fire were omitted because crossdating showed they originated within a few years of the fire. A) two stands from each of two fires that were 38 and 41- years-old were sampled (*n* = 27 trees; 12, 3-m radius plots were searched in total, as well as the area surrounding these plots). B) Two stands from each of four fires that were 58 and 59-years-old were sampled (*n* = 107 trees; 24, 3-m radius plots were searched in total, as well as the area surrounding these plots).

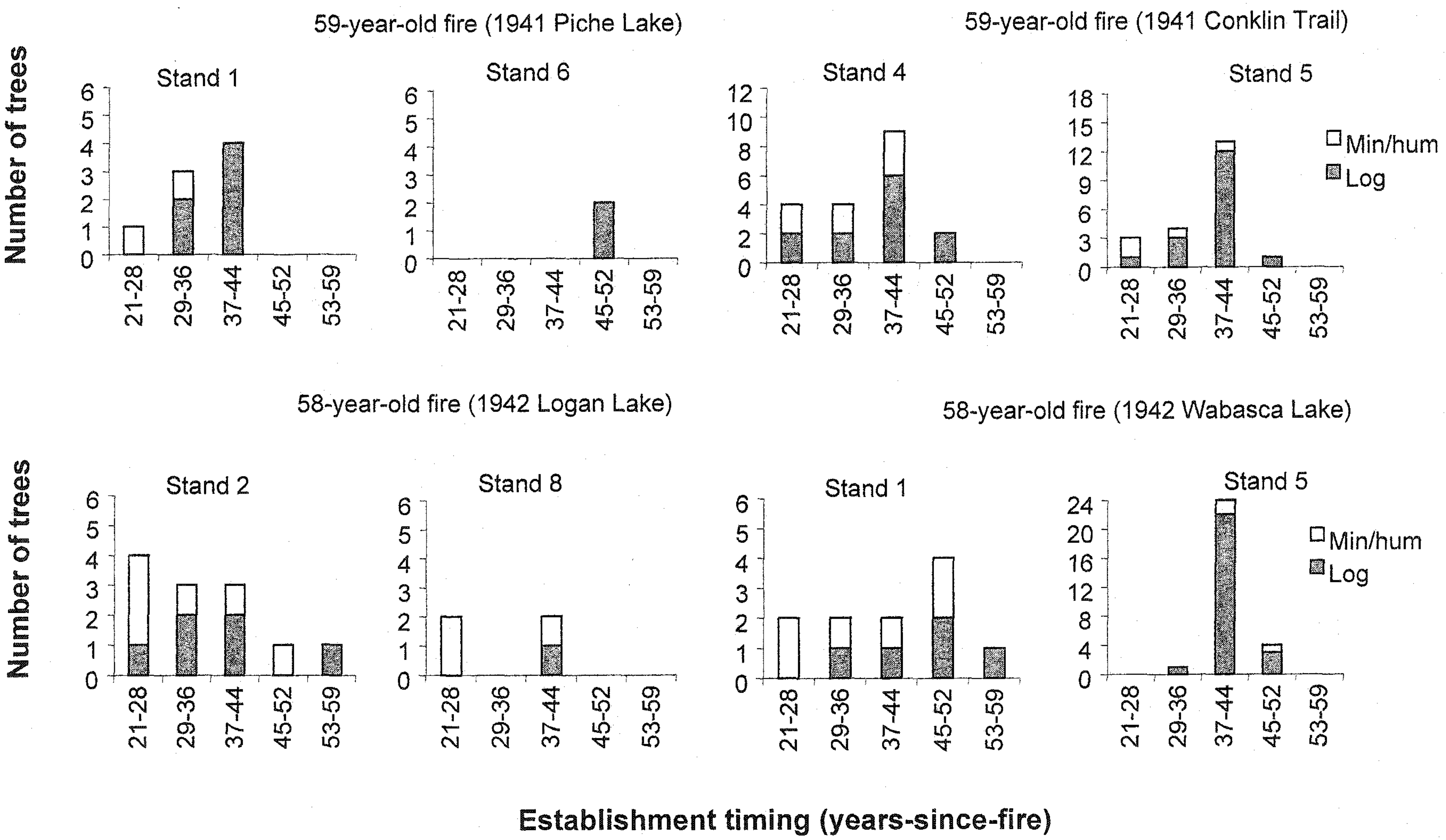


Figure 5.3: The timing of delayed establishment in 59 and 58-year-old fires (*n* = 2 stands / fire). Thirty trees were collected per stand; trees that established more than 20 years post-fire were classified as delayed regeneration and are depicted here. Trees were grouped by establishment substrate: mineral soil or humus (location of root collar in these substrates could not always be distinguished), versus downed logs.

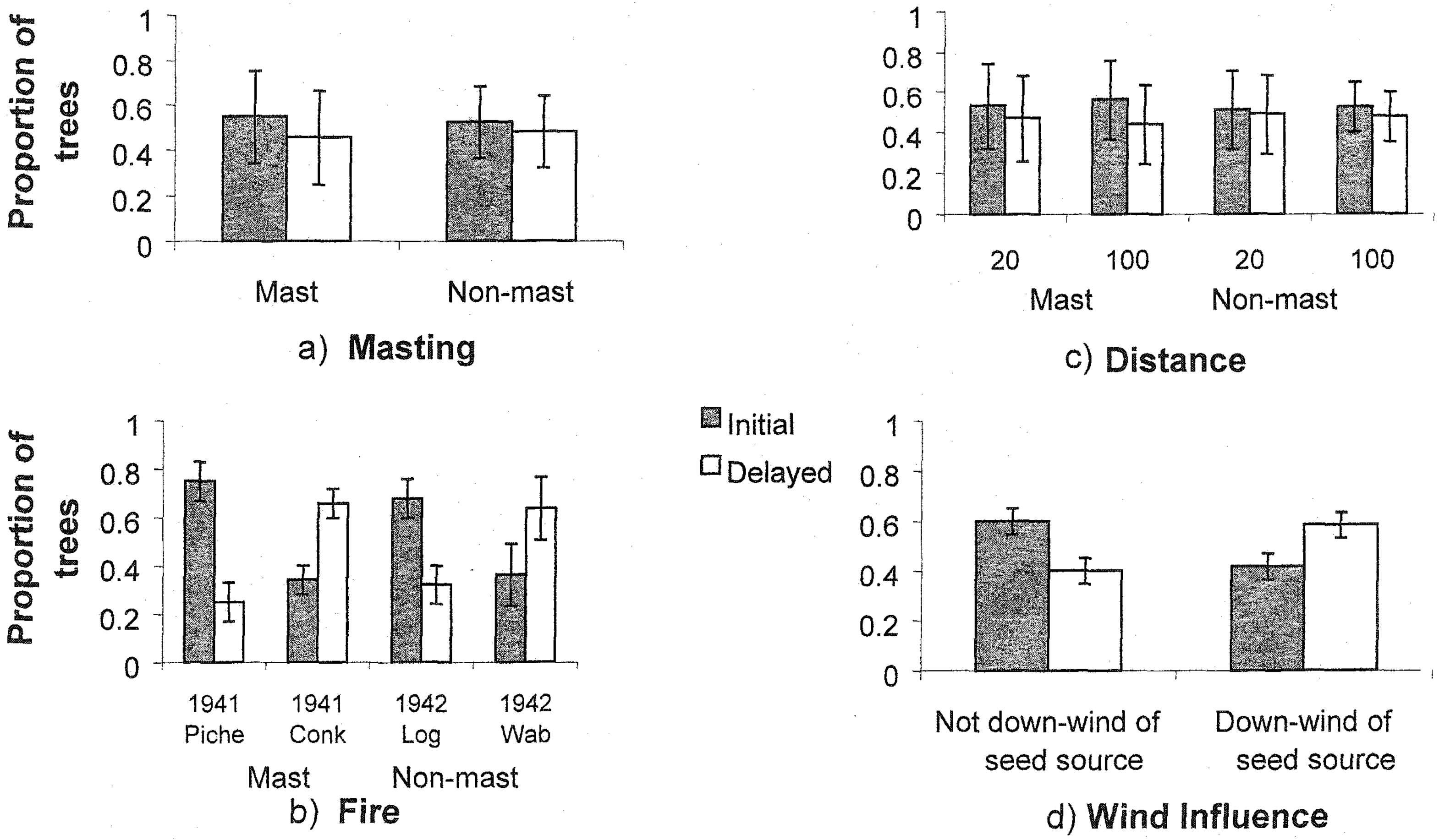


Figure 5.4: Influence of temporal and stand location effects on the proportion of initial regeneration (established between 1 - 20 years post-fire, see section 5.3.1 and 5.3.2) versus delayed regeneration (more than 20 years post-fire). Effects include: a) mast year burns (1941) versus non-mast year burns (1942), b) replicate fires, c) distance from seed source, and d) direction relative to prevailing winds dispersing seed from live seed sources (downwind is 60 - 150°, while not downwind is all other directions). Bars depict means from two fires +/- 1 std. error. Five stands were sampled per fire.

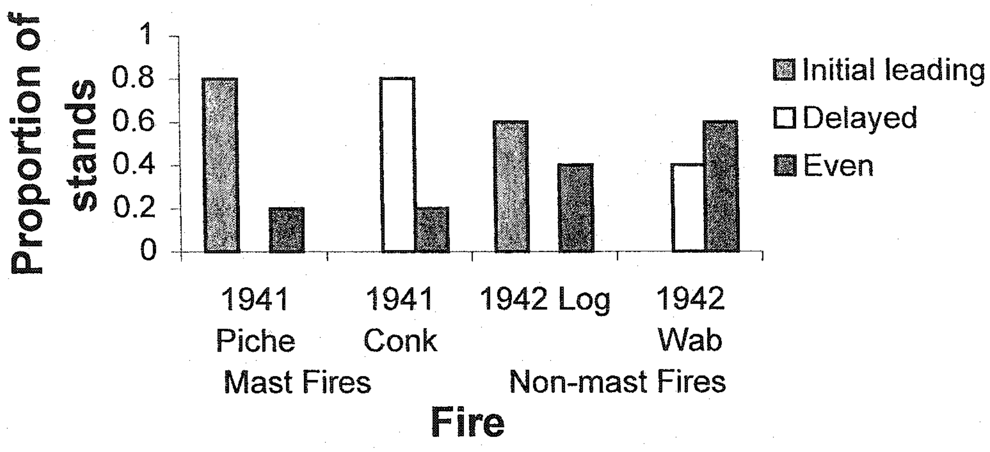


Figure 5.5: Frequency of stands dominated by initial regeneration versus stands dominated by delayed regeneration, on mast and non-mast year fires. Stands with 60 percent or more initial regeneration were classified as initial leading, stands with more than 60 percent delayed regeneration were classified as delayed, stands with more than 40 and less than 60 percent of initial and delayed regeneration respectively, were classified as even. Five stands were aged per fire.

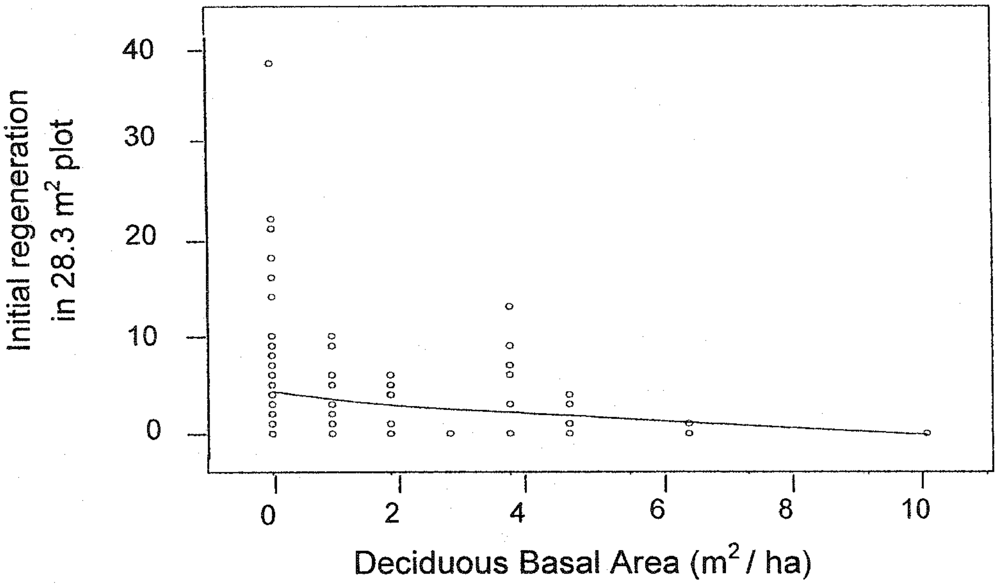


Figure 5.6: Relationship between density of initial regeneration relative to basal area of deciduous trees surviving the fire on plots in the 58 and 59-year-old fires (*n* = 117 plots, deviance explained = 10.0 %, $p < 0.001$).

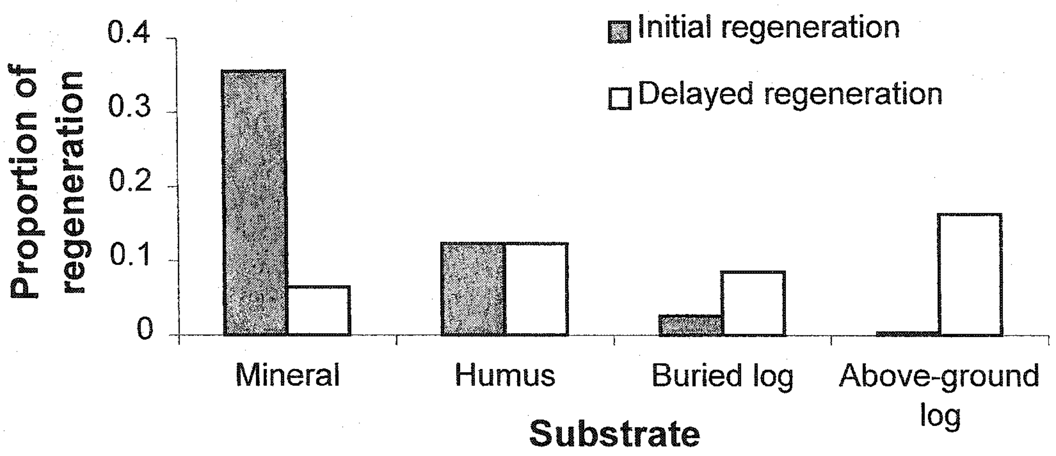


Figure 5.7: Proportion of total regeneration that was initial or delayed and that occurred on different substrates in 58 and 59-year-old fire origin stands (n = 20 stands). All trees were excavated, and were classified according to the location of the root collar. Fallen logs with a visible outline were classified as above-ground logs, while buried logs were not visible prior to excavation of the tree.

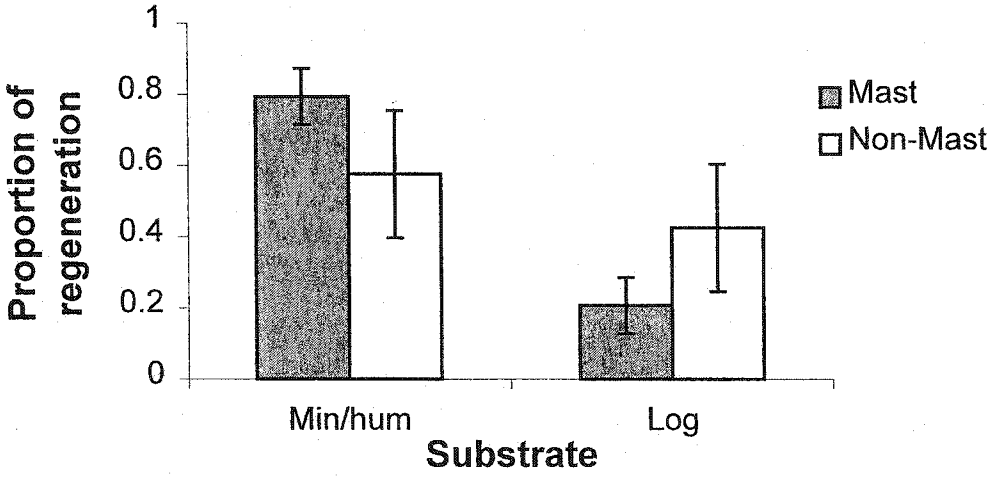


Figure 5.8: Proportion of regeneration found on different establishment substrates on mast (1941) versus non-mast (1942) fires. Mineral soil and humus are substrates typically available immediately after fire while logs are available more than 20 years after fire. Bars depict means from two fires, +/- 1 std. error. Eight stands were sampled per fire.

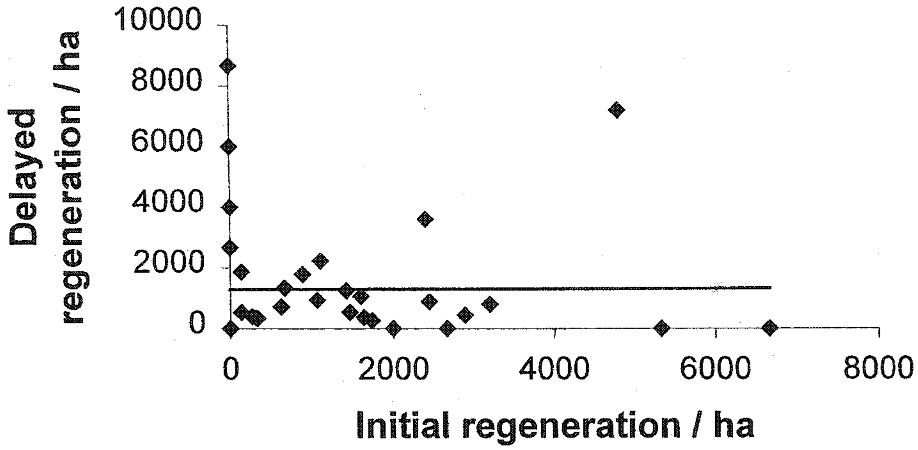


Figure 5.9: Relationship between the mean density (three 28.3 m^2 plots) of delayed regeneration at 58 and 59-year-old sites versus the density of initial regeneration (n = 39 sites). See table 5.5a for the statistical analysis.

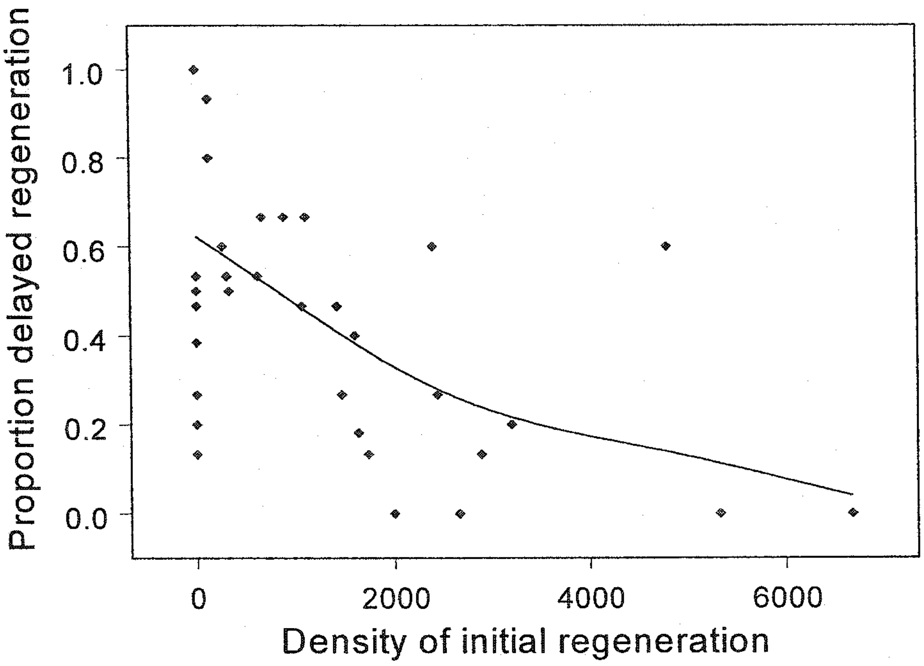


Figure 5.10: Relationship between the mean density of delayed regeneration at 58 and 59-year-old sites versus the proportion of initial regeneration (n = 39 sites). See table 5.5b for the statistical analysis.

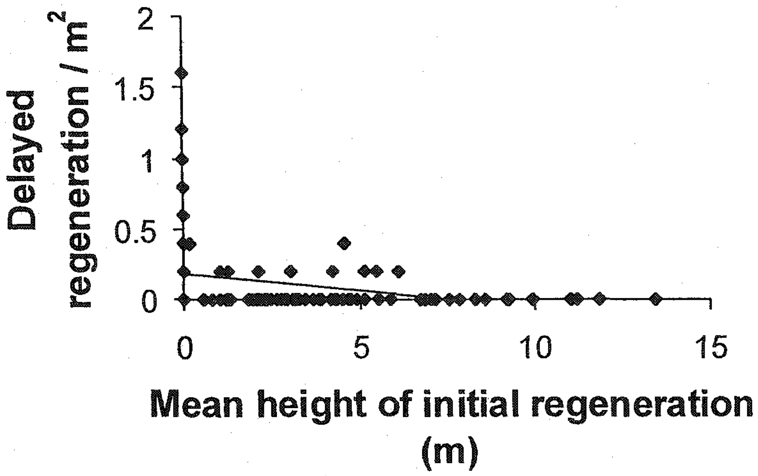


Figure 5.11: Relationship between the density of delayed regeneration and mean height of initial regeneration in plots (58 and 59-year-old fires). Height of initial regeneration was obtained within a 28.3 m^2 plot centered on the $5m^2$ subplot containing delayed regeneration (n = 116 plots). See table 5.6a for the statistical analysis.

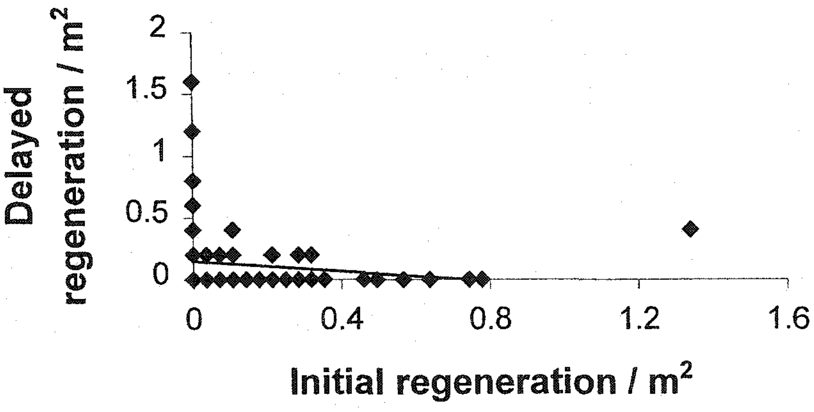


Figure 5.12: Density of delayed regeneration in the center 5 m^2 subplots in relation to the density of initial regeneration in the surrounding 28.3 m^2 plots (n = 117 plots). See table 5.6a for the statistical analysis.

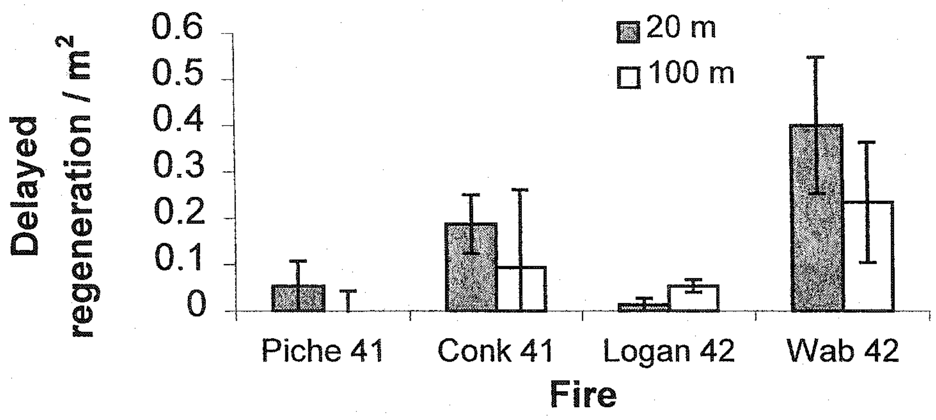


Figure 5.13: Density of delayed regeneration relative to distance from seed source on 58 and 59-year-old fires (1942 and 1941 respectively).

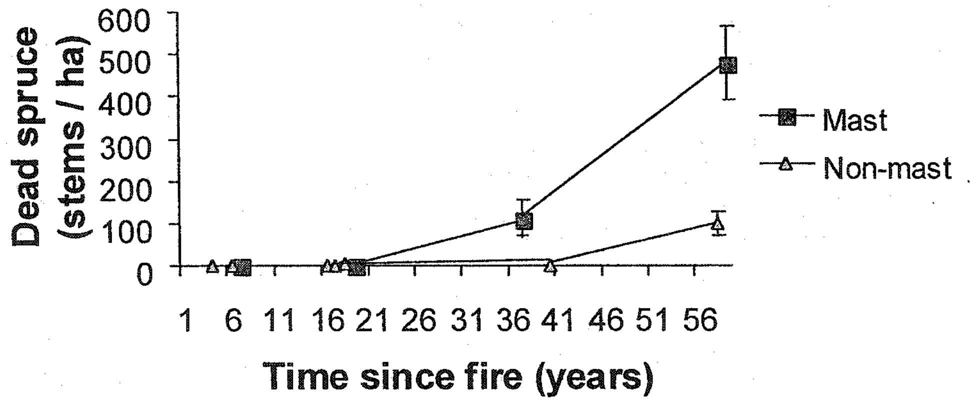


Figure 5.14: The density of spruce regeneration that subsequently died relative to time since fire for mast and non-mast fires. Standing and fallen stems of all sizes were included in counts. Means and standard error bars are from at least 7 stands for a single fire in most years, except years 16, 17, 18, 38, 58, and 59 which reflect means and standard error from two fires (at least 14 stands).

5.9 Literature Cited

Alberta Environmental Protection. 1999. Natural regions and sub-regions of Alberta. AB. Nat. Heritage Inf. Centre, Edmonton, AB.

Alberta Forestry Lands and Wildlife. 1985. Alberta phase 3 forest inventory - An Overview. AB. For. Serv., Edmonton, AB.

Alberta Sustainable Resource Development. 2001. Historical wildfire information. For. Prot. Branch. http://envweb.env.gov.ab.ca/env/forests/fpd.

Alexander, M.E., Lawson, B.D., Stocks, B.J., and Van Wagner, C.E. 1984. User guide to the Canadian forest fire behavior prediction system: rate of spread relationships, Envt. Canada, Can. For. Ser. Fire Danger Group. Interim edition.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology **81**: 1500-1516.

Bishop, Y.M., Fienberg, S.E., and Holland, P.W. 1975. Discrete Multivariate Analysis: Theory and Practice, Cambridge, United States.

Carleton, T.J., and Wannamaker, B.A. 1986. Mortality and self-thinning in black spruce. Annals of Botany. **59**: 621-628.

Coates, D.K., Haeussler, S., Lindeburgh, S., Pojar, R., and Stock, A.J. 1994. Ecology and Silviculture of Interior Spruce in British Columbia. For. Canada, B.C. Min. For., B.C., Canada, FRDA Rep. 220.

Connell, J.H., and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Am. Nat. 111: 1119-1144.

Day, R.J. 1964. The microenvironments occupied by spruce and fir regeneration in the Rocky Mountains, Can. Dept. For., For. Res. Branch Pub. 1037.

Delong, H.B., Lieffers, V.J., and Blenis, P.V. 1997. Microsite effects on first-year establishment and overwinter survival of white spruce in aspen-dominated boreal mixedwoods. Can J. For. Res. **27**: 1452-1457.

DesRochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? Can. J. For. Res. **27**: 1263-1267.

Dobbs, R.C. 1976. White spruce seed dispersal in central British Columbia. For. Chron. **52**: 225-228.

Eberhardt, K.E. and Woodard, P.E. 1987. Distribution of residual vegetation associated with large fires in Alberta. Can. J. For. Res. **17**: 1207-1212.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old field vegetation development. Vegetatio **4**: 412-417.

Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. **27**: 139-147.

Glenn-Lewin, D.C. and van der Maarel, E. 1992. Patterns and processes of vegetation dynamics. Pages 11-59 *In* D.C. Glenn-Lewin, R.K. Peet, and T.T. Veblen (eds.). Plant Succession: Theory and prediction. Chapman and Hall, London.

Greene, D.F., and Johnson, E.A. 2000. Tree recruitment from burn edges. Can. J. For. Res. **30**: 1264-1274.

Gutsell, S.L., and Johnson, E. A. 2002. Accurately ageing trees and examining their height- growth rates: implications for interpreting forest dynamics. J. Ecol. **90:** 153-166.

Harmon, M.E., Franklin, J.F., Swanson, F.J., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack, K. Jr., and Cummin, K.W. 1986. Ecology of coarse woody debris in temperate ecosystems. Adv. Ecological Res. **16**: 133:302.

Horn, H.S. 1981. Some causes of variety in patterns of secondary succession. Pages 24 - 35 *In* D.C. West, H.H. Shugart, and D.B. Botkin (eds.). Forest Succession: Concepts and Application. Springer-Verlag, New York.

Kabzems, R.D., and Lousier, J.D. 1992. Regeneration, growth and development of *Picea glauca* under *Populus* spp. canopy in the Boreal White and Black Spruce Zone, Forestry Can., B.C. Min. For., Victoria, B.C., FRDA Rep. 176.

Kobe, R.K., and Coates, K.D. 1997. Models of sapling mortality as a function of growth to characterize interspecific variation in shade tolerance of eight tree species of northwestern British Columbia. Can. J. For. Res. **27**: 227-236.

Lee, P. 1998. Dynamics of snags in aspen-dominated midboreal forests. For. Ecol. Manage. **105**: 263-272.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K., and Stewart, J.D. 1996a. Semi-natural and intensive silvicultural systems for boreal mixedwood forest.

For. Chron. **72**(3): 286-292.

______, Stadt, K.J., and Navratil, S. 1996b. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. **26**: 1002-1007.

McCullagh, P., and Nelder, J.A. 1983. Generalized Linear Models. Chapman and Hall, London, England.

Mills, S. 2001. Bryophyte species composition and diversity at different scales in conifer-dominated boreal forest stands. M. Sc. Thesis, University of Alberta, Edmonton, AB.

Nienstaedt, H., and Zasada, J.C. 1990. *Picea glauca*. Pages 165-185 *In* R.M.Burns, and B.H. Honkala (eds.). Silvics of North America. Vol. 1, Conifers. USDA For. Serv., Agric. Handbook 654.

Olson, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Bot. Gaz. **119**: 125-170.

Palik, B.J., and Pregitzer, K.S. 1995. Height growth of advance regeneration under an even-aged bigtooth aspen (*Populus grandidentata*) overstory. Am. Midl. Nat. **134**: 166-175.

Pickett, S.T.A., Collins, S.L., Armesto, J.J. 1987. Models, mechanisms and pathways of succession. Bot. Rev. **53**: 335-371.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fennica. **36**: 289-306.

Rowe, J.S. 1955. Factors influencing white spruce reproduction in Manitoba and Saskatchewan. Ottawa, Dept. North. Affairs. Nat. Res., For. Res. Div. Tech. Note 3.

S-Plus 2000 Professional Release 2. MathSoft, Inc., Seattle, WA.

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

SPSS 1999. SPSS for windows release version 10.0. Chicago, IL.

Tymstra, C. *pers com.* Forester, Wildfire and Air. Oper. Br., For. Prot. Br., Sust. Res. Devt., Edmonton, AB.

Youngblood, A.P. 1995. Development patterns in young conifer-hardwood forests of interior Alaska. J. Veg. Sci. **6**: 229-236.

Zar, J.H. 1996. Biostatistical Analysis. 3rd ed. Prentice-Hall, Inc. Upper Saddle River, New Jersey, USA.

Zasada, J.C., and Gregory, R.A. 1969. Regeneration of white spruce with reference to interior Alaska: a literature review. For. Serv., Pac. NW For. Exp. Sta. Gen. Tech. Rep. PNW-79.

Zasada, J.C., Lovig, D. 1983. Observations on primary dispersal of, *Picea glauca*, seed. Can. Field-Nat. **97**: 104-106.

Zasada, J.C. 1985. Production, dispersal, and germination of white spruce and paper birch and first year seedling establishment after the Rosie Creek fire. University of Alaska, Fairbanks, Misc. Publ. 85.

CHAPTER 6

The Concordance Between Pre-fire and Post-fire White Spruce Composition in Boreal Mixedwood Stands

---

6.1 Abstract

White spruce is less likely to show concordance between pre- and post-fire occurrence than most boreal tree species because it relies on wind dispersed seed from living trees for regeneration. We examined whether the density of white spruce and trembling aspen pre-fire, and fire timing relative to mast seed years affected the density of white spruce regeneration after fire. On fires that occurred between 1979 and 1994, we sampled a total of 81 stands containing a wide range of aspen, white spruce, and other tree species pre-fire. White spruce regeneration was positively related to its pre-fire density on most fires that had a zero or one year delay before a mast year, but this relationship did not occur on fires with delays of two or more years. Spruce regeneration was negatively related to the density of aspen pre-fire. The density of immediate regeneration was greater than pre-fire density in most stands on mast year and 1 year delay fires, but the reverse was true for fires with longer delays before a mast year. These findings have important implications for the population dynamics of white spruce and the succession and management of mixedwood forests.

6.2 Introduction

The reproductive strategies of many boreal tree species are adapted to permit *in situ* regeneration immediately after fire via serotiny or asexual reproduction from below-ground meristems (Dix and Swan 1971; Johnson 1992; Greene and Johnson 1999; Lavoie and Sirois 1998). This strategy maintains populations over time, and suggests that species composition may be similar within stands over many stand-replacing disturbances. White spruce has a different reproductive strategy, relying on wind dispersed seeds to recolonize fires (Galipeau *et al.* 1997; Greene and Johnson 1999). Furthermore, white spruce is non-serotinous and lacks a seedbank (Johnson 1992; Coates *et al.* 1994); therefore, the likelihood of spruce replacing itself after a stand-replacing fire is lower than most boreal tree species. The proximity of seed sources determines the likelihood of spruce regeneration (see chapter 4, section 4.6.1 and 4.6.2; Zasada 1985; Greene and Johnson 2000; Purdy *et al.* 2002); hence, local populations of spruce may decline, or go extinct, after fire if dispersal distances are great. The replacement of pre-fire spruce populations may also be affected by temporal variability in seed production. We found that mast year burns had twice as much regeneration as fires with a one year delay before a mast year, and further declines were observed in fires with longer delays (see Chapter 4, section 4.6.2). Mixedwood stands of aspen and white spruce may be an exception to the predictable pattern of similar species composition over multiple fire events in the boreal forest.

Fire intensity is another factor that affects the concordance between pre-fire and post-fire tree species composition. This has been observed in divergent forest types such as the tropical rain forests (Hill and Read 1984), as well as black spruce and jack pine forests in boreal regions (Lavoie and Sirois 1998). In boreal forests, tree species composition and age can greatly affect fire behavior (Alexander *et al.* 1984; Cumming 2000). The rates of fire spread, and fire intensities required for crowning differ considerably between spruce and aspen (Alexander *et al.* 1984; Johnson 1992). As the proportion of spruce increases within a stand, the rate of fire spread increases and the fire intensity required for crowning decreases (Alexander *et al.* 1984; Johnson 1992). The density of spruce versus aspen pre-fire may affect the amount of duff consumed (Johnson 1992), and the creation of microsites suitable for spruce regeneration.

In situ regeneration by aspen from root suckers may reduce the success of spruce regeneration because aspen grow much more quickly than spruce (Lieffers and Beck 1994; Nienstadt and Zasada 1990) and aspen leaf litter can cause mortality of spruce seedlings (Youngblood 1995). Aspen sucker density is related to pre-fire aspen basal area (Greene and Johnson 1999); consequently, spruce seedlings may experience less competition and show better survivorship on sites dominated by spruce pre-fire.

Overall the evidence suggests that pre-fire composition may influence the density and success of white spruce regeneration. We predict that sites with greater white spruce density pre-fire will have greater post-fire regeneration because seed sources may be greater, higher fire intensities may create more microsites, and there will be less competition with aspen. Our objective was to determine whether the density of white spruce regeneration post-fire is affected by the pre-fire composition of white spruce and trembling aspen. In so doing, we test the concordance between pre-fire and post-fire composition of white spruce in boreal mixedwoods. This study is unique on two counts: 1) concordance has not been quantified for white spruce, and 2) no study has looked at this relationship relative to mast years and disturbance timing. We tested our prediction on burned stands that had a wide range of aspen, white spruce, and other tree species pre-fire. This study has important implications for the population dynamics of white spruce and the succession and management of mixedwood forests.

6.3 Study Area

See chapter 4, section 4.3 for a detailed description of the study area.

6.4 Methods

To test the concordance between the density of white spruce pre- and post-fire, we selected 10 fires that occurred in 1979, 1980, 1981, 1982, 1990, 1991 and 1994 (fires are described in Chapter 4, section 4.4 and 4.5). Sampled fires occurred in mast years, as well as one, two, three, and four years before a mast year. We confined our analyses of pre-fire species composition to fires 20 years old and younger at the time of sampling because we could not visually distinguish dead trees to species in older fires. We used the same sampling procedures that are discussed in chapter 4, section 4.4. Hence, we sampled 7 to 10 burned stands per fire for a total of 81 stands. Each stand was adjacent to a white spruce seed source that was seed producing at the time of the fire. We recorded the density of pre-fire trees (standing and fallen) to species within the 5 m radius center plot at the 20 and 100 m sites. In some stands there were no sites 100 m away from a seed source so the total number of sites was 147 (see Chapter 4, Fig. 4.3). Only trees rooted within the plots were counted. There was homogeneity in pre-fire tree species composition at the site level; therefore, we assumed that one plot at each distance adequately reflected pre-fire forest composition. Pre-fire trees in the 5 m radius plots were identified to species by examining crown shape, bark, or cones if present. Burned stands ranged from pure deciduous to pure white spruce, although many stands had varying densities of black spruce, jack pine, paper birch, balsam poplar, and balsam fir (Fig. 6.1). We recorded the density of white spruce regeneration in each of the three, 3 m radius plots at the 20 and 100 m sites ($n = 441$ plots from 147 sites; see Chapter 4, Fig. 4.3). The furthest plots at each site were up to 45 m apart. We used the age data from Chapter 4, Fig. 4.6 for identifying fires between 1979 and 1994 with large mast cohorts. We also used the age data from the 1994 fire (trees were collected and aged according to the procedures in Chapter 4, sections 4.4.1 and 4.4.2), presented in Appendix 6.1. No age data are presented for the 1992 fire because only three seedlings were found, despite extensive searching.

Statistical analyses of data were based solely on the center plot at each site and are presented in Tables 6.1 to 6.3. Figures 6.2 to 6.5 show the densities of spruce regeneration from all three plots at each site compared to the pre-fire density from the 5 m radius plot at each site. Data in figures is presented this way in order to show that relationships at the plot level (in statistical analyses) occurred at the site level too. We classified all sites according to the density of regeneration versus pre-fire stems, using the categories greater, equal, less, and no spruce. The category equal was given to sites with a similar number of spruce pre- and post-fire, +/- 10%; categories of greater or less were outside this range.

6.5 Data Analysis

We tested whether the density of white spruce regeneration increased with spruce density pre-fire using generalized linear models (GLM). Separate analyses were performed for fires that occurred between 1979 and 1982 (older fires), and between 1991 and 1994 (younger fires), because the accuracy of pre-fire stem counts and the density of surviving spruce regeneration may differ with time since fire. Data analyses were based solely on the center plot at each distance (see Chapter 4, Fig. 4.3) because both pre-fire and post-fire spruce were recorded in these plots ($n = 147$ plots respectively). The density of spruce regeneration in the 3 m radius plot was regressed against the density of spruce pre-fire in the surrounding 5 m radius plot. We also tested if the relationship between pre- and post-fire spruce was affected by whether fires contained a large mast cohort in their age structure. We used the categorical variable delay length to distinguish fires by the presence or absence of a large mast cohort. In the older fires, all mast and 1 year delay fires (1979, 1982) had a large mast cohort, while fires with a 2 or more year delay (YD) did not (see Chapter 4, Fig. 4.6). In the younger fires, the mast year fire (1991) had a mast cohort (see Fig. 4.6), while the 1 and 4YD fires (1992, and 1994) did not (Appendix 6.1). In the results and discussion, we will refer to each fire by its delay length (mast year fires, 1, 2, 3, and 4YD fires) when discussing the analysis of either the older or younger fires. The following model was used for both the older and younger fires:

$$Y_r = u + \beta_s S + \beta_d D + \epsilon$$

Where Y_r = regeneration density, u = the slope intercept, β_s = the coefficient of pre-fire spruce, S = the density of pre-fire spruce, β_d = the coefficient for delay length, D = delay length, and ϵ = residual error. Stepwise selection was used to determine whether both variables were significant predictors of white spruce regeneration. A quasi-likelihood function was used to model the data because there was considerable overdispersion (McCullagh and Nelder 1983). The appropriate link and variance functions were used in the model. Non-linear effects were tested for using a generalized additive model; however, they did not improve the model fit, and were therefore omitted. S-PLUS version 2000 was used for GLM analyses (S-PLUS 2000).

We tested the correlation between the density of pre-fire spruce and seed tree abundance (within 60 m of the 20 m center plot) to determine whether stronger seed sources were associated with higher densities of spruce pre-fire. A Spearman rank correlation test was used because pre-fire spruce data could not be normalized. A separate test was performed on older fires and on younger fires. SPSS version 11.0 was used for these analyses (SPSS 2001).

Using a similar GLM model to the one above, we tested whether the density of spruce regeneration (in the center 3 m radius plot) decreased with increasing densities of aspen pre-fire, on older fires and on younger fires. The term $\beta_s S$ was replaced with $\beta_a A$, where β_a = the coefficient of aspen density pre-fire, and A = the density of pre-fire aspen. All other terms remained the same. Significant non-linear effects were modeled with a polynomial term (McCullagh and Nelder 1983).

6.6 Results

The density of spruce regeneration increased significantly with increasing density of spruce pre-fire on older fires (1979 to 1982; $p < 0.001$; Tables 6.1a and 6.2). This relationship was stronger on mast year and one year delay fires than on fires with two or more year delays before a mast year (Figures 6.2a and 6.2b respectively). On younger fires (1991 to 1994), spruce regeneration decreased significantly with increasing spruce pre-fire (Tables 6.2 and 6.3a). The decrease in spruce regeneration only occurred on the 1991 mast year fire (Fig. 6.3a). The density of spruce pre-fire was correlated with the number of seed trees on older fires ($r^2 = 0.580, p < 0.001, n = 107$) and younger fires ($r^2 = 0.520, p < 0.001, n = 45$).

Spruce regeneration decreased significantly with increasing densities of aspen pre-fire on older and younger fires ($p < 0.001$, respectively; Tables 6.1, 6.2, and 6.3). The decrease in spruce regeneration only occurred on mast year and 1YD fires in older fires (Fig. 6.2c) and the 1991 mast year fire (Fig. 6.3c).

Spruce regeneration density usually exceeded pre-fire spruce density in sites burned in mast year fires and 1YD fires, (69.5% of stands; Fig. 6.4). Spruce regeneration occasionally exceeded pre-fire density in fires with a two or more year delay before a mast year (23.9% of stands; Fig. 6.4). Overall, there was an identical proportion of sites with more spruce post-fire than pre-fire (0.455 for all ratios combined in Figures 6.5a and 6.5b, respectively). Many sites had much more spruce post-fire than pre-fire (4.1 to 32 times greater after fire; Fig. 6.5a), while fewer sites had much less spruce post-fire than pre-fire (0.24 – 0.031; Fig. 6.5b). We did not find spruce regeneration (i.e. in the sampled plots) on a large proportion of sites with spruce before fire (0.170; Fig. 6.5b); a smaller proportion of sites (0.122) had regeneration after fire even though no spruce occurred before fire (Fig. 6.5a).

6.7 Discussion

6.7.1 Pre- and post-fire concordance

The relationship between white spruce regeneration and pre-fire spruce varied substantially between fires with a different delay length before a mast year. Regeneration density increased significantly with pre-fire spruce density on most fires with a delay length up to one year. In contrast, the 1991 mast year fire showed a negative relationship (Fig. 6.3a), but sampled sites in that fire had a much lower and narrower range of pre-fire spruce densities. Pre-fire spruce density had little effect on regeneration density for fires with two year delays or longer. White spruce seedbeds deteriorate rapidly after fire (Purdy *et al.* 2002, Zasada *et al.* 1978; Zasada 1985; Wurtz and Zasada 2001) and most regeneration occurs in the first mast year after fire on fires with a short delay before a mast year (see Chapter 4, section 4.6.3). Seedbeds may no longer have been sufficiently receptive on fires with two year delays or longer for replacement of pre-fire spruce.

It is important to note that the majority of sites in mast burns and one year delay fires had more spruce post-fire than pre-fire, while the proportion of sites with less spruce post-fire increased with longer delay lengths. The 1992 fire was a one year delay fire with fewer spruce post-fire on most sites (only 3 seedlings were found in total). This fire was much smaller than all other fires (only 66 ha versus 389 ha for the next smallest fire) and may not have burned intensely enough to permit much spruce regeneration.

Age structure data from chapter 4, section 4.6.3 showed that the proportion of trees originating from the first mast cohort declined significantly as delay length increased. Delay length before a mast year is important for a large mast cohort, and the size of this cohort appears important for the replacement of pre-fire spruce. Mast year burns and one year delay fires appear to be on a trajectory towards a composition that resembles pre-fire spruce composition, while this rarely occurs on fires with longer delay lengths. We recognize that sapling densities will decrease by 38 to 59 years after fire due to mortality (see Chapter 5, section 5.6.4) and this will affect the likelihood of canopy replacement. Nonetheless, it appears that stands burned in non-mast years will have less spruce content at maturity than they did pre-fire unless substantial delayed regeneration occurs (i.e. trees establishing more than 20 years after fire).

Competition with aspen suckers may have affected white spruce survival at seedling and sapling stages. Although we did not test the effect of aspen sucker density on white spruce, we suspect that sucker density was related to the density of pre-fire aspen (e.g. Greene and Johnson 1999). Spruce density declined significantly with increasing aspen pre-fire; however, our data does not indicate whether spruce mortality was affected by competition with aspen. Aspen suckers can contribute to the mortality of spruce seedlings through leaf litter fall (Youngblood 1995) and at sapling stages by the reduction of light levels to below 25% of full light transmission (Comeau, pers. com.; Lieffers pers. com). There was little evidence of spruce mortality on younger and older fires that we studied (see Fig. 5.14); however, our estimates of seedling mortality are likely conservative because dead seedlings are unlikely to persist for several years.

White spruce is a non-serotinous species (Johnson 1992); consequently, its presence in stands prior to fire is unlikely to elevate regeneration densities directly through seed survival in burned cones. White spruce may, however, produce cones for one or two years after fire, depending on the extent of fire damage (Macdonald unpublished). We sampled a minimum of four years after fire; consequently, we may have sampled some stands where mortality was not immediate, and *in situ* seed production occurred after fire. Seed production after fire by trees that die subsequently may be important in some cases for replacement of white spruce at sites beyond the dispersal distance of unburned seed sources. Most regeneration does, however, originate from unburned seed sources (Nienstadt and Zasada 1990; Purdy *et al.* 2002; Greene and Johnson 2000).

Significant relationships between pre- and post-fire spruce are not surprising given the close proximity of sampled sites to mature seed sources. One reason for this relationship is that a significant correlation existed between pre-fire spruce density and the number of seed trees within 60 m of the 20 m site. The number of seed trees within 60 m of the fire was a significant predictor of regeneration (see Chapter 4, sections 4.6.1 and 4.6.2) and would therefore contribute to the observed relationship between pre- and post-fire density of white spruce. Several previous studies have found a similar relationship between seed tree abundance and white spruce regeneration (Densmore 1985; Kneeshaw and Bergeron 1996; Purdy *et al.* 2002). It is likely that burned stands were similar in spruce composition to adjacent unburned stands, because previous studies have found little evidence to indicate that species composition affects residual formation or affects the location of fire edges (Smyth 1999; Wong 2002).

6.7.2 Fire behavior effects

Vegetation shifts after fire are frequently attributed to fire intensity because it affects the availability of suitable substrates and seed sources (Hill and Read 1984; Lavoie and Sirois 1998; Kabzems and Lousier 1992). There are considerable differences in fire behavior as the amount of white spruce increases in boreal mixedwood stands (Alexander *et al.* 1984; Johnson 1992). Intense crown fires are more common in white spruce stands, while less intense surface fires occur more frequently in aspen dominated stands (Johnson 1992). The high rates of spread required to maintain crown fires in aspen (Alexander *et al.* 1984) may have resulted in a frequent shift from crown to surface fire as the aspen content increased in mixedwood stands. Crown fires generally expose more mineral soil than surface fires (Johnson 1992); consequently, increasing spruce density pre-fire may have facilitated greater spruce regeneration through the creation of more regeneration microsites.

Conifer needles at the base of spruce trees permit greater mineral soil exposure by fire around tree boles, leading to more white spruce seedlings (pers. obs.; Schoplick 1997). Our statistical models were at the plot level; consequently, plots with several spruce pre-fire likely had greater mineral soil exposure and therefore better microsites for regeneration. Jack pine and black spruce have fuel properties that are more similar to white spruce than to aspen (Johnson 1992) and their presence in stands may have further contributed to mineral soil exposure. Parent tree replacement by regeneration at the microsite level has been reported in seed reliant species (Ne'eman and Izhaki 1998); however, this was attributed to better microsite quality which led to greater survivorship on the microsite of the parent tree, rather than tree-level influences on substrate combustion. Many aspen-dominated mixedwood stands have favorable conditions for spruce establishment (Lieffers *et al.* 1996a); therefore, the absence of spruce post-fire has usually been attributed to low fire intensity or the absence of proximal seed sources (Kabzems and Lousier 1992; Lieffers *et al.* 1996a), rather than less favorable conditions for spruce establishment.

6.7.3 Fire frequency and spruce persistence in mixedwoods

One of the predominant hypotheses for the similarity in boreal forest tree species over several fire events is the prevalence of fire return intervals that are shorter than the lifespan of trees (Johnson 1992; Greene and Johnson 1999). Coupled with reproductive adaptations to fire (serotiny and asexual sprouting), the likelihood of tree populations going extinct is therefore very low. The persistence of white spruce in fire dominated landscapes hinges upon fire severity and fire return intervals exceeding 40 to 50 years (Nienstadt and Zasada 1990). Fire return intervals may need to be much longer in mixedwoods for white spruce persistence because regeneration frequently occurs about 40 years after fire (see Chapter 5, section 5.6.1), and trees take at least 80 to 100 years to produce substantial amounts of seed when they grow in the understory of aspen (pers. obs.). Fire return intervals in the mixedwoods of Alberta have been estimated at between 50 to 200 years (Van Wagner 1978; Cumming in Armstrong 1999) depending on the method used. These estimates are comparable to the average fire cycle of 100 years reported for the boreal forest in North America (Hunter 1993; Johnson 1992). We think that many non-mast fires will not attain concordance to pre-fire canopy composition because: 1) a lot of delayed regeneration is necessary for this to occur, 2) fires will burn a large number of stands in the additional time required for most delayed regeneration to occur and the much longer time required for them to reach the canopy (assuming they survive this long). Delayed regeneration may grow at a similar rate as initial regeneration because growth rate comparisons by Lieffers *et al.* (1996b) indicated that trees established on logs versus on mineral soil had similar rates of growth. This suggests that the additional 38 – 44 year time interval for most delayed regeneration to occur (Chapter 5, section 5.6.1), may add a similar number of years to the time required by them to produce seed. Thus seed production on some mixedwood sites may require approximately 120 to 140 years.

A case can be made from our data for the importance of delayed regeneration to the persistence of white spruce in mixedwoods. Sampled fires spanned a typical time interval between mast years (approximately 4 years, based on 60 years of data from Fig. 4.1 and Table 12 in Chapter 4), and we sampled a similar number of fires for each year of the mast interval. Initial regeneration appears to maintain a similar density of spruce before and after fire on sites that are located within 100 m of mature seed sources. That is, half of the sites had higher densities of spruce post-fire than pre-fire, while half of the sites had higher densities pre-fire than post-fire. We expect that pre-fire densities would be "replaced" on fewer than 50% of stands if: 1) pre-fire populations had been sampled at random distances from fire edges, 2) spring fires and fires with less crown mortality were selected (i.e. lower fire severity), and 3) a random distribution of age classes of unburned stands surrounded the sampled fires. These conditions reflect the natural post-fire landscape, and differ from portions of the landscape that we sampled. This simple comparison suggests that delayed regeneration may contribute to spruce persistence in mixedwoods because immediate post-fire regeneration would not be able to maintain an even balance of pre- and post-fire populations.

6.7.4 Management implications

One recent priority in forest management has been the maintenance of all tree species at the stand level following harvesting (Grover, pers. com.). Due to the prolific suckering ability of aspen after clear-cutting and competition with spruce (Doucet 1989), intensive silviculture is often required to reestablish spruce at pre-harvest densities (Lieffers *et al.* 1996a). While this is important for preserving tree diversity at the stand level, this approach does not resemble the shifting mosaic of spruce composition in mixedwood stands following fire. Our findings show that forest recovery after fire is not a unidirectional process in mixedwoods. Lieffers *et al.* (1996a) propose a variety of silvicultural options that allow forest managers to manipulate forests to resemble stand structures that occur naturally. Forest managers may adopt a landscape level approach to species maintenance in mixedwoods rather than a stand level approach. This perspective on management may also reduce costs and stand tending efforts because spruce does not have to establish at the same densities as occurred at the time of cutting. To ensure that this approach does not result in reduced establishment of spruce, deliberate efforts are needed to establish and monitor spruce at the landscape level because it remains the more difficult species to establish.

6.8 Conclusions

Unlike most boreal tree species, white spruce abundance changes considerably between fire events even when an adjacent seed source is present. White spruce regeneration was greater on sites dominated by spruce pre-fire than on sites dominated by aspen. Relationships between spruce regeneration and pre-fire tree species were most apparent on mast year fires and fires with a short delay length before a mast year. Immediate regeneration after fire appears sufficient for concordance between pre-and post-fire spruce density in most stands on mast year and one year delay fires. Ingress must occur in most stands from fires with longer delay lengths before a mast year in order for concordance with pre-fire density. Our findings support mixedwood management approaches that maintain tree species composition at the landscape level rather than at the individual stand level.

Table 6.1: Results of a generalized linear model testing whether the density of spruce regeneration in fires between 1979 and 1982 (older fires) was affected by the density of: (a) spruce trees pre-fire, and (b) aspen trees pre-fire. The categorical variable delay length (before a mast year) was also tested in the model, and distinguished fires by the presence or absence of a large mast year cohort in the age structure. Fires that occurred in a mast year or one year before a mast year had a large mast cohort, while fires with a two or three year delay did not. Using a stepwise procedure, the percent of total deviance that each variable explained was determined along with its significance (p). *df* = degrees of freedom. See table 6.2 for the slopes and intercepts.

Variable	*df*	Deviance	p
a)			
Null	104		
Spruce stems pre-fire	103	32.7	< 0.001
Delay length	102	11.7	< 0.001
Total		**44.4**	
b)			
Null	103		
Aspen stems pre-fire	102	9.4	< 0.001
Delay length	101	12.0	0.005
Total		**21.4**	

Note: Models are based on spruce regeneration counts in the 3 m radius plots (28.3 m^2) and pre-fire stem counts in 5 m radius plots (78.5 m^2).

Table 6.2: The intercept and slope values from generalized linear models in Tables 6.1 and 6.3. A polynomial function with 3 degrees of freedom was used to account for a significant non-linear relationship between aspen pre-fire and white spruce regeneration

Model	Fires	u	β_d(delay length)	β_s (spruce pre-fire)	β_a(aspen pre-fire)
Table 6.1a	1979 - 1982	0.170	1.219	0.152	
Table 6.1b	1979 - 1982	0.152	1.246		-0.112
Table 6.3a	1991 - 1994	1.580	-0.677	-0.117	
Table 6.3b	1991 - 1994	-0.282	-0.639		-3.454 6.040 -6.867

Note: Models are based on spruce regeneration counts in the 3 m radius plots (28.3 m^2) and pre-fire stem counts in 5 m radius plots (78.5 m^2).

Table 6.3: Results of a generalized linear model testing whether the density of spruce regeneration in 1994, 1992, and 1991 fires (younger fires) was affected by the density of: (a) spruce trees pre-fire, and (b) aspen trees pre-fire. The categorical variable delay length (before a mast year) was also tested in the model, and distinguished fires by the presence or absence of a large mast year cohort in the age structure. Fires that occurred in a mast year or one year before a mast year had a large mast cohort, while fires with a two or three year delay did not. Using a stepwise procedure, the percent of total deviance that each variable explained was determined along with its significance (*p*). *df* = degrees of freedom. See table 6.2 for the slopes and intercepts. Significant non-linear effects were modeled with a polynomial term for variables with a ●.

Variable	*df*	Deviance	*p*
a)			
Null	43		
Spruce stems pre-fire	42	4.7	< 0.001
Delay length	41	9.7	< 0.001
Total		**14.4**	
b)			
Null	43		
Delay length	42	4.8	< 0.001
Aspen stems pre-fire●	39	41.7	< 0.001
Total		**46.5**	

Note: Models are based on spruce regeneration counts in the 3 m radius plots (28.3 m^2) and pre-fire stem counts in 5 m radius plots (78.5 m^2).

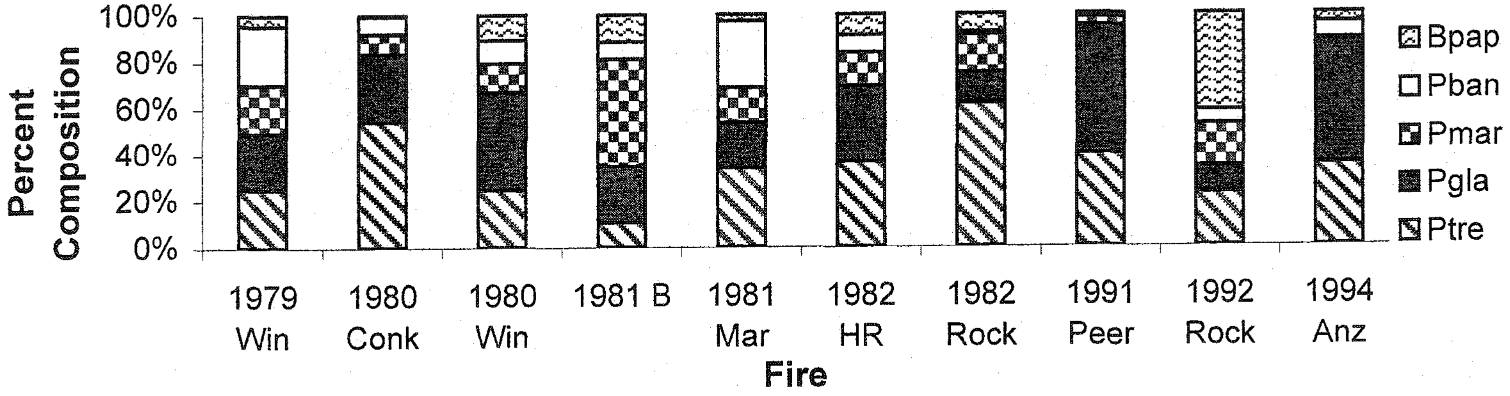


Figure 6.1: Pre-fire composition of tree species based on stem density in sampled stands (n = 7 to 10 stands per fire). Species abbreviations are Bpap (*Betula papyrifera*), Pban (*Pinus banksiana*), Pmar (*Picea mariana*), Pgla (*Picea glauca*), and Ptre (*Populus tremuloides*). *Abies balsamea* and *Populus balsamifera* occurred infrequently in stands, and were excluded from these estimates of pre-fire stand composition.

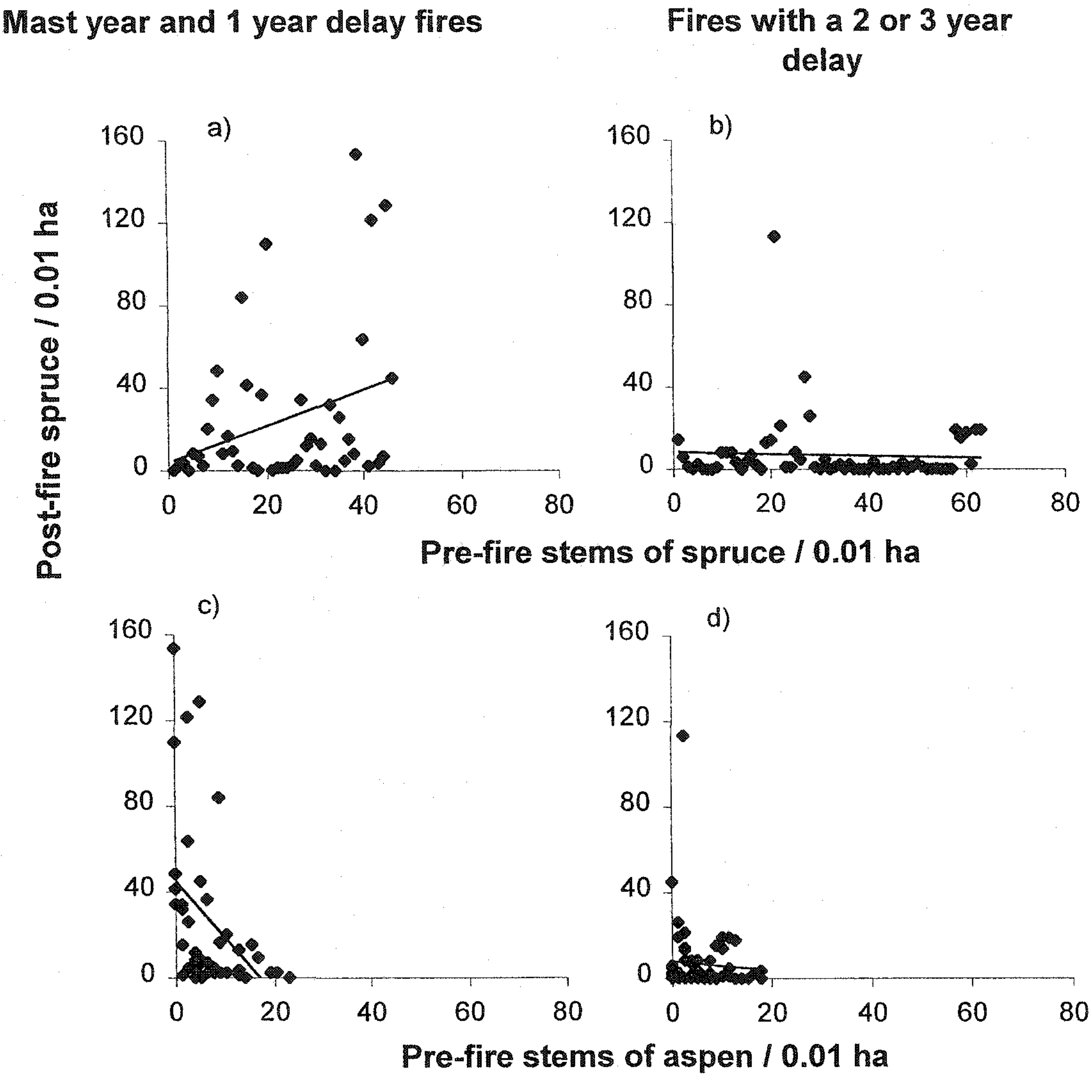


Figure 6.2: Relationship between the density of post-fire spruce regeneration and: pre-fire spruce density (a,b), pre-fire aspen density (c, d) on all sites from 1979 to 1982 fires. Fires that occurred in mast years and 1 year after a mast year (1979 and 1982 respectively) had a large mast year cohort (a, c), while fires with a 2 or 3 year delay before a mast year (1981 and 1982 respectively) did not have a large mast cohort (b, d). A total of 147 sites were sampled. See table 6.1 for the results of statistical analyses.

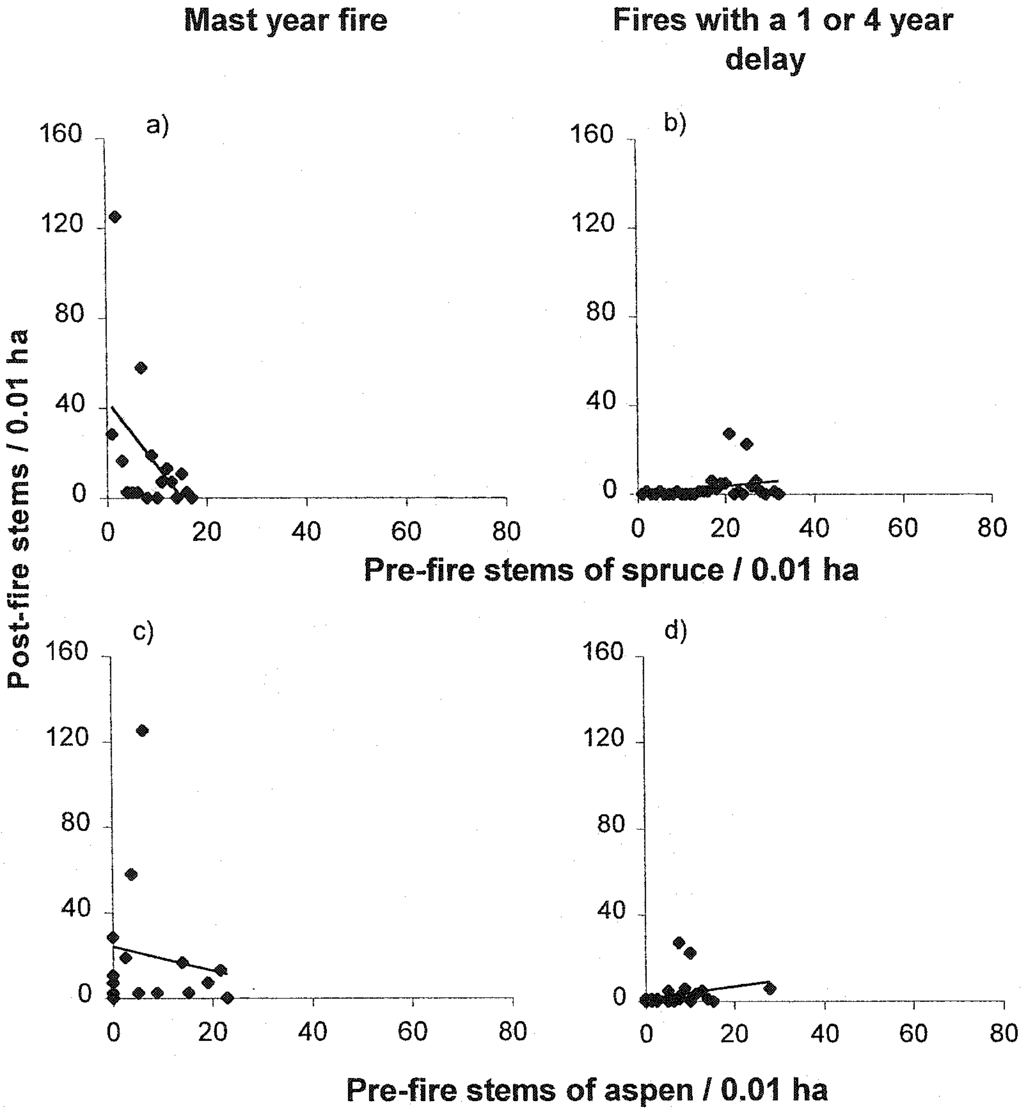


Figure 6.3: Relationship between the density of post-fire spruce regeneration and: pre-fire spruce density (a,b), pre-fire aspen density (c, d) on all sites from 1991, 1992, and 1994 fires. The 1991 fire occurred in a mast year and had a large mast year cohort (a, c), while the 1992 and 1994 fires had a 1 and 4 year delay, respectively, before a mast year, and did not have a large mast cohort (b, d). A total of 147 sites were sampled. See tables 6.2 and 6.3 for the results of statistical analyses.

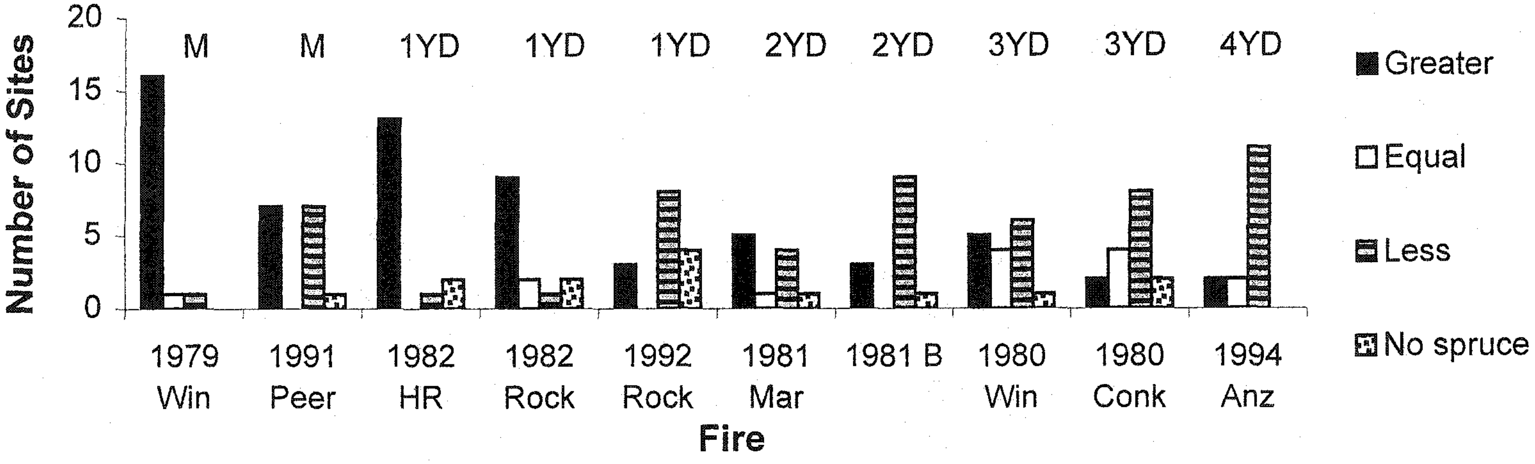
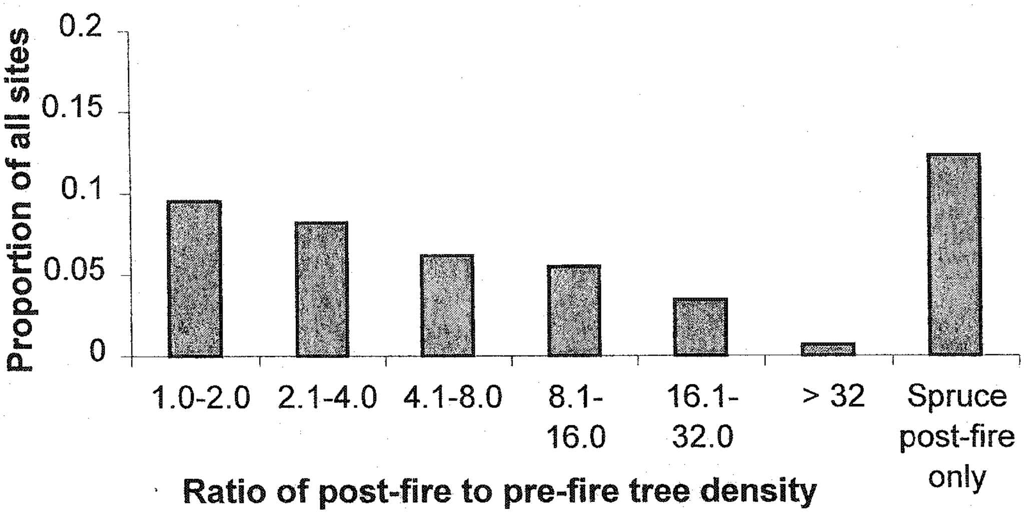


Figure 6.4: A comparison of sites with respect to the density of spruce regeneration after fire relative to pre-fire spruce density. The mean density (3 plots) of regeneration was used for each site. A total of 147 sites from 81 stands were sampled (sites were situated at both 20 and 100 m from live seed sources in each stand). Fires that occurred in mast years are marked with a M, while YD (year delay) indicates the number of years that fires occurred before a mast year. Fires occurred between 4 to 20 years prior to sampling. The category equal was given to sites with a similar number of spruce pre- and post-fire, +/- 10 %.

a) Sites with greater post-fire white spruce density than pre-fire density



b) Sites with lower post-fire white spruce density than pre-fire density

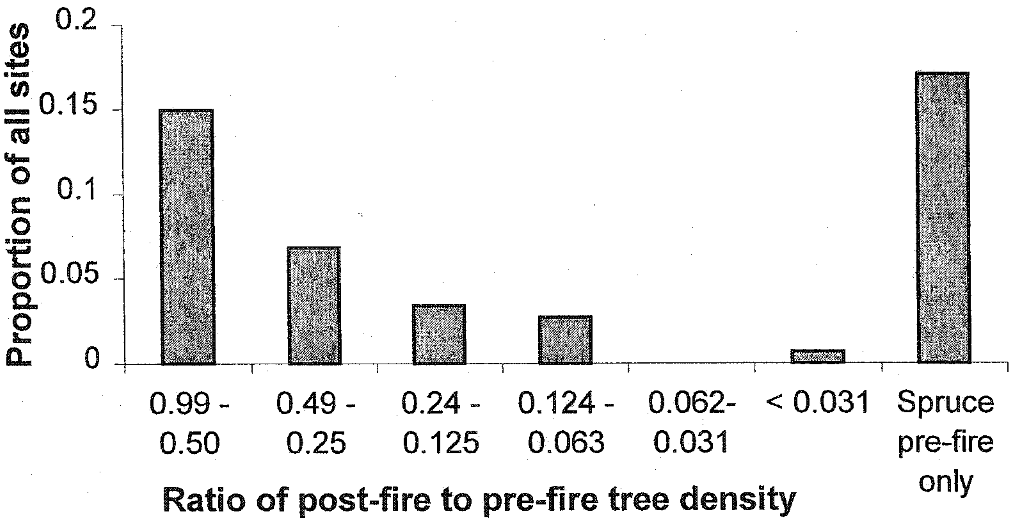


Figure 6.5: Replacement of pre-fire white spruce trees by post-fire regeneration that established within a few years of the fire. A total of 147 sites from 81 stands were sampled. Fires occurred between 4 and 20 years prior to sampling (1994 - 1979). The proportion of sites with no spruce either before or after fire was 0.09, and is not shown here.

6.9 Literature Cited

Alexander, M.E., Lawson, B.D., Stocks, B.J., and Van Wagner, C.E. 1984. User guide to the Canadian forest fire behavior prediction system: rate of spread relationships, Envt. Canada, Can. For. Ser. Fire Danger Group. Interim edition.

Armstrong, G. 1999. A stochastic characterization of the natural disturbance regime of the boreal mixedwood forest with implications for sustainable forest management. Can. J. For. Res. **29**: 424-433.

Coates, D.K., Haeussler, S., Lindeburgh, S., Pojar, R., and Stock, A.J. 1994. Ecology and Silviculture of Interior Spruce in British Columbia. For. Canada, B.C. Min. For., B.C., Canada, FRDA Rep. 220.

Comeau, P. 2001. Competition dynamics and competition management in young mixedwood stands. Oral presentation, Landscape ecology seminar series, Jan. 11. University of Alberta, Edmonton, AB.

Cumming, S.G. 2000. Forest type, fire ignition, and fire frequency in boreal mixedwood forests. Edmonton, Sust. For. Mgmt. Net. Working Paper 2000-11.

Densmore, R. 1985. Effect of microsite factors on establishment of white spruce seedlings following wildfire. *In:* Early results of the Rosie Creek fire research project, 1984. Juday, G.P. and Dyrness, C.T. (eds.). Fairbanks, Alaska, Univ. Alaska: 38-39.

Dix, R.L., and Swan, J.M.A. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Can. J. Bot. **49**: 657-676.

Doucet, R. 1989. Regeneration silviculture of aspen. For. Chron. 66: 85-90.

Galipeau, C., Kneeshaw, D., and Bergeron, Y. 1997. White spruce and balsam fir colonization of a site in the southeastern boreal forest as observed 68 years after fire. Can. J. For. Res. **27**: 139-147.

Greene, D.F., and Johnson, E.A. 1999. Modelling recruitment of *Populus tremuloides*, *Pinus banksiana*, and *Picea mariana* following fire in the mixedwood boreal forest. Can. J. For. Res. **29**: 462-473.

Greene, D.F., and Johnson, E.A. 2000. Tree recruitment from burn edges. Can. J. For. Res. **30**: 1264-1274.

Grover, B. pers. com. Environmental Research Team Coordinator, Alberta Pacific

Forest Industries, Boyle, AB.

Hill, R.A., and Read, J. 1984. Post-fire regeneration of rainforest and mixed forest in western Tasmania. Aust. J. Bot. **32**: 481-493.

Hunter, M.L. 1993. Natural fire regimes as spatial models for managing boreal forests. Biol. Conserv. **65**: 115-120.

Johnson, E.A. 1992. Fire and Vegetation Dynamics: Studies from the North American boreal forest. Cambridge University Press, Cambridge, Great Britain.

Kabzems, R.D., and Lousier, J.D. 1992. Regeneration, growth and development of *Picea glauca* under *Populus* spp. canopy in the Boreal White and Black Spruce Zone, For. Can. and B.C. Min. For. FRDA 176.

Kneeshaw, D.D., and Bergeron, Y. 1996. Ecological factors affecting the abundance of advance regeneration in Quebec's southwestern boreal forest. Can. J. For. Res. **26**: 888-898.

Lavoie, L., and Sirois, L. 1998. Vegetation changes caused by recent fires in the northern boreal forest of eastern Canada. J. Veg. Sci. **9**: 483-492.

Lieffers, V.J., and Beck, J.A. 1994. A semi-natural approach to mixedwood management in the prairie provinces. For. Chron. **70**: 260-264.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K. and Stewart, J.D. 1996a. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. **72**: 286-292.

_____, Stadt, K.J., and Navratil, S. 1996b. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. **26**: 1002-1007.

McCullagh, P. and Nelder, J.A. 1983. Generalized linear models. Chapman and Hall, London, Great Britain.

Ne'eman, G., and Izhaki, I. 1998. Stability of pre- and post-fire spatial structure of pine trees in Aleppo pine forest. Ecography **21**: 535-542.

Nienstaedt, H., and Zasada, J.C. 1990. *Picea glauca*. Pages 165-185 *In:* R.M.Burns and B.H. Honkala, (eds.). Silvics of North America. Vol. 1, Conifers. U.S. Dept. Agric. For. Serv., Agric. Handbook 654.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fenn. **36**(1):

289-306.

S-PLUS 2000 Professional Release 2. MathSoft, Inc., Seattle, WA.

Schoplick, J. 1997. Natural regeneration of white spruce after wildfire in the boreal forest of northeastern Alberta. ALPAC For. Ind. Inc., AB, and Friedrich-Alexander-Universitaet-Erlangen-Nuernberg, Germany, Report.

Smyth, C.L. 1999. Overstory composition of live residuals in fire affected landscapes of northern Alberta. M.Sc. Thesis. Univ. of AB, Edmonton, AB.

SPSS 2001. SPSS for windows release version 11.0. Chicago, IL.

Van Wagner, C.E. 1978. Age-class distribution and the forest fire cycle. Can. J. For. Res. **8**: 220-227.

Wong, A.S. 2002. Topographic characteristics and plant community structure of fire residuals in Virginia Hills, Alberta. M.Sc. Thesis. Univ. AB., Edmonton, AB.

Youngblood, A.P. 1995. Development patterns in young conifer-hardwood forests of interior Alaska. J. Veg. Sci. **6**: 229-236.

Wurtz, T.L., and Zasada, J.C. 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. Can. J. For. Res. **31**: 999-1011.

Zasada, J.C. 1985. Production, dispersal, and germination of white spruce and paper birch and first year seedling establishment after the Rosie Creek fire. Univ. AK, Fairbanks, Misc. Publ. 85.

Zasada, J.C., Foote, M.J., Deneke, F.J., and Parkerson, R.H. 1978. Case history of an excellent white spruce cone and seed crop in interior Alaska: cone and seed production, germination, and seedling survival. USDA. For. Serv., Pac. NW For. Exp. Sta., Gen. Tech. Rep. PNW-65.

CHAPTER 7

Conclusions and Implications of Research

7.1 Conclusions

The principal objective of this study was to determine whether the timing of fire relative to mast years of white spruce has a lasting effect on its abundance and timing of establishment, and hence, the successional development of boreal mixedwoods. I found that significantly more spruce established in mast year fires than in fires with a one, two, or three year delay before a mast year. Greater densities of white spruce were found in mast year fires than in non-mast year fires for stands up to 41-years-old; this suggests that establishment in the first few years is critical to spruce regeneration and density in the stand over many years of successional development. Further to this objective, I determined whether spruce age structures showed a large mast cohort in the year immediately after fire; this led to three questions that had to be answered first. 1) Do ground-level ring counts underestimate the true age of white spruce? 2) Do aging errors increase with stand age? 3) What are the factors contributing to age underestimation?

I determined that ground-level ring counts underestimated true age, and that aging errors increased significantly with stand age. Age underestimation ranged from 0 to 10 years in trees from 18-year-old stands, and from 0 to 27 years in trees from 59-year-old stands. After accounting for aging errors, I concluded that: 1) the period of immediate regeneration after fire was significantly shorter than estimated without using crossdating, 2) most trees established within 5 years of the fire (in stands up to 20 years old), and 3) a mast cohort comprised the majority of regeneration in recent mast burns (60% in 7 and 20-year-old stands), but this percentage declined significantly in fires with longer delays between fire and the next mast year (15.6% in fires with 3 year delays).

I found that that the length of buried stem below the humus layer increased significantly with stand age. This led to considerable age underestimation in stands older than seven years because ground-level disks did not contain the earliest growth rings (i.e. the root collar), and many later growth rings were also missing. Using clipping experiments, I found that browsing like that inflicted by snowshoe hares reduced ring width, and even caused a missing ring in some trees. I concluded that hare browsing may contribute to substantial age underestimation in repeatedly browsed trees.

A further objective of this study was to determine if fire history and seed availability of white spruce were critical to succession in mixedwoods over a 59 year period. I found that a similar number of stands were dominated by initial regeneration of white spruce, by "even" mixtures of initial and delayed regeneration, and by delayed regeneration (35, 35, and 30%, respectively). Spruce age structures over the 59 year period were not affected by seed source proximity or the timing of mast years relative to fire years. A distinct regeneration pulse occurred between 38 and 44 years after fire on decayed logs, suggesting that facilitation processes are important to mixedwood succession. Finally, I determined the concordance between pre- and post-fire populations of white spruce. The density of immediate regeneration was greater than pre-fire density on most fires with no delay or a one year delay before a mast year, but the reverse was true for fires with longer delays. These results suggest that large amounts of delayed regeneration must occur on fires with delays of two years or longer before a mast year, in order to maintain similar densities of spruce before and after fire.

7.2 Limitations of Research

I used relatively coarse indices to identify mast years and non-mast years, while acknowledging the potential for variation in seed production over large areas. My justification for these indices (cone production and squirrel trapping records) is that they are significantly correlated throughout Alberta and indicative of mast years (Kemp and Keith 1970), and significant synchrony in masting occurs at still greater distances among *Picea* species in North America (Koenig and Knops 1998). Furthermore, a lack of synchrony, along with a multitude of other factors (i.e. fire intensity, variation in precipitation during key germination years, variation in seed predator populations, post-fire competition, successful regeneration in non-mast years, etc.), would more likely prevent the detection of a mast year effect than reduce the validity of my findings that mast years are important.

The estimation of aging error with the crossdating techniques described must be regarded as conservative (Desrochers and Gagnon 1997); therefore, the apparent regeneration periods that I identified should be interpreted with some caution (i.e. the initial regeneration period in stands 38 years old and older are likely as short as in younger stands). A complete stem analysis using skeleton plots is necessary to obtain a truly precise count of all missing rings in suppressed trees. The regeneration periods I identified may differ from forests where regeneration substrates deteriorate more slowly after fire, and particularly in stands where regeneration of deciduous tree species does not occur.

The age structures of spruce regeneration that I found cannot be extended to all burned mixedwood stands where fire intensity, season of burn, seed source availability at the time of fire, and masting history are not known. I controlled for these factors as much as possible so that hypotheses could be tested in stands where regeneration was likely to occur. Stands adjacent to spruce trees that are too young to produce seed at the time of the fire, or beyond the dispersal distance of surviving seed sources are unlikely to have immediate regeneration (Lieffers *et al.* 1996b) even in a mast year. Season of burn may limit direct comparison of age structures in the oldest fires in this study (58 and 59-year-old stands originated from spring fires) with the fires up to 41 years old (primarily summer fires). Spring burns are less likely to expose the mineral soil because of greater duff moisture (Johnson 1992); however, this may depend on the year and the site. Ratios of initial to delayed regeneration in the oldest stands should not be regarded as stable. As stands age, initial regeneration may continue to self-thin, while later ingress may continue to occur (Simard *et al.* 1998). Complete mortality of later recruiting cohorts may also occur prior to reaching the canopy (Johnson 1992; Gutsell and Johnson 2002).

The comparison of pre-and post-fire concordance of spruce populations described here is useful for showing trends in recovery after fire, but does not address the final population size. Processes occurring within the stand will undoubtedly affect population size over time. My findings in Chapter 6 reflect concordance under conditions with an adjacent seed source and intense fires, and cannot be extended to different stand history conditions.

7.3 Implications for Mixedwood Dynamics

This study shows that aging errors have contributed to the uncertainty in the dating of white spruce establishment. It now seems apparent that the first few years after fire are critical for establishment of white spruce in mixedwoods, and that gradual ingress does not account for the majority of regeneration (Peters *et al.* 2002). My data suggest that a rapid decline in seedbed receptivity limits further regeneration of white spruce. These findings concur with many short-term studies of seedling recruitment (Zasada and Gregory 1969; Zasada 1985; Zasada and Wurtz 2001; Purdy *et al.* 2002) and thus reconcile short-term studies with retrospective studies in older stands. The occurrence of delayed regeneration is also supported by the literature (Lieffers *et al.* 1996b; Youngblood 1995); however, previous studies have not recognized delayed regeneration as episodic, nor have they related this to the abundance of fire-killed logs which have reached a suitable decay stage.

The short period available for spruce regeneration immediately after fire demonstrates why the timing of fire relative to mast years is critical to spruce persistence in mixedwood landscapes. Many studies in the ecological literature have suggested that mast cohorts are more important than non-mast cohorts (Silvertown 1980; Sork 1983; Keely and Bond 1999), but this has rarely been demonstrated. The mast cohorts observed in this study indicate that mast years for white spruce do result in greater regeneration than non-mast years. Fire return intervals are short in the boreal forest (Johnson 1992) relative to the time required for the sexual maturity of white spruce. Consequently, the initial mast cohort appears critical to mixedwood dynamics because many stands may burn before delayed cohorts reach the canopy and provide seed for future forest recovery. Furthermore, there is some evidence that delayed regeneration in mixedwoods experiences higher mortality and may not reach the canopy (Gutsell and Johnson 2002). Fire and masting history contribute to the stochastic nature of spruce composition in mixedwood stands over time. The temporal variability in mixedwood forest composition over several fire cycles may thus be described as a shifting mosaic.

This study provides empirical evidence that early succession in mixedwoods occurs via different successional mechanisms. Succession in many stands readily conforms to Egler's (1954) initial floristic model because white spruce is frequently present immediately after fire along with other coniferous and deciduous tree species, and can eventually dominate the canopy (Lieffers *et al.* 1996a). Tolerance mechanisms, as described by Connell and Slatyer (1977), are important to the recruitment of white spruce into the canopy (Bergeron 2000). Such mechanisms are exhibited by tolerance to repeated browsing, and the extended survival of suppressed spruce despite missing growth rings. White spruce does not easily fit into the relay floristics model because regeneration is not restricted to later periods, and it rarely replaces deciduous species completely. Furthermore, it tolerates post-fire conditions well, and possesses a number of characteristics of early successional species such as light seeds and long distance seed dispersal by wind (Begon *et al.* 1990; Coates *et al.* 1994). I have also shown that facilitation mechanisms, such as establishment on decayed logs, are also important to white spruce regeneration. Delayed regeneration on logs (versus immediate regeneration) represents a fundamentally different successional pathway in mixedwoods and should be recognized as such. The occurrence of succession via multiple pathways (even within the same community) as described by Odum (1969) and Pickett *et al.* (1989) is an appropriate paradigm of succession in mixedwoods.

7.4 Management Implications

White spruce is a species of high economic importance to Canada's forest industry. The aging errors I found indicate that the growth of white spruce is slower and more variable than previously thought. I recommend that additional crossdating studies be performed in different stand types and geographic locations to assess the prevalence and range in age underestimation. An accurate picture of growth is critical to establishing cut rotation length, predicting yield, and identifying suitable silvicultural systems for mixedwoods. Currently, Alberta's regeneration standards require spruce saplings in stocked plots to exceed 50 cm in height eight years after harvesting (Anonymous in Lieffers and Beck 1994). Forest managers are concerned about meeting these standards (Lieffers and Beck 1994), and these concerns appear well-founded, because the standards greatly exceed the growth rates of natural regeneration. I observed a mean height of only 66.3 cm in fires 16 to 20 years old (*n* = 39 stands, 883 trees, Peters unpublished data). This is well below the height of 1.3 m (breast height) that white spruce is often assumed to reach in 15 years (age is frequently estimated at breast height, and 15 years is the standard correction factor added to these estimates; Anonymous 1991). My results suggest that yield differences between artificially regenerated and fire-origin trees (Coates *et al.* 1994) may be even greater than previously believed.

My results indicate that many mixedwood stands are even-aged, even though understory spruce display a tremendous range in size. Individuals of "all sizes" in even-aged populations have been reported for other tree species (Oliver 1980; Crawley 1997), but there is still a widespread perception that the wide range in size of white spruce also reflects age differences. Foresters frequently substitute the size of trees for age for species where small old trees grow similarly to small young trees after release (Lieffers, pers. com.). Several uneven-aged forest management systems that have been proposed for mixedwoods (Lieffers *et al.* 1996a) may be equally valid as management prescriptions for uneven-sized stands (that are even-aged), because suppressed spruce release well (Coates *et al.* 1994). Thus, increased awareness that many mixedwood stands are actually even-aged may require very little modification at the operational level.

Partial cut systems with several entries remain a good approach for maximizing fibre production on fire-origin stands. Removal of aspen canopies with understory protection and wind protection will permit greater release of understory white spruce trees (Lieffers *et al.* 1996a). Subsequent partial cuts may permit good use of the uneven size distribution in many even-aged stands because spruce can release well even after 100 years of suppressed growth (Coates *et al.* 1994). Many of the stands sampled were uneven-aged, and can be managed as such. Planting white spruce in the understory of aspen stands may be a viable means of regenerating white spruce and increasing mixedwood productivity (Lieffers and Beck 1994). My results suggest that understory planting approximately 40 years after fire mimics delayed regeneration, and may allow better growth because shrub cover was lowest at this time. Planting at this time may necessitate wind protection later on (i.e. due to high height to diameter ratios), depending on how much spruce have grown by the time deciduous species are cut. These systems favor conifer over deciduous regeneration (Graham and Jain 1998), but this bias may be necessary in order to maintain a viable saw log industry considering the short harvest rotations in mixedwoods. Furthermore, maintenance of white spruce in mixedwoods is vital to the preservation of biodiversity (Lieffers and Beck 1994; Stelfox 1995).

Salvage logging of burned mixedwood stands presents several natural regeneration issues for white spruce. It is important that seed source strength and suitable substrate conditions after fire are not compromised as a result of salvage logging. In stands with good mineral soil exposure, green and partly burned seed trees (i.e. veteran trees, and trees in unburned residuals and the forest edge) should be retained to increase the likelihood of spruce regeneration within a few hundred meters of the forest edge. In such stands, whole-tree harvesting should be done in the winter to minimize disruption of the seedbed and limit the amount of slash. If mast years coincide with the year of the fire, or occur one year after fire, harvesting of seed trees in the winter after seed cast will allow natural regeneration. Harvesting at this time will not greatly limit the amount of natural regeneration that would have occurred if seed trees were retained, because little regeneration occurs in the subsequent 35 years. Stands that are lightly burned are unlikely to have exposed mineral soil or much natural spruce regeneration, so harvesting of green trees and summer logging may be valid options. If summer logging must occur on poorly burned sites in a good seed year, seed trees should be retained and the seedbed scarified immediately after harvest, to increase natural regeneration. These options may be economical because they permit wiser use of burned and green timber, increase opportunities for natural regeneration, and reduce the need for artificial regeneration.

7.5 Future Research

The overall influence of fire and masting on spruce regeneration may vary considerably depending on the relationship between fire occurrences and mast years. Fire events may be greater in the year prior to mast years because hot, dry weather during bud differentiation permits greater cone production in the following year (Eis 1967). Research is needed to determine whether the same synoptic climate variables that affect fire, also affect masting. This relationship is particularly important because climate change is expected to increase fire frequency in the western boreal region (Flannigan *et al.* 1998), and species like white spruce that take a long time to mature are most likely to be adversely affected. Research on the effects of climate change on masting is also important because the frequency, scale, and synchrony of masting may change. The amount of climate change is expected to vary throughout North America, particularly with respect to latitude and elevation. White spruce already shows variability in the frequency and scale of masting relative to latitude and elevation. Masting may be particularly sensitive to climate change in areas where small changes in climate will affect critical periods during the pollination and maturation periods of seed development. The contribution of mast years to regeneration depends largely on interactions with numerous seed predators (e.g. mammals - red squirrels, deer mice, and red-backed voles; birds – crossbill spp., chickadees; insects – spruce seedworm, spiral spruce coneborer) and pathogens (cone rust) (Coates *et al.* 1994); consequently, the effects of climate change on their populations should be explored concurrently.

An emerging issue in mixedwood dynamics is whether there is regional variation in delayed regeneration throughout the boreal, and whether later cohorts recruit into the canopy and contribute to forest regeneration. Studies in the Prince Albert area of Saskatchewan indicate that there is little delayed regeneration in 80 to 140-year-old stands (Gutsell and Johnson 2002), but in eastern Alberta this appears to occur frequently in 38 to 80-year-old stands (see Chapter 5, section 5.6.2; Lieffers *et al.* 1996b). Further research into the establishment, growth, and mortality of these cohorts in similar stand ages is warranted. A thorough characterization of secondary substrates, forest microclimates, and a comparison of precipitation records may indicate why differences in delayed regeneration occur within the Mixedwood Ecoregion.

Further research into the factors contributing to missing rings is vital. The frequency of missing rings should be quantified relative to previous growth, tree height and age, canopy cover, species composition, latitude, and elevation. Information on the likelihood of encountering aging errors will be extremely useful for forest regeneration studies so that appropriate aging techniques are used.

7.6 Literature Cited

Anonymous, 1991. Alberta vegetation inventory standards manual version 2.1. Land Inf. Serv. Div., Res. Inf. Branch.

Begon, M., Harper, J.L., and Townsend, C.R. 1990. Ecology: Individuals, Populations, and Communities. 2nd ed. Blackwell Scientific Publications, Boston, USA.

Bergeron, Y. 2000. Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. Ecology **81**: 1500-1516.

Coates, D.K., Haeussler, S., Lindeburgh, S., Pojar, R., and Stock, A.J. 1994. Ecology and Silviculture of Interior Spruce in British Columbia. For. Canada, B.C. Min. For., B.C., Canada, FRDA Rep. 220.

Connell, J.H., and Slatyer, R.O. 1977. Mechanisms of succession in natural communities and their role in community stability and organization. Amer. Nat. **111**: 1119-1144.

Crawley, M. 1997. Plant Ecology. 2nd ed. Blackwell Science Ltd. Oxford, U.K.

Desrochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? Can. J. For. Res. **27**: 1263-1267.

Egler, F.E. 1954. Vegetation science concepts. I. Initial floristic composition - a factor in old field vegetation development. Vegetatio **4**: 412-417.

Eis, S. 1967. Cone crops of white and black spruce are predictable. For. Chron. **43**: 247-252.

Flannigan, M.D, Bergeron, Y., Englemark, O., and Wotton, B.M. Future wildfire in circumboreal forests in relation to global warming. J. Veg. Sci. **9**: 469-476.

Graham, R.T., and Jain, T.B. 1998. Silviculture's role in managing boreal forests. Cons. Ecol. **2**(2):8. Available from the Internet. URL: http://www.consecol.org/vol2 /iss2/art8.

Gutsell, S.L., and Johnson, E. A. 2002. Accurately ageing trees and examining their height-growth rates: implications for interpreting forest dynamics. J. Ecol. **90**: 153-166.

Johnson, E.A. 1992. Fire and Vegetation Dynamics: Studies from the North American Boreal Forest. Cambridge University Press, Cambridge, Great Britain.

Keely, J., and Bond W. 1999. Mast flowering and semelparity in bamboos: the bamboo fire cycle hypothesis. Am. Nat. **154**: 383-391.

Kemp, G.A., and Keith, L.B. 1970. Dynamics and regulation of red squirrel (*Tamiasciurus hudsonicus*) populations. Ecology **51**: 763-779.

Koenig, W.D., and Knops, J.M.H. 1998. Scale of mast-seeding and tree-ring growth. Nature **396**: 225-226.

Lieffers, V.J., and Beck, J.A. 1994. A semi-natural approach to mixedwood management in the prairie provinces. For. Chron. **70**: 260-264.

Lieffers, V.J., Macmillan, R.B., MacPherson, D., Branter, K. and Stewart, J.D. 1996a. Semi-natural and intensive silvicultural systems for the boreal mixedwood forest. For. Chron. **72**: 286-292.

______, V.J., Stadt, K.J., and Navratil, S. 1996b. Age structure and growth of understory white spruce under aspen. Can. J. For. Res. **26**: 1002-1007.

Odum, E.P. 1969. The strategy of ecosystem development. Science. **164**: 262-270.

Oliver, C.D. 1980. Even-aged development of mixed species stands. J. For. **78**: 201-203.

Olson, J.S. 1958. Rates of succession and soil changes on southern Lake Michigan sand dunes. Bot. Gaz. **119**: 125-170.

Peters, V.S, Macdonald, S.E., and Dale, M.R.T. 2002. Aging discrepancies of white spruce affect the interpretation of static age structure in boreal mixedwoods. Can. J. For. Res. **32**: 1-6.

Pickett, S.T.A., Collins, S.L., Armesto, J.J. 1987. Models, mechanisms and pathways of succession. Bot. Rev. **53**: 335-371.

Purdy, B.G., Macdonald, S.E., and Dale, M.R.T. 2002. The regeneration niche of white spruce following fire in the mixedwood boreal forest. Silva Fenn. **36**: 289-306.

Silvertown, J. 1980. The evolutionary ecology of mast seeding in trees. Biol. J. Linn. Soc. **14**: 235-250.

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

Stelfox, J. B. 1995. Relationships between stand age, stand structure, and biodiversity in aspen mixedwood forests in Alberta. AB Env. Centre, Can. For. Serv., Edmonton, AB, No. 001A.

Sork, V. L. 1983. Mast-fruiting in hickories and availability of nuts. Am. Mid. Nat. **109**: 81-88.

Wurtz, T.L., and Zasada, J.C. 2001. An alternative to clear-cutting in the boreal forest of Alaska: a 27-year study of regeneration after shelterwood harvesting. Can. J. For. Res. **31**: 999-1011.

Youngblood, A.P. 1995. Development patterns in young conifer-hardwood forests of interior Alaska. J. Veg. Sci. **6**: 229-236.

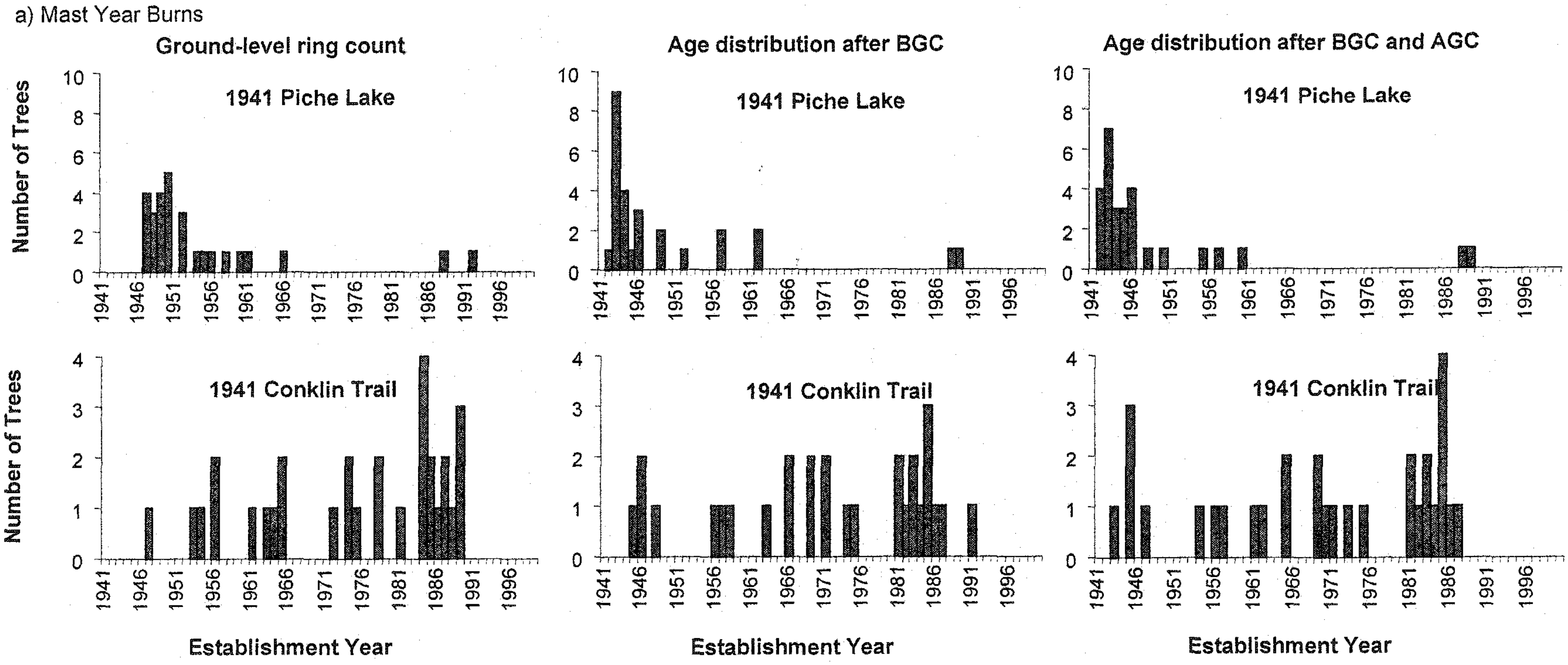
Zasada, J.C. 1985. Production, dispersal, and germination of white spruce and paper birch and first year seedling establishment after the Rosie Creek fire. University of Alaska, Fairbanks, Misc. Publ. 85.

Zasada, J.C., and Gregory, R.A. 1969. Regeneration of white spruce with reference to interior Alaska: a literature review. For. Serv., Pac. NW For. Exp. Sta., Gen. Tech. Rep. PNW-79.

APPENDICES

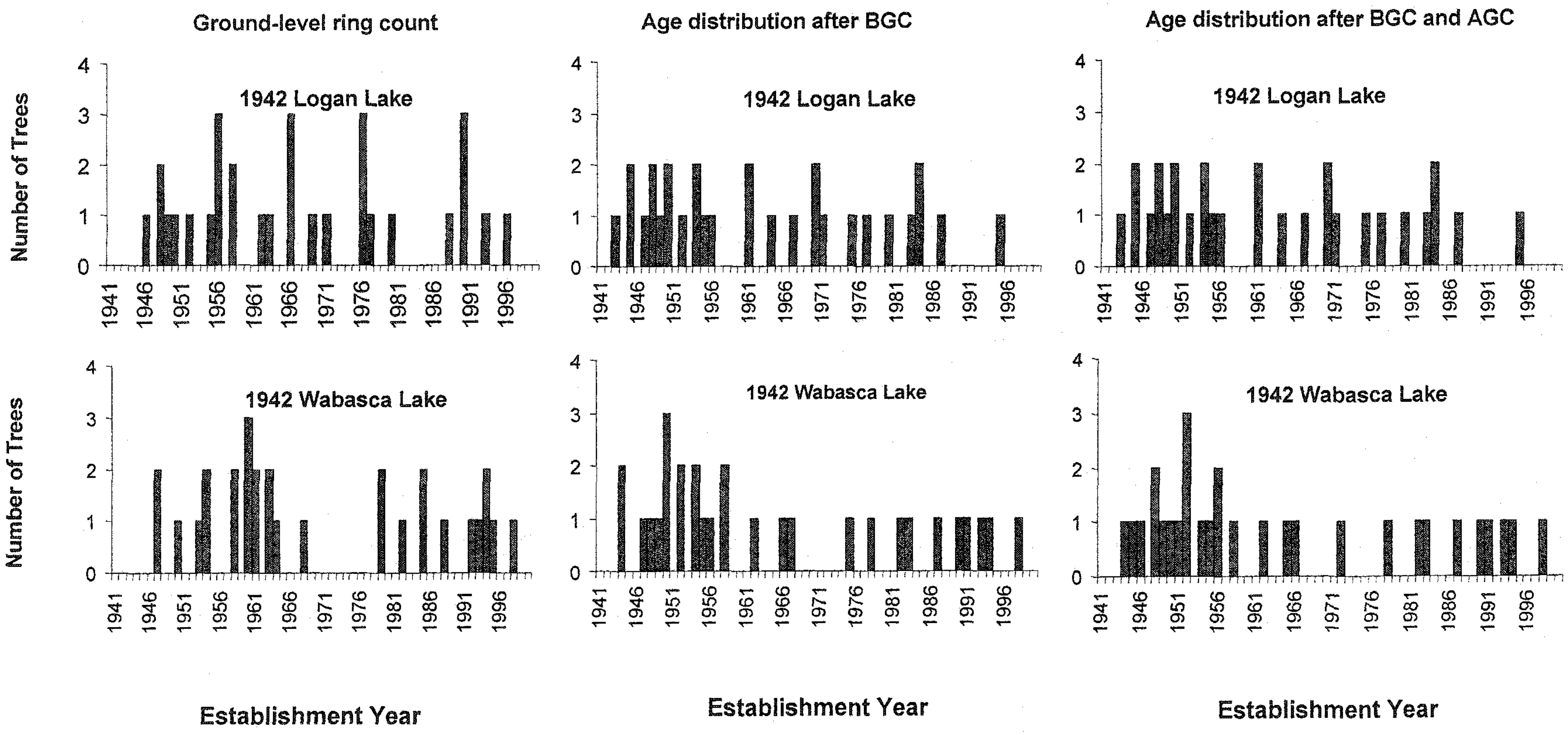
Appendix 2.1: Correlation values of 38-year-old stands crossdated with Cofecha before and after accounting for missing rings. Within stands, crossdating was performed seperately for trees in plots located 20 m versus 100 m from the seed source. Flagged sections are 10 year sections that correlate better in another location, or show significant differences in growth (ring sequences were not adjusted further because of reduced match to the master chronology). The master stand is the reference stand that was used for the master chronology (approximately 57-years-old).

Stand # - Distance (m)	Before identifying missing rings		After crossdating (rings added)	
	Correlation	Flagged sections (%)	Correlation	Flagged sections (%)
2-20	0.227	73.9	0.302	64.2
2-100	0.237	59.1	0.325	47.8
3-20	0.370	47.8	0.294	57.1
3-100	0.306	68.0	0.304	67.7
Master	0.140	73.2	0.619	31.6



Appendix 5.1: Estimate of age distribution on a) 59-year-old mast fires, and b) 58-year-old non-mast fires, based on different approaches to age estimation: ground level ring counts, addition of missing rings located with below-ground crossdating (BGC), and addition of missing rings from above-ground crossdating (AGC) and BGC. One stand was randomly selected from each fire (*n* = 30 trees / stand). Aging errors identified in these stands were used for methods in Chapter 5 for distinguishing initial regeneration from delayed regeneration.

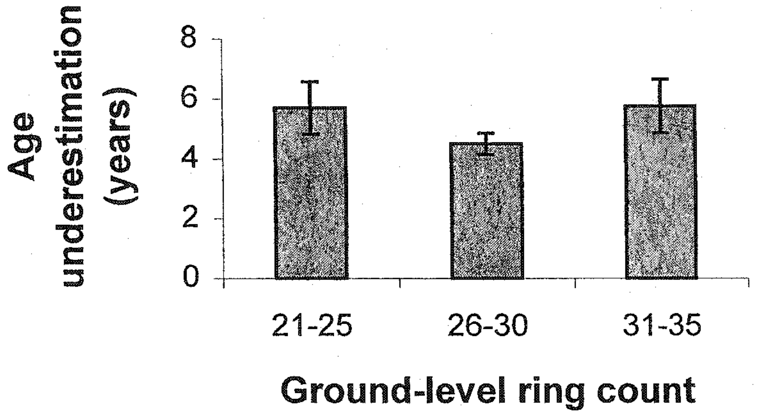
b) Non-mast Year Burns



Ground-level ring count

Age distribution after BGC

Age distribution after BGC and AGC

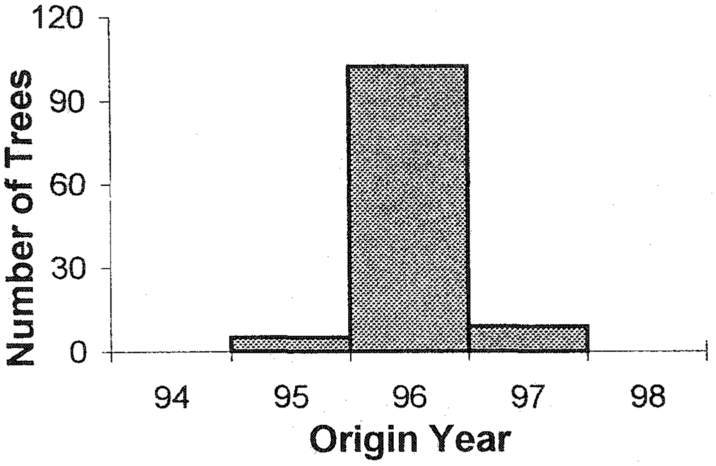


Appendix 5.2: Age underestimation of trees relative to ground-level ring counts. Age underestimation was determined by crossdating below ground with skeleton plots, and obtaining the root collar age. These mean errors were added to trees with ground-level ages corresponding to the categories shown in this figure, in order to identify initial regeneration (established within 20 years of the fire), versus delayed regeneration (established 21-59 years after fire; see Fig. 5.1).

Appendix 5.3: Frequency of aged trees in stants that were either initial or delayed regeneration, relative to distance from seed source (on sampled fires). Stands originated from independent seed sources with non-overlapping seed shadows. Fifteen trees were collected per site. Several trees are not reported because they were either lost, damaged during collection, or orginated prior to the fire.

Fire	Stand	Distance	Delayed	Initial
1961 House River	2	20	1	13
1961 House River	2	100	4	10
1961 House River	3	20	1	14
1961 House River	3	100	0	14
1958 Lawrence Lake	1	20	6	9
1958 Lawrence Lake	1	100	5	8
1958 Lawrence Lake	6	20	4	8
1958 Lawrence Lake	6	100	2	13
1941 Piche Lake	1	20	2	8
1941 Piche Lake	1	100	5	10
1941 Piche Lake	3	20	0	15
1941 Piche Lake	3	100	2	13
1941 Piche Lake	5	20	10	5
1941 Piche Lake	5	100	4	11
1941 Piche Lake	6	20	0	15
1941 Piche Lake	6	100	2	13
1941 Piche Lake	8	20	6	9
1941 Piche Lake	8	100	5	9
1941 Conklin Trail	1	20	6	9
1941 Conklin Trail	1	100	7	8
1941 Conklin Trail	4	20	10	5
1941 Conklin Trail	4	100	9	6
1941 Conklin Trail	5	20	12	3
1941 Conklin Trail	5	100	10	5
1941 Conklin Trail	7	20	8	7
1941 Conklin Trail	7	100	14	1
1941 Conklin Trail	8	20	15	0
1941 Conklin Trail	8	100	7	7
1942 Logan Lake	2	20	6	9
1942 Logan Lake	2	100	7	8
1942 Logan Lake	3	20	8	7
1942 Logan Lake	7	100	8	7
1942 Logan Lake	5	20	2	13
1942 Logan Lake	5	100	8	7
1942 Logan Lake	6	20	4	11
1942 Logan Lake	6	100	3	11
1942 Logan Lake	8	20	2	13
1942 Logan Lake	8	100	0	15
1942 Wabasca Lake	1	20	10	5
1942 Wabasca Lake	1	100	3	12
1942 Wabasca Lake	2	20	9	6
1942 Wabasca Lake	2	100	4	11
1942 Wabasca Lake	3	20	•	•
1942 Wabasca Lake	3	100	15	0
1942 Wabasca Lake	5	20	15	0
1942 Wabasca Lake	5	100	15	0
1942 Wabasca Lake	6	20	7	8
1942 Wabasca Lake	6	100	8	7

• Missing data



Appendix 6.1: White spruce establishment timing on a 1994 fire (*n* = 8 stands, 110 trees). Trees were aged by counting growth rings at the root collar. This fire occurred four years prior to the mast year of 1998.