SMALL SCALE DISTURBANCES AND STAND DYNAMICS IN *INONOTUS TOMENTOSUS* INFECTED AND UNINFECTED OLD-GROWTH AND PARTIAL

CUT WET, SUB-BOREAL FORESTS IN BRITISH COLUMBIA

by

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B.Sc. The University of Northern British Columbia, 1997

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF MASTER OF SCIENCE

in

NATURAL RESOURCES MANAGEMENT

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THE UNIVERSITY OF NORTHERN BRITISH COLUMBIA

May 2001

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ABSTRACT

Disturbance and stand dynamics were compared for old-growth and partial cut forests with and without *Inonotus tomentosus* (Fr.) Teng caused root disease in wet, cool Sub-Boreal Spruce forests near Prince George, British Columbia, Canada. Two methodologies (a time since death model and tree ring growth rate criteria) were developed to support two studies – a gap level analysis and a stand level analysis. The objectives of the studies were to: 1) Determine the spatial and temporal patterns of small-scale disturbance in oldgrowth and partial cut forests with and without the influence of *I. tomentosus*; 2) Determine how stand composition and structure differ between *I. tomentosus* infected and non-infected old-growth forests; 3) Determine how *I. tomentosus* affects stand dynamics in partial cut forests and how its effects differ from its effects in old growth forests.

In the gap level analysis, four forest types were sampled in 10 meter fixed radius plots (Old-growth with *I. tomentosus* (OGT) (n=21), and partial cut with *I. tomentosus* (PCT) (n=22), Old-growth without *I. tomentosus* (OGNT) (n=23) and partial cut without *I. tomentosus* (PCNT) (n=23)). *P. glauca* × *engelmannii* mortality was 50% lower in partial cut forests than in old-growth forests regardless of infection status. The functional gap size caused by a single tree averaged 16.76 m². Summed gap-size measures for all trees dying in a decade indicated that between 6.9 and 8.1% of stand area was made available to understory trees per decade. Due to high mortality rates and low recruitment rates to the canopy for *P. glauca* × *engelmannii*, old-growth forests are shifting to a canopy dominated by *A. lasiocarpa*. In the partial cut plots, higher relative *P. glauca* × *engelmannii* populations may rise relative to present densities.

ii

In old-growth forests, the spatio-temporal patterns of canopy disturbance and canopy patch structure were quantified from 0.49ha (n=6) stem-mapped plots using Moran's I and Standard Normal Deviates. Canopy disturbance and canopy composition were similar for *I. tomentosus* infected and uninfected stands at low levels of incidence. For stand types pooled, average decadal canopy disturbance ranged from 5.09%-6.0%. Gaps size averaged < 7m in diameter and were irregularly distributed across the forests. Species patch structure analysis indicated that *P. glauca* × *engelmannii* is found in small patches which are probably remnants of a once nearly homogenous spruce canopy. These results show that small-scale disturbances are important successional mechanisms in old-growth Sub-Boreal Spruce forests because of their effects on stand structure and dynamics.

TABLE OF CONTENTS

ABSTRACT	ii
TABLE OF CONTENTS	iv
LIST OF TABLES	ix
LIST OF FIGURES	x
ACKNOWLEDGEMENT	xii
PREFACE	1
CHAPTER 1. INTRODUCTION TO SUB-BOREAL STAND DYNAMICS: LITERATURE REVIEW.	3
1.1 Species Associations, Range and Climate	3
1.2 Succession	5
1.3 Small and Medium Scale Disturbances in Boreal, Sub-Boreal and Sub-Alpine Forests	7
1.4 Stand Development In Sub-Boreal, Boreal And Sub-Alpine Forests	9
1.5 Resource Dynamics in Gaps	11
1.6 Inonotus tomentosus as a Cause of Small Scale Disturbance	13
1.7 Research Questions	17
1.8 LITERATURE CITED	19
CHAPTER 2. ESTIMATING TIME SINCE DEATH IN <i>PICEA GLAUCA</i> × <i>ENGELMANNII</i> AND <i>ABIES LASIOCARPA</i> IN A WET-COOL SUB-BOREAL SPRUCE FOREST.	
2.0 ABSTRACT	26
2.1 INTRODUCTION	28
2.2 METHODS	31
2.21 Study Area	31

2.22 General Approach	31
2.23 Explanatory Variables	32
2.24 Analysis and Modeling	35
2.3 RESULTS	38
2.31 Model Validation	39
2.4 DISCUSSION	40
2.5 CONCLUSIONS	43
2.6 LITERATURE CITED	44
2.7 APPENDIX	47
CHAPTER 3. A METHODLOLOGY FOR ESTIMATING YEAR OF DEATH IN SBS FORESTS USING TREE RING GROWTH RATES.	
3.0 ABSTRACT	59
3.1 INTRODUCTION	61
3.2 METHODS	63
3.21 Study Area and Site Selection	63
3.22 Sampling Design and Plot Measurements	64
3.23 Analysis	64
3.3 RESULTS AND DISCUSSION	70
3.31 Comprehensive Analysis	70
3.32 Selective Analysis	71
3.4 CONCLUSIONS	76
3.5 LITERATURE CITED	77

v

CHAPTER 4. SPATIOTEMPORAL PATTERNS OF SMALL-SCALE DISTURBANCES IN SUB-BOREAL SPRUCE FORESTS: IMPLICATIONS FOR PARTIAL CUT HARVESTING AND INONOTUS TOMENTOSUS ROOT DISEASE.

4.() ABSTRACT	82
4.1	4.1 INTRODUCTION	
4.2	4.2 METHODS	
	4.21 Study Area	87
	4.22 Site Selection	88
	4.23 Sampling Design and Measurements	89
	4.24 Data Analysis	91
4.3	4.3 RESULTS	
	4.31Stand Composition	94
	4.32 Disturbance	95
	4.33 Accumulated Mortality	95
	4.34 Functional Gap Size	96
	4.35 Transition Probabilities	97
	4.36 Simulations of Future Stand Compositions	97
4.4	4 DISCUSSION	99
4.:	5 CONCLUSIONS	105
4.0	6 LITERATURE CITED	106

CHAPTER 5. STAND LEVEL SPATIO-TEMPORAL DISTURBANCE PATTERNS CAUSED BY *INONOTUS TOMENTOSUS* AND OTHER AGENTS IN SUB-BOREAL SPRUCE-FIR FORESTS.

5.0 ABSTRACT	115
5.1 INTRODUCTION	116
5.2 METHODS	
5.21 Study Area	119
5.22 Site Selection	120
5.23 Sampling Design and Plot Measurements	121
5.24 Interpretation of Growth Patterns	123
5.25 Analysis for Spatial Patterns of Disturbance	123
5.3 RESULTS	126
5.31 Canopy Composition	126
5.32 Canopy Ascension by Species	126
5.33 Canopy Ascension by Decade	126
5.34 Spatial Patterns of Canopy Disturbance	127
5.35 Spatial Patterns of Species Patches	128
5.4 DISCUSSION	129
5.41 Spatial Patterns of Disturbance	129
5.42 Species Patch Structure	130
5.5 CONCLUSIONS	131
5.6 LITERATURE CITED	133

CHAPTER 6. SUMMARY OF FINDINGS, MANAGEMENT RECOMENDATIONS AND CONCLUSIONS.

6.0 STUDY RATIONALE	144
6.1 SUMMARY OF RESEARCH	
6.11 Canopy Disturbance	149
6.12 Gap Size	150
6.13 Canopy Mortality By Species	150
6.14 Stand Composition, Canopy Replacement and Future Stand Composition	150
6.15 Impacts of Inonotus tomentosus and Partial Cutting on Disturbance and Stand Composition	151
6.2 MANAGEMENT APPLICATIONS	
6.21 Prescribed Harvest Intensity for Partial Cut Harvesting in Wet- Cool SBS Forests	153
6.22 Harvest Dispersion	153
6.23 Harvest Timing	153
6.24 Development of Methodology	154
6.25 Future Research	156
6.3 CONCLUSIONS	158
6.4 LITERATURE CITED	159

LIST OF TABLES

CHAPTER 1. INTRODUCTION TO SUB-BOREAL STAND DYNAMICS: LITERATURE REVIEW.

Table 1. Climatic comparisons for various sub-boreal, sub-alpine andboreal forests present in British Columbia.	23
CHAPTER 2. ESTIMATING TIME SINCE DEATH IN <i>PICEA GLAUCA</i> × <i>ENGELMANNII</i> AND <i>ABIES LASIOCARPA</i> IN A WET-COOL SUB-BOREAL SPRUCE FOREST.	
Table 1. Bivariate regression statistics.	51
Table 2. Correlation matrix for spruce model and fir.	52
Table 3a. Summary of regression statistics for the spruce models.	53
Table 3b. Summary of regression statistics for the fir models.	54
Table 4. Comparison of mean years since death.	55
CHAPTER 4. SPATIOTEMPORAL PATTERNS OF SMALL-SCALE DISTURBANCES IN SUB-BOREAL SPRUCE FORESTS: IMPLICATIONS FOR PARTIAL CUT HARVESTING AND INONOTUS TOMENTOSUS ROOT DISEASE.	
Table 1. Summary of stand composition and mortality data.	109
Table 2. Species composition dynamic over the next 200 years.	110
CHAPTER 5. STAND LEVEL SPATIO-TEMPORAL DISTURBANCE PATTERNS CAUSED BY <i>INONOTUS TOMENTOSUS</i> AND OTHER AGENTS IN SUB-BOREAL SPRUCE-FIR FORESTS.	
Table 1. Proportion of canopy accession types by treatment type, and species.	136
Table 2. Summary of spatial autocorrelation of species association using joins-count statistics.	137

LIST OF FIGURES

CHAPTER 1. INTRODUCTION TO SUB-BOREAL STAND DYNAMICS : LITERATURE REVIEW.	
Figure 1. Location of Sub Boreal Spruce biogeoclimatic zone and the Aleza Lake Research Forest.	24
Figure 2. Models of Succession.	25
CHAPTER 2. ESTIMATING TIME SINCE DEATH IN <i>PICEA GLAUCA</i> × <i>ENGELMANNII</i> AND <i>ABIES LASIOCARPA</i> IN A WET-COOL SUB-BOREAL SPRUCE FOREST.	
Figure 1. Regression fit for spruce model.	56
Figure 2. Regression fit for fir model.	57
Figure 3. Plotted values of dates of tree mortality.	58
CHAPTER 3. A METHODLOLOGY FOR ESTIMATING YEAR OF DEATH SBS FORESTS USING TREE RING GROWTH RATES.	IN
Figure 1. Demonstration of various incremental growth patterns used assess date of canopy ascension.	to 79
Figure 2. Box-plots showing the range in initial 10-year average growt rate.	:h 80
Figure 3. Decision set for determining year of canopy ascension.	81
CHAPTER 4. SPATIOTEMPORAL PATTERNS OF SMALL-SCALE DISTURBANCES IN SUB-BOREAL SPRUCE FORESTS: IMPLICATIONS FOR PARTIAL CUT HARVESTING AND INONOTUS TOMENTOSUS ROOT DISEASE.	
Figure 1. Disturbance chronologies for the four forest types.	111
Figure 2. Transition probability data from 1930-1950.	112
Figure 3. Transition probability data from 1950-1970.	113
Figure 4. Transition probability data from 1970-1997.	114

CHAPTER 5. STAND LEVEL SPATIO-TEMPORAL DISTURBANCE PATTERNS CAUSED BY *INONOTUS TOMENTOSUS* AND OTHER AGENTS IN SUB-BOREAL SPRUCE-FIR FORESTS.

Figure 1. Canopy ascension by decade and by species for <i>Inonotus</i> tomentosus infected plots.	138
Figure 2. Canopy ascension by decade and by species for <i>Inonotus</i> tomentosus uninfected plots.	139
Figure 3. Locations of canopy ascension dates for trees in the three non- infected plots.	140
Figure 4. Locations of canopy ascension dates for trees in the three <i>Inonotus tomentosus</i> infected plots.	141
Figure 5. Correlogram showing Moran's I coefficients for <i>Inonotus</i> tomentosus infected plots.	142
Figure 6. Correlogram showing Moran's coefficients for <i>Inonotus tomentosus</i> uninfected plots.	143
CHAPTER 6. SUMMARY OF FINDINGS, MANAGEMENT RECOMENDATIONS AND CONCLUSIONS.	
Figure 1. Diameter class distribution (dbh) of dead trees in old-growth forests.	160

ACKNOWLEDGEMENT

"If you know how long its going to take, how much money it will cost and what to expect, isn't research". It took lots of time, quite a bit of money and there were several unexpected obstacles along the way. That said there are many people to thank for all of their time and efforts, financial contributions and guidance in this project. Alison –you tolerated 3 ½ years of this! How will I every repay you? You gave me time to work and time to play. To Mike and Kathy who trusted I could do and learn – you are important mentors. Thanks to my assistants Elana, Lorraine and Christian. For their financial contributions I would like to thank Forest Renewal British Columbia, The Science Council of British Columbia, Grant Smith at Canfor, and Terry Kuzima at Carrier Lumber – your contributions were greatly appreciated. I would also like to thank Richard Kabzems, my external reviewer, Mike Jull and Joe Ackerman for your careful reviews and important perspectives. Your participation greatly improved the quality of this research!

Thanks to Mom, Dad and Tim for many enjoyable days in the woods.

To Edward and Andrina Newbery

PREFACE

"The outstanding scientific discovery of the twentieth century is not television, or radio, but rather the complexity of the land organism. Only those who know the most about it can appreciate how little is known about it. The last word in ignorance is the man who says of an animal or plant: 'what good is it?' If the land mechanism as a whole is good, then every part is good, whether we understand it or not. If the biota, in the course of æons, has built something we like but do not understand, then who but a fool would discard the seemingly useless parts? To keep every cog and wheel is the first precaution of intelligent tinkering." *Aldo Leopold, 1966.*

The practice of forest management in British Columbia is evolving from traditional ideas of sustained yield management to ecosystem management approaches as suggested above by Aldo Leopold. With this paradigm shift, strategies are being developed to maintain the complexity of the land organism and thus maintain healthy ecosystems. It has been proposed that one way of maintaining healthy ecosystems is to use harvest patterns that mimic natural disturbance regimes so as to provide for more natural levels of stand and landscape level diversity.

Secondary succession in wet sub-boreal, spruce-fir forests in central British Columbia is thought to be initiated by catastrophic fire, with return intervals ranging 227-6, 250 years. Due to the relative infrequency of fire in this area compared to drier forest ecosystems, small-scale disturbance agents that cause mortality of individual or small groups of trees can be important processes affecting succession. In areas where small disturbances are known to be a predominant successional mechanism, partial cut harvesting is used to mimic the natural disturbance regime. However, little is known about small-scale disturbance regimes and associated forest dynamics in the sub-boreal, forests of western North America. Without precise information on these attributes, we may not be able to develop partial cut harvesting protocols that mimic the natural smallscale disturbance regime. An important small-scale disturbance agent in wet, sub-boreal,

spruce-fir forests is *Inonotus tomentosus* (Fr.) Teng. The root disease caused by this fungus can spread to adjacent trees and inoculum can remain active in stumps and roots for decades. These characteristics may create important differences in disturbance regime and stand development compared to other disturbance agents (*e.g.* bark beetles and windthrow). Moreover, *I. tomentosus* caused mortality may be exacerbated by partial cut harvesting because inoculum could be transferred more readily from infected stumps to new regeneration and residual trees. Given the need for partial cut guidelines in wet, subboreal forests and the potential interaction of *I. tomentosus* with partial cutting, there is a need to quantify the disturbance regime and subsequent stand dynamics for forests infected by *I. tomentosus* and those uninfected by *I. tomentosus*.

This thesis addresses three main questions for wet-cool sub-boreal forests located east of Prince George, British Columbia:

- 1. What are the spatial and temporal patterns of small-scale disturbance for old-growth and partial cut forests with and without the influence of *I. tomentosus*?
- 2. How does stand composition and structure differ between *I. tomentosus* infected and non-infected old-growth forests?
- 3. How does *I. tomentosus* affect stand dynamics in partial cut forests and how does this differ from its affects in old-growth forests?

These questions are addressed at both the tree and stand level by combining information from two investigative approaches that measure stand dynamics at different spatial scales. In combination, these approaches provide a multi-scale understanding of small-scale natural disturbance regimes, stand dynamics and succession in wet, sub-boreal forests. It is hoped that these studies will improve our understanding of small-scale disturbances in sub-boreal forests, particularly the ecology of *I. tomentosus*, and provide a biological basis for *I. tomentosus* management and partial cut silviculture.

CHAPTER 1. INTRODUCTION TO SUB-BOREAL STAND DYNAMICS: LITERATURE REVIEW

1.1 Species Associations, Range and Climate

The sub-boreal forest region of North America is composed of a variety of forest ecosystems transitional to the southern boundary of the boreal forest. The southern boundary of the sub-boreal zone varies from east to west. In eastern North America, the sub-boreal forest is bounded to the south by the deciduous forest region, beginning in south-central Ontario and ranging into the northeastern United States (Rowe 1972). In this area, sub-boreal forests are mixtures of eastern conifers (eastern white pine, red pine and eastern hemlock), eastern hardwoods (yellow birch, sugar maple, red maple, red oak, basswood, white elm, poplars, beech, white oak, butternut and white ash), and boreal species (white and black spruce, balsam fir, jack pine, poplars and white birch) (Rowe 1972). In central North America, the sub-boreal forest is absent due to the abrupt boundary between the boreal forest in the north and the grassland region of the Great Plains to the south (Farrar 1995). In western North America the sub-boreal forest is comprised of mixtures of *Picea glauca* × *engelmannii* Voss × Parry (hybrid spruce, hereafter referred to as spruce) and Picea mariana B.S.P. (black spruce), Abies lasiocarpa Nutt. (sub-alpine fir, hereafter referred to as fir), Pinus contorta Dougl. (lodgepole pine), Populus tremuloides Michx. (trembling aspen), Betula papyrifera Marsh (paper birch), Populus trichocarpa Torr. & Gray (black cottonwood) and Pseudotsuga menziesii Franco (Douglas-fir) (Pojar et al. 1982). Here, sub-boreal forests are transitional to higher elevation forests and the boreal forest northward.

The sub-boreal climate is slightly less continental than the boreal (Table 1). It has shorter winters, longer growing seasons, higher precipitation, and lower rates of

evapotranspiration. Generally, the average growth rates of trees are higher in sub-boreal than boreal forests due to the slightly more favorable macroclimate (Pojar et al. 1982). In British Columbia, large areas of the sub-boreal forest are classified as Sub-Boreal Spruce (SBS) forests. The SBS forest region is located in central interior British Columbia between 52° and 57° North latitude and 122° and 128° West longitude (Pojar et al. 1982; Meidinger and Pojar 1991) (Figure 1). This diverse zone is transitional to higher elevation montane Douglas-fir and sub-alpine forests in the south and the boreal forests in the north (Pojar et al. 1982; Meidinger and Pojar 1991). Generally, the SBS is dominated during late seral stages by spruce and fir. SBS forests typically occur at low to medium elevations (500 to 1300 meters above sea level) on the gently rolling terrain of the Fraser and Nechako plateaus and the Fraser basin (Pojar et al. 1982). The climate of the SBS is broadly continental with seasonal extremes of long, cold, snowy winters and short, warm, moist summers (DeLong et al. 1993). Mean annual temperature ranges from 1.7°C to 5°C and average temperatures are below 0°C for 4-5 months and above 10°C for 4-5 months of the year (Table 1) (Meidinger and Pojar 1991). The mean annual precipitation is widely variable, between 440 mm and 900 mm, but extremes in precipitation of 415 mm and 1650 mm have been recorded from short-term data (Table 1) (Meidinger and Pojar 1991). A second sub-boreal zone also found in British Columbia is the Sub-Boreal Pine-Spruce. This zones' climate is slightly drier and cooler than the SBS (Table 1) and lodgepole pine-engelmann spruce (Picea engelmannii) mixtures dominate late seral ecosystems.

1.2 Succession

Stand Initiation

SBS forests originate by fire and the stand initiation stage is characterized by the development of a single cohort of several tree species initially achieving high densities. On most sites, shade intolerant species, generally faster growing and with regeneration strategies that are fire adapted: lodgepole pine, paper birch, trembling aspen, spruce and Douglas-fir, establish quickly while more shade tolerant species and those less fire adapted: fir, western hemlock (*Tsuga heterophylla* Sarg.) and western red cedar (*Thuja plicata* Donn) fill in over time and gradually increase in abundance (Oliver and Larson 1996). Spruce, due to its moderate shade tolerance is also found in the understory of these forests.

Stem Exclusion

Following stand initiation, the single cohort stand undergoes a period of density dependent mortality called stem exclusion (Oliver and Larson 1996). Canopy closure and limited resources prevent further understory initiation (germination) and vigorous individuals out-compete weaker and smaller individuals resulting in their mortality and/or suppression to subordinate canopy positions (Waring and Schlesinger 1985; Davis and Johnson 1987; Oliver and Larson 1996). More shade tolerant trees, such as fir and spruce, may survive in sub-canopy positions, however, this stage is characterized by high mortality rates for all species regardless of shade tolerance (Kneeshaw and Burton 1997). *Understory reinitiation*

Towards the end of the stem exclusion stage, mortality starts to occur in the overstory creating growing space for a second post-fire cohort. In the SBS a variety of shade tolerant trees: fir (especially), spruce, and occasionally western red-cedar, and

western hemlock undergo a second period of germination and/or growth from advanced regeneration (Oliver and Larson 1996). In some cases paper birch and Douglas-fir, relatively shade intolerant species, are able to regenerate successfully. The understory reinitiation stage continues to influence stand structure and composition in SBS forests due to competition induced mortality and mortality caused by small and medium scale disturbances mainly caused by *Inonotus tomentosus*, spruce beetle outbreaks (*Dendroctonus rufipennis*) (Humphreys and Safranyik 1993), windthrow and snow or ice breakage.

Old-growth

Oliver and Larson (1996), define old-growth as the complete replacement of the initial fire-origin cohort. This is achieved by the absence of stand replacing disturbances and continued mortality of trees, due to small and intermediate scale disturbances (Kneeshaw and Bergeron 1998). Spruce, and fir mixtures with a wide representation of size and age classes typically characterize old-growth SBS forests. The time frame for old-growth development is variable and the definition of old-growth given above may only rarely be realized in the SBS. However, once a post-fire cohort begins to replace the fire-origin cohort in the canopy, the development of an old-growth forest has begun.

In particularly wet SBS forests, fire may be so infrequent that true old-growth forests are common place. Hawkes *et al.* (1997) reports that fire return intervals in very wet and cool SBS forests near the Rocky Mountains likely range 1200-6250 years. DeLong and Tanner (1996) reported intervals ranging 227-345 years in slightly drier SBS forests in the foothills of the Rocky Mountains. In between these long return intervals, small scale disturbances caused by root rot fungi (e.g. *Inonotus tomentosus*), wood feeding insects (e.g. *Dendroctonus rufipennis*), tree life spans, and abiotic factors such as

windthrow and snow loading, kill individual or small groups of trees. These small disturbances create old-growth forests and facilitate the maintenance and renewal of forest structure in forests with long fire return intervals. Furthermore, it is acknowledged that they are becoming important processes where fire suppression or climatic change has excluded or reduced fire's influence on the ecosystem (Clark 1994; Frelich and Reich 1995; Andison 1996; Kneeshaw and Bergeron 1998).

1.3 Small and Medium Scaled Disturbances in Sub-Boreal, Boreal and Sub-Alpine Forests

In wet SBS forests, and other similar forest regions such as sub-alpine and eastern North American and Asian (sub)-boreal forests, small scale disturbance agents are important processes to forest dynamics and succession during the inter-fire period (Veblen 1989; Lertzman 1992; Veblen *et al.* 1994; Frelich and Reich 1995; Kubota 1995; Yamamoto 1995; Kneeshaw and Burton 1997; Kneeshaw and Bergeron 1998; Yong *et al.* 1998; Lewis and Lindgren 1999). However, knowledge about the patterns and processes created by these small disturbances is limited, especially in northern interior British Columbian forests. This is partly because of the previously held belief that SBS forests had short fire return intervals that minimized the importance of small and intermediate sized disturbances. However, a body of literature is beginning to demonstrate the importance of small to medium sized disturbances to stand dynamics in many sub-alpine, boreal and sub-boreal forest types.

In a Rocky Mountain sub-alpine fir forest in southern British Columbia, Veblen (1986) reported that spruce beetle outbreaks averaged 200 hectares in size and return intervals were 116.5 years. In a SBS forest near Smithers, British Columbia, Kneeshaw and Burton (1997) reported that spruce beetle caused 5 – 90% mortality over areas

ranging from 1-6, 200 hectares. Another key disturbance in sub-boreal forests is *Inonotus* tomentosus which reportedly caused 0-10% mortality in patches ranging in size from < 1 hectare to 100 hectares (Van Groenewoud and Whitney 1969; Merler *et al.* 1988).

Kneeshaw and Bergeron (1998) characterized the percent area in recently formed gaps as a function of stand age for southeastern boreal forests in northwestern Quebec. For young forests (65 years), 7.1% of the study area was occupied by gaps whereas old forests (230 years) were found to have 40.4% of stand area in gaps. Mortality was mainly attributed to overstory tree senescence and spruce budworm.

In a sub-alpine forest in central Japan, Yamamoto (1995) reported that of the total stand area studied, 7.4% was occupied by gaps, gap density equaled 17.2 ha $^{-1}$ and mean gap size was 43.3 m², with the data highly skewed to smaller gap sizes. Of these gaps, 65.3% were caused by single tree deaths, with about 55% of these attributed to wind. In a sub-boreal forest in northern Japan, Kubota (1995) reported different disturbance patterns in four similar systems dispersed widely across their study area. Some forests were affected by continuous small disturbances mainly due to wind, killing one to a few trees in isolated areas. Other forests were affected periodically by slightly larger disturbances such as typhoon.

A few studies have examined disturbance across multiple scales (Veblen *et al.* 1994; Frelich and Reich 1995). In a southern boreal forest in Minnesota, Frelich and Reich (1995) demonstrated the importance of scale in succession. Five models of succession were tested in their study: 1) *Cyclic Model*, succession begins at stand A then evolves to stand B, then C, then D, and back to A (Figure 2a); 2) *Convergent Model*, two dissimilar forests succeed towards the same stand composition (Figure 2b); 3) *Divergent Model*, stand A succeeds into two different stand compositions (Figure 2c); 4) Parallel

Model, stand A and stand B maintain their characteristics even after disturbance (Figure 2d); 5) *Individualistic Model*, the stand begins at point A and is driven to an array of potential points depending on a variety of mechanisms and relationships (Figure 2e). At small spatial scales, they reported the divergence hypothesis best described successional patterns with small groups of trees (35 m²), of the same species, age, height, etc., developing from a homogeneous fire origin stand. At a larger scale (1-16 hectares) succession lead to a convergent model (Figure 2b) with one stand comprised of mixtures of several species with no patchiness pattern evident as in the small scale study (Frelich and Reich 1995). In both cases, succession was driven by openings in the canopy 10-30 meters in diameter caused by wind, insects and disease, but the results clearly show how different interpretations can be made depending on the scale examined. It is important to realize that disturbance occurs across this hierarchy of scales, and single scale disturbance investigations do not explicitly take this approach. Thus, the combined interpretations of different studies will reveal the true outcome of disturbances operating at multiple scales.

1.4 Stand Development in Sub-Boreal, Boreal and Sub-Alpine Forests

Stand development following a disturbance is contingent upon the nature of the disturbance, the age of the stand, the health of the stand, abiotic factors such as soil texture, biotic factors such as herbivory, and chance. However, some simplifications of stand characteristics are possible even with generalizations regarding disturbance regime. Throughout the regions discussed above, *Abies spp.* and *Picea spp.* dominate late successional boreal and sub-boreal forests. Generally, *Picea spp.* has greater basal area due to a greater number of larger trees but *Abies spp.*, is generally found in higher total

densities (about 8:1, *Abies:Picea*) (Veblen 1986; Veblen *et al.* 1994; Frelich and Reich 1995; Yamamoto 1995; Kneeshaw and Burton 1997; Kneeshaw and Bergeron 1998; Jull and Farnden *unpublished data*).

In *Picea spp.-Abies spp.* forests horizontal stand structure has been reported to be generally clumped with groups of individuals surrounded by open patches (Lewis and Lindgren 1999) and there is a high degree of vertical canopy stratification in old forests (Veblen 1986; Veblen *et al.* 1994; Frelich and Reich 1995; Yamamoto 1995; Kneeshaw and Burton 1997; Kneeshaw and Bergeron 1998; Jull and Farnden *unpublished data*). Age class and diameter distributions range from uneven (exponential decay) (Kubota 1995; Jull and Farnden *unpublished data*) to bimodal or irregular in old forests (Johnson *et al.* 1994).

Mortality appears mainly in upper canopy positions in mature forests (Veblen 1986; Frelich and Reich 1995; Kubota 1995; Kneeshaw and Burton 1997; Kneeshaw and Bergeron 1998; Jull and Farnden *unpublished data*), and in most cases (but see Johnson *et al.* 1994), recruitment from the understory occurs reliably, replacing lost stems and maintaining canopy cover. There appears to be agreement that these ecosystems are self-maintaining in the absence of fire, with small scale disturbances being a key process allowing understory species to replace lost canopy trees. Generally, various mixtures of *Abies spp.* and *Picea spp.* maintain the canopy. In some cases, *Betula spp.* (Jull and Farnden *unpublished data*; Frelich and Reich 1995; Kubota 1995; Yamamoto 1995; Kneeshaw and Bergeron 1998), *Tsuga spp.*, and *Thuja spp.* (Frelich and Reich 1995; Yamamoto 1995) are maintained in small numbers due to the presence of suitable germination substrate, gap environments or chance.

In most cases, it is thought that Picea spp. and Abies spp. are able to coexist indefinitely in these forests due to differences in their mortality schedules and recruitment strategies (Kneeshaw and Bergeron 1998). However, Johnson et al. (1994) inferred from his results that a long period of *Picea glauca* exclusion during stem exclusion will not allow it to be maintained without fire. Differences in shade tolerance and seed germination may be responsible for these apparent differences in recruitment strategies. Fir mortality rates reported by Jull and Farnden (unpublished data) from long-term permanent sample plot data, increase linearly with diameter or age of the tree. Spruce appears to have a U-shaped mortality curve, with slightly higher mortality rates for sapling to small pole sized trees than fir. Spruce mortality decreases from pole (7 cm diameter) to mature trees (55 cm diameter) then increases again as trees become susceptible to pests and reach old age (Jull and Farnden unpublished data). Fir survival is higher than spruce for young trees while the opposite relationship holds for older trees. Furthermore, fir regenerates and subsists in the understory in higher densities than spruce due to greater shade tolerance and more successful germination on thick humus layers (Jull et al. 1996). These recruitment-mortality relationships appear to maintain Abies spp.- Picea spp. coexistence in many forests throughout the world.

1.5 Resource Dynamics in Gaps

The maintenance of these forests through understory establishment and recruitment to the canopy is due largely to the above and below ground resource dynamics resulting from recently dead or dying canopy trees. Light, nutrition, moisture and temperature regimes are all affected by disturbance and these resources and environments can become more abundant or favorable to potential recruits currently

living in or germinating in the gaps. In this thesis, resource availability in gaps is not measured, thus the relationships between gap formation, resource availability and tree growth cannot be examined. Based on previous research (Walters and Reich 1997) understory trees are assumed to be limited by multiple resources, thus the increase in growth of understory trees is attributed to increases in several limiting resources, as described below.

Light

Canopy gaps change many physical ecosystem components, however the most obvious effect is on light regimes. Canham (1989), found that with the exception of forests with extreme canopy height to crown width ratios (common in *Picea-Abies* forests), single tree-fall gaps significantly increase the quantity and quality of light an understory tree receives. However, the actual duration of this increased light is short in northern latitudes even in large gaps (several trees), since increasing latitude results in decreasing overhead light duration throughout the day (Canham 1989). In addition to this effect, the light received falls north of the gap with increasing latitude. Therefore, the quantity and quality of light is higher a few meters north of the dead canopy tree (Canham 1989).

As mentioned, forests with extreme canopy height to crown width ratios tend to reduce the total impact of light regimes in gaps. Tall trees with narrow crowns characterize *Picea-Abies* forests, but due to deep live crowns typical of spruce and subalpine fir, the impact of increased light should be at least partially responsible for increased understory growth rates in these forests (Kneeshaw and Burton 1997).

A number of studies have linked increased light with increased plant productivity in the field and *in vitro* (Walters and Reich 1997). Regardless of variation in species

shade tolerance, growth rates are higher with greater light levels. Many studies have also shown that trees will respond with increased height and diameter growth rates following release from shade (Canham 1989; Veblen 1989; Yong *et al.* 1998). Canham (1989) suggests that even single tree gaps increase light regimes as much as two-fold and that this additional light can trigger strong growth releases especially in shade tolerant species. Shade tolerant species are favored in these environments because they can regenerate under low light, closed canopy environments and out-survive less tolerant species at any given low light level. When a gap forms, they are able to respond quickly by increasing leaf area (Canham 1989). Shade intolerant species follow a different mode of establishment. These species colonize larger gaps germinating on mineral substrate in high light and grow quickly into the newly available space (Canham 1989). Thus, the size of a disturbance may favor a particular species of tree due to the gaps' physical and environmental characteristics and the trees' ecophysiological adaptations.

Nutrients, Temperature and Moisture

While increased light may be the most obvious change in resources caused by gap formation, nutrient availability, moisture, and temperature also increase in response to gap formation (Picket and White 1985, Pritchett and Fisher 1987, Schmidt et al. 1988, Walters and Coates, unpublished data). Thus increased seedling growth following gap formation in SBS forests may be due to increases in light, moisture, temperature and nutrient availability and not just increases in light alone

1.6 Inonotus tomentosus as a Cause of Small Scale Disturbance

One important cause of gap formation in wet SBS forests is *Inonotus tomentosus* (Fr.) Teng (Merler *et al.* 1988; Lewis and Hansen 1991a; Lewis *et al.* 1992; Lewis 1997).

This root pathogen induces gradual decline in tree vigor and eventually mortality (Lewis and Hansen 1991b) due to dysfunctional roots, or windthrow due to weakened root systems (Lewis and Hansen 1991b; Lewis 1997). *I. tomentosus* generally produces pockets of infection and mortality that are distributed throughout the forest (Lewis *et al.* 1992). Due to its slow colonization processes, mortality is particularly evident in older forests (Lewis *et al.* 1992). This disease has a wide host range but *Picea spp.* suffers the most damage (Lewis and Hansen 1991a; Meidinger and Pojar 1991; Hunt and Unger 1994). Other tree species such as lodgepole pine and Douglas-fir are moderately affected by the disease and *Abies spp.* even less. Hardwoods appear to be immune (Whitney 1993).

I. tomentosus can spread from host to host in two known ways. Root contact provides bridges for hyphae to move from infected to healthy trees (Lewis and Hansen 1991b). Basidiospores also spread the disease, and are thought to cause new infection centers but the mechanism of this infection process is not known (Lewis and Hansen 1991b). Once a new host is infected, possibly beginning in small feeder roots, the fungus accesses the root heartwood (Lewis *et al.* 1992). Its presence in the heartwood is indicated by reddish brown stain proceeding to darker and thicker bands of stain and finally to pockets of advanced decay characterized by longitudinal pitting (Lewis *et al.* 1992). In roots smaller than 2 cm in diameter, the fungal mycelium can be located in the bark or the cambium. This difference may be due to the thinner bark and lack of defense mechanisms in these small roots and the lack of significant heartwood accumulation (Lewis *et al.* 1992).

In large roots, the infection gradually weakens the trees' support making it susceptible to windthrow (Lewis and Hansen 1991b). The disease can infect a significant

portion of these large roots before reductions in growth occur, since the heartwood is not involved with the transport of resources (Hunt and Unger 1994; Lewis 1997). Mortality of the roots occurs when the sapwood becomes significantly decayed (Lewis *et al.* 1992) or when structural integrity is degraded to the point where tree fall occurs. Whitney (1980) speculates that mortality of the tree itself occurs when root mortality reaches 80%. However, mortality is probably more common due to weakened roots, resulting in windthrow (Whitney 1980). Following tree mortality, colonization of the root sapwood occurs rapidly due to the inactivity of active defense mechanisms. In the large roots, the decay will progress radially from the heartwood to the sapwood, thereby increasing probability that inoculum will contact a new host (Lewis *et al.* 1992).

Since the fungus spreads through root-to-root contact and prefers *Picea spp.* as a host, the gaps it forms may spread outward from the original infection center (Lewis *et al.* 1992). Therefore it can be hypothesized that *Picea spp.* may be eliminated from these progressive gaps and resistant species, especially sub-alpine fir in SBS forests, may be the species that is favored in the colonization of these gaps. Therefore, the disturbance regime and subsequent stand development could potentially be quite different compared to gaps and forests without the disease because it may reduce mature and regenerating hybrid spruce in wet, cool SBS forests in central British Columbia.

This hypothesized effect of *I. tomentosus* may have important forest health implications in both managed and unmanaged forests. For example, the choice of harvest systems in British Columbia is guided by the principle of ecosystem management (British Columbia Ministry of Forests 1995). One of the central tenants of this management philosophy is that imitating natural disturbance patterns with harvesting patterns will aid in achieving sustainable forest development (British Columbia Ministry of Forests 1995).

Due to the small scale disturbances that are common in wet SBS forests, partial cut silviculture systems might be appropriate tools for forest management because they may more closely mimic the natural disturbance process between long fire return intervals (Davis and Johnson 1987; Oliver and Larson 1996; Jull 1997). However, applying partial cut silviculture systems to sites where root disease is present may cause the disease to spread faster, due to a hypothesized increase in inoculum volume that may occur in the roots and stumps of harvested trees. This is known to occur with other root diseases such as *Armillaria ostoyae* and *Heterobasidion annosum* (Koening 1969; Cruickshank *et al.* 1997; Garbelotto *et al.* 1997), but the effect of harvesting on inoculum volume for *I. tomentosus* is unknown. This result was not supported by Whitney (1993) who reported that partial cut forests of *Picea glauca* had a lower proportion of individuals infected with *I. tomentosus* than unthinned forests. He proposed various reasons for this including discontinuity of spruce roots preventing root to root contact and increased due to more abundant resources following thinning.

It can be hypothesized that a combination of several factors may lead to increased infection and mortality of residual trees. The acceleration of disease-related mortality might be caused by harvesting infected trees, which when cut, lose the ability to actively limit root colonization, and therefore inter-tree spread. Furthermore larger trees are typically favored over smaller diameter trees in most partial cut or selective systems including diameter limit, stand improvement, seed tree, shelter wood, group selection, and single tree selection systems (Smith 1986). Since these larger trees are more likely to be infected with *I. tomentosus* (Lewis 1997) the effect of the cut may increase the probability of residual tree or regenerating tree contact with mycelium in an infected stump, and potentially, mortality rates and/or gap demography may be altered. Thus, it is

critical to understand the impacts of partial cutting on the incidence of *I. tomentosus* caused spruce mortality and its implications for stand structure.

1.7 Research Questions

This research addresses two main questions associated with small scale disturbances in old-growth and partially cut forests. First, does small-scale disturbance and forest dynamics differ between Inonotus tomentosus infected and uninfected forests? The answers to this question will enhance our understanding of how old-growth SBS forests developed to their present condition and may help predict future forest conditions. This information would aid resource managers in understanding how well old-growth forests will continue to provide the values for which they were preserved. Furthermore, this study will provide quantitative information necessary for forest managers to design partial cut systems that mimic old-growth dynamics and provide information on the longterm sustainability of small-scale forest dynamics in old-growth SBS forests. The second question is: Does partial cutting increase the incidence of I. tomentosus compared to uncut forests and if so, what implications does this have for differences in stand dynamics between infected and uninfected forests? This information could provide guidelines for partial cutting in *I. tomentosus* infected stands and predictions about future stand conditions where partial cutting is applied. Therefore, the objectives of this thesis are to quantify and compare fine and coarse spatial scale disturbance regimes and stand dynamics in *I. tomentosus* infected and non-infected stands for both partial cut and oldgrowth SBS forests.

These objectives are addressed in the following chapters. Chapter 2 describes the development of a methodology used to help recreate a fine-scaled disturbance chronology

for unmanaged and partially cut forests with and without *I. tomentosus*. This new method, called the Time Since Death model (TSD model) estimates when a tree died based on its state of decomposition.

Chapter 3 is a second methodology study developed to utilize tree ring growth rate patterns in canopy trees to determine the date a tree ascended to the canopy. Chapter 4 summarizes the gap-scale disturbance regime of wet SBS forests. This study combines the methodologies developed in Chapters 2 and 3 to recreate the disturbance dynamics occurring in four forest stand types (*I. tomentosus* infected, and uninfected old-growth forests and *I. tomentosus* infected and uninfected partial cut forests). Basic stand composition and attribute data are also sampled to compare these data across forest stand types. Chapter 5 summarizes the stand scale study. This study uses spatial autocorrelation analysis of tree ring data and species association to determine differences in the canopy level disturbance regime and canopy patch structure for *I. tomentosus* infected and uninfected old-growth forests using six 0.49 ha plots with 7 meter resolution. Chapter 6 integrates the results of the fixed radius plot and grid plot studies and draws conclusions regarding disturbance regimes, stand development, and implications for forest management.

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Forest	Mean Annual	Average	Average	Mean Annual	Percent
Zone	Temperature	Months	Months	Precipitation	Precipitation
	Range (°C)	Below 0 °C	Above 10	(mm)	as Snow
			°C		
				440 (415) –	
Sub-Boreal	1.7 – 5	4 - 5	2-5	900 (1650)	25 – 50
Spruce					
Research	09-49	N/A	N/A	682.4 -	380/
Forest	0.9 – 4.9	N/A	11/21	1315.3	5670
1 01 010					
Sub Boreal					
Pine-	0.3 - 2.7	4 – 5	1 – 3	335 - 580	30 - 50
Spruce					
	-2.0 - 2	5.7	2 /	330 570	35 55
Boreal	-2.7 - 2	5-1	2 - 4	550 - 570	55 - 55
	-2-2	5 – 7	2	400 - 2000	50 - 70
Sub-Alpine			_		

Table 1. Climatic comparisons for various sub-boreal, sub-alpine and boreal forests present in British Columbia. Numbers in parenthesis denote extremes taken from short term weather data. Derived from Meidinger and Pojar (1991) and Sagar 1993.



Figure 1. Location of Sub Boreal Spruce biogeoclimatic zone and the Aleza Lake Research Forest in central interior British Columbia (Government of British Columbia, Ministry of Environment Lands and Parks and Ministry of Forests 2001).



Figure 2. a) Cyclic model of succession, b) Convergent model of succession, c) Divergent model of succession, d) Parallel model of succession, e) Individualistic model of succession. Each arrowed line represents a disturbance and the state the stand reaches due to succession (comes from Frelich and Reich 1995)

CHAPTER 2. ESTIMATING TIME SINCE DEATH IN *PICEA GLAUCA* × ENGELMANNII AND ABIES LASIOCARPA IN A WET-COOL SUB-BOREAL SPRUCE FOREST

2.0 ABSTRACT

Age class analysis, direct gap measurements, and dendrochronology, are retrospective methods used to quantify disturbance regimes in forest ecosystems, but each method has limitations. This paper presents a new method that helps overcome some of the limitations current methods have in disturbance regime studies. The method is a set of multiple regression models that estimate the year of death for *Picea glauca* × *engelmannii* and *Abies lasiocarpa* from the tree characteristics: species, position (standing/down), decay class, proportion of decay, bark presence and integrity, primary branch presence and integrity, and fine branch presence and integrity.

The model was developed from a sample of 183 trees with known dates of death from 0-70 years before present (± 2.5 for periods 1926-1963, 1988-1998 and ± 12.5 yrs for period 1963-1988) determined from permanent sample plot data obtained from the Aleza Lake Research Forest, in east central British Columbia, in the wet-cool foothills of the Rocky Mountains. Four models were developed, two for each species based on their current position (standing or down). The *P. glauca* × *engelmannii* model explained 87.3% and 75.3%, and the *A. lasiocarpa* model explained 76.8% and 84.7% of the variation in years since death for standing and down trees, respectively. On an independent sample of dead trees (N = 48), time since death was estimated with the parameterized model. These values were compared to year of release determined from tree ring cores in understory trees that were subordinate to the modeled dead trees. The two estimates were strongly related (R²= 92.4%), indicating that model estimates provide

acceptable estimates for year of death in the two species. Other benefits the models provide are a quick (yet accurate) field approach for estimating year of death, and they can be used to determine year of death for small trees that fail to cause growth increases in understory trees and for trees that do not have subordinate individuals that release following overstory mortality.

In this study, *P. glauca x engelmannii* and *A. lasiocarpa* decayed at similar rates but these species were found to decay much faster than *Thuja plicata* in coastal rainforests and slower than *Abies* (spp.) and *Pinus* (spp.) in the Sierra Nevada. Climate, log size and species may be important sources of variation in these results.

2.1 INTRODUCTION

The study and quantification of small-scale disturbance regimes is difficult without extensive long-term documentation of the scale and timing of these disturbances as they occur. Due to the paucity of these real time assessments, a variety of retrospective techniques have been developed. One technique, the interpretation of static age-class distributions, is generally not appropriate in forests of complex age structure because different species of trees have different recruitment and mortality schedules. These differences can lead to misconceptions about the disturbance regime (Johnson *et al.* 1994). Therefore, tree ring analysis or direct gap measurements are often used to quantify the patterns of canopy level disturbance (Veblen 1986; Lorimer and Frelich 1988; Frelich and Lorimer 1991; Lertzman 1992; Veblen *et al.* 1994; Abrams *et al.* 1995; Frelich and Reich 1995; Kubota 1995; Yamamoto 1995; Cherubini *et al.* 1996; Kneeshaw and Bergeron 1998; Yong *et al.* 1998).

Tree ring analysis uses dramatic and sustained increased radial growth patterns, minimum growth rate thresholds that indicate gap-origin probability, and other interpretive patterns about incremental diameter growth to indicate the temporal and spatial patterns of tree mortality. These techniques are useful in describing small to largescale canopy level disturbances, but are limited to situations where canopy mortality causes an understory tree to increase markedly in growth rates. Since diameter growth is a more sensitive measure of stand competition than any other growth index (Assman 1970), these techniques are considered reliable, but they require extensive local calibration of growth rate criteria in order to assign a year of death to tree release criteria. Furthermore, these methods may not be applicable where large increases in understory resources might not accompany overstory tree death. The tall, narrow crowned boreal and

sub-boreal forests are one such example as are stands with low density such as might be found on water-logged or very dry sites.

For direct measures of gap size, the percent area of stand disturbance is calculated using geometric formulae. However, the resultant value must be restricted to recent gaps; about 30 years old (Veblen 1986; Lertzman 1992; Kubota 1995; Yamamoto 1995; Kneeshaw and Bergeron 1998; Yong *et al.* 1998). Another problem with applying this method are that the sampled gap-makers are usually restricted to canopy trees. Therefore, the percent gap area is underestimated because it does not include sub-canopy trees, which also contribute to gap dynamics. There also is limited ability to quantify temporal and spatial gap dynamics with this approach. Therefore, it is unknown if the rate of gap formation is constant, variable over time, randomly distributed, or has some underlying spatial pattern. Perhaps the main limitation with this approach, at least in subboreal forests, is that gaps are not single definable features of the canopy or any other layer. Therefore, it is nearly, if not entirely impossible to determine where one gap starts and another one ends.

Due to limitations of these current methodologies, a study was initiated to develop an alternative method for reconstructing stand dynamics. The method is based on estimating time since death from a tree's decomposition characteristics. To do this, decay characteristics of dead *Picea glauca* × *engelmannii* (Parry ex Engelm.) (hybrid spruce, hereafter referred to as spruce and *Abies lasiocarpa* (Hook.) Nutt. (sub-alpine fir, hereafter referred to as fir) trees of known dates of death were collected from permanent sample plots in central British Columbia. Then, multiple regression models using decay characteristics as predictor variables and time since death as the dependent variable were developed. Resultant Time Since Death models (TSD models) were then validated with

an independent data set where time since death was estimated by tree ring release of suppressed trees subordinate to dead canopy trees.

Specifically the objectives of this study are to:

- Construct a set of TSD models that accurately estimate the year of death for trees using variables that are easily measured in the field to indicate the degree of decomposition after death.
- 2. Assess the capabilities and limitations of the models.
- 3. Validate the models with independent samples of dead trees.
- 4. Compare the decay characteristics of spruce and fir, and species from other ecosystems.

2.2 METHODS

2.21 Study Area

To develop a multiple regression model that estimates the time since death for trees, a known and reliable date of death is needed. The date of death data was provided for trees from long-term growth and yield sample plots at the Aleza Lake Research Forest (ALRF) (British Columbia Ministry of Forests, Inventory Branch). The ALRF is located at 54° 07' N, 122° 04' W, about 60 kilometers east of Prince George, British Columbia, Canada. It lies between 600 and 750 meters above sea level on the Nechako plain of the Fraser River Basin in the Interior Plateau physiographic region (Holland 1976). The ALRF is located in a wet, cool type of the Sub-Boreal Spruce (SBS) biogeoclimatic zone, and is classified as the SBSwk1 according to a biogeoclimatic system in common usage in British Columbia (see Meidinger and Pojar, 1991, for details). The SBSwk1 climate is characterized by cold, snowy winters and moist, cool summers. The climate is slightly less continental than typical for more westward SBS areas due to the orographic influence of the Northern Rocky Mountains to the east, resulting in higher precipitation than usual for the rest of the zone (Meidinger and Pojar 1991).

2.22 General Approach

In 1928, a series of growth and yield plots were established at the ALRF and trees greater than 10 cm diameter were stem-mapped and tagged for future identification. Diameter, species, and height were measured on the trees in these plots beginning in 1928, and remeasured every 5 years until 1963. A shift in government policy prevented further remeasurements until 1988, with the most recent occurring in 1998. Observational data on the predictor variables were collected for model development on a sample of 192

trees with known dates of death determined from ALRF growth and yield records in six Experimental Plots (106, 107, 112, 148, 149, 150). These variables were chosen from a review of previous studies, which found relationships between certain components of tree morphology and decomposition rates (Henry and Swan 1974; Grier 1978; Graham and Cromack 1982; Sollins 1982; Raphael and Morrison 1987; Carpenter *et al.* 1988; Kelsey and Harmon 1989; Harmon *et al.* 1994; Daniels *et al.* 1997).

The final measurement of a tree in the permanent sample plot records at the ALFR indicates it died somewhere during the remeasurement interval, which is inferred to be the mid-point of the remeasurement interval. Therefore, there are records of when trees died \pm 2.5 years for the 5 year remeasurement intervals and \pm 12.5 years for the one interval between 1963 and 1988. Trees which died many years ago were difficult to locate. Old stem-maps and metal detectors were used to locate the metal tags that were used to identify trees in the permanent sample plots.

2.23 Explanatory Variables

Tree species: Studies have shown that species vary in decomposition rates and this variation is related to differences in phenol concentrations (Daniels *et al.* 1997), agents of mortality, and post-mortality decay organisms (Carpenter *et al.* 1988; Kelsey and Harmon 1989; Harmon *et al.* 1994). The dominant species at the ALRF are spruce and fir. All other species are uncommon in mature forests, usually representing less than 5% of stand composition. Therefore, data were collected only for spruce and fir. Previous studies (Daniels *et al.* 1997) indicated that modeling should be species specific, so models were developed independently for spruce and fir.

Tree position: Whether a tree remains standing or falls down after it dies and how long it has been in each position effects exposure to physical weathering and access to decay organisms, with downed trees decomposing faster (Carpenter *et al.* 1988). Trees were recorded as either standing (1) or down (2). It was not known how long the tree remained standing after it died because the permanent sample plot records have only recently included this attribute. Thus, only the current position of the tree was recorded and no attempt was made to project the length of time in each position.

Proportion of Decay: Trees rot from both the bark towards the pith and from the pith towards the bark depending on species and presence of decay organisms (Daniels *et al.* 1997). However, dead sapwood is generally less resistant to decay than the heartwood and trees do not generally decay from the outside, until they die (Kelsey and Harmon 1989). Therefore depth of decay on the outer bole is proportional to how long sapwood decay has been occurring. Using the methods of Daniels *et al.* (1997) the depth of decay from the bark towards the pith was recorded, using an axe to chop into the wood and a ruler to measure the depth to sound wood (cm). When the entire radius was decayed, it was recorded as half of the diameter of the tree. This was done at several points within the first two meters from the roots of the tree to develop an average depth of decay. Proportion of decay was calculated by dividing the average depth of decay by one-half of the tree's diameter. Depth of decay because this variable incorporates the difference in decay rate due to tree size.

Decay Class: Decay class is a qualitative, categorical index based on cumulative decomposition of the main bole. The density of the bole was estimated at several points within the first 10 meters from the roots of the tree as suggested by Daniels *et al.* (1997).

Decay Class (DC) I trees are solid with no decay in the sap or heartwood. DC II trees are solid but have some preliminary signs of decay. DC III trees are in stages of advanced decay but the wood still has structural integrity and can still support its own weight. DC IV trees are completely rotten, able to be kicked apart and cannot support their own weight. DC V trees are similar to DC IV trees in structure but are assimilated into the duff and have coniferous or deciduous vegetation well established and roots ramified throughout.

Primary Branches: Primary branches were assessed as two separate variables, branch presence and branch integrity. Branch presence had four categories: (1) all branches remaining; (2) partial branch remains; (3) only broken stubs and; (4) no primary branches. Branch integrity had 3 categories: (1) branches cannot be moved in the knot; (2) branches are loose in the knot; and (3) no primary branches.

Fine Branches and Needles: Fine branches were also assessed as two variables: fine branch presence and fine branch integrity. Fine branch presence had three categories: (1) trees with 75-100% of original branches; (2) trees with 1-75%; and (3) no fine branches remaining. Fine branch flexibility had three categories (1) pliable, (2) brittle, or (3) none. Needle abundance had the same categories as fine branch presence.

Bark: Bark is also important for estimating recent mortality (Raphael and Morrison 1987). Bark was assessed as two variables: Bark integrity: (1) tight, (2) variable, (3) loose and (4) missing; and bark presence (1) present, (2) variable, and (3) missing).

2.24 Analysis and Modeling

Years since death and proportion of decay were treated as continuous variables. Tree species was treated as nominal and the remaining variables were treated as ordinal. For the two continuous variables, a Shapiro-Wilk W test was used to test for normality. The nominal and ordinal variables were assessed for normality using a Chi-square likelihood ratio test based on hypothesized probabilities totaling one with equal probability distributed across the categories. The distributions for the variables were nonnormal. Due to the large sample size: N = 69 for spruce and, N = 114 for fir, and because regression is robust to non-normality, parametric methods were used (Lewis – Beck 1980).

Outliers were examined by assessing residual plots of each independent variable against the predicted values of years since death and with normal quantile plots of the studentized residuals. Leverage values were calculated to determine overly influential data points. Nine trees out of 192 total trees were omitted from the analysis due to large residuals (1.5 * interquartile range), which are likely due to a measurement error or errors in the ALRF data set.

A number of variables included in the analysis had significant heteroscedasticity (unequal variance in error terms). For both models, heteroscedastic error terms were indicated by the Brown-Forsythe test (Fox 1991). For spruce, bark class, and bark integrity had significant heteroscedasticity. For fir, density, branch integrity, and bark integrity had significant heteroscedasticity ($\alpha = 0.05$). For heteroscedastic variables, attempts were made to improve the condition by creating new variable categories. None of these attempts decreased heteroscedasticity that was due to high variation in the final category relative to preceding categories, since the final category is applicable to infinite

times since death. However, including variables with heteroscedastic error terms is justified since the goal was not to develop a parsimonious model but to develop a robust model for predicting time since death. Eliminating variables with not statistically significant partial slopes (resulting from the heteroscedasticity) or conducting best subsets regression was not done because all explanatory variables are required to avoid specification error and maximize the coefficient of multiple determination. For example, eliminating all the variables in the down spruce model with not statistically significant partial slope coefficients would lower the R² from 0.753 to 0.680. An R² difference test comparing the two R² values indicates this is a significant (p>0.05) loss in explanatory power.

The variables were initially screened using bivariate regressions and correlation matrices, to examine linearity and multicollinearity. Needle presence, fine branch presence, and primary branch presence were eliminated from analysis due to very poor correlation ($R^2 < 0.05$) with years since death and high collinearity between them.

Interactions between the position of the tree and the remaining explanatory variables were tested. These analyses were performed by plotting each variable for each position and comparing the slopes using standard procedures (Fox 1991). Significant interactions were found and justified the splitting of each species into a positional model (standing and down).

Ordinary least squares regression was then used to develop each model. The models were then externally validated by estimating time since death on an independent sample (dates of death unknown) of previously dominant or co-dominant dead trees (n = 48, 27 spruce, 21 fir). The decomposition variables were collected and increment cores were taken from one nearby understory tree for each dead tree. Estimated dates of death

from the TSD model were regressed on dates of understory tree release (for trees releasing at least 50%) determined from the increment cores using ordinary least squares regression.

2.3 RESULTS

For both species, all variables had a significant linear relationship to years since death (Table 1) as determined by bivariate linear regression analysis. It appeared that proportion of decay had a non-linear relationship with years since death, however, no transformation improved the R^2 value. Therefore these data were considered to be best described by a linear model. For both species, years since death was most strongly related to decay class (Table 1). Since position is a binomial category, linearity cannot be evaluated, however, for both species the trend indicates that downed logs are older than standing logs.

A correlation matrix (Table 2) shows relationships among the independent variables. For both species, decay class is highly correlated with proportion of decay and bark class is highly correlated with bark integrity. This is because each pair of variables is measuring similar attributes: the degree of decomposition on a tree's main bole and the bark retention on the tree, respectively.

To determine the degree of influence multicollinearity had on the models, variable inflation factor analysis was conducted. Variable inflation factors (VIF) are equal to $1/(1-R^2)$, where the R^2 is equal to the coefficient of determination for one explanatory variable regressed against the other explanatory variables. The higher the regression coefficients between some set of explanatory variables, the higher the VIF (StatSoft 1997). Thus, a high VIF (>9) indicates that collinearity is strongly affecting the precision of estimation (Fox 1991). For both spruce and fir, no VIF exceeds 9 for all possible combinations, therefore the multicollinearity is not extreme (StatSoft 1997) which justified keeping highly correlated predictor variables in the model.

Interactions between position and all the remaining explanatory variables were assessed independently for each species by plotting each predictor variable against years since death at the two levels of position. For spruce (p = 0.009) and fir (p = 0.047) a significant interaction between position and decay class was found indicating that for both species, decomposition rates of the main bole are faster in down trees. These interactions were justified by separating each species model into two models based on position.

Thus four models, ((2) species × (2) position) were generated, each using the following predictor variables: decay class, branch integrity, fine branch flexibility, bark class, bark integrity, and proportion of decay. The mixed model for each species (Table 3a and 3b; Figures 1 and 2) indicates that the explanatory variables explain a significant proportion of the variation in years since death, and range from a low of $R^2 = 75.30\%$ for the down spruce model to a high of $R^2 = 87.30\%$ for the standing spruce model.

2.31 Model Validation:

Using an independent sample, the year of death for 48 dead trees (27 spruce and 21 fir) was estimated with one of the four TSD models and then death dates were compared to year of tree ring release measured on near by understory trees with ordinary least squares regression (Figure 3). The two estimates of tree mortality were very close $(R^2 = 92.4\%)$. Note the regression line does not intersect the x and y axis in a perfect 1:1 relationship. For older mortality the regression line falls slightly above the x-y intersections and slightly below for recent mortality. This is likely because of continual increasing variance in the TSD model estimate with increasing values of the tree ring estimate as seen in the data (Figure 3).

2.4 DISCUSSION

The TSD models developed from dead tree characteristics accurately predicted time since death for spruce and fir in the wet SBS forests of central interior British Columbia. The results suggest that the TSD models can be used to estimate the year of death for spruce and fir with a minimum diameter of 10 cm DBH up to about 70 years since death. These estimates can be applied towards describing disturbance history in the SBSwk1 forests around Aleza Lake.

The relative importance of the explanatory variables can be attributed to their "longevity of measurability". For instance, fine branches fall off the tree quickly following mortality. Thus, they are irrelevant in predicting mortality beyond the time they disappear yet, to remove them from the model would eliminate the most sensitive variables in estimating recent mortality. This suggests that variables which are sensitive to recent mortality as well as older mortality are most useful in terms of their predictive capability. With respect to the variables examined here, decay class, bark integrity, bark class and proportion of decay would be the most widely useful predictors of years since death because they blend the ability to be sensitive to recent as well as past mortality.

The heteroscedasticity present in these variables is caused by larger variance in the last category of each variable relative to the preceding categories. For example, the condition of no bark class had the widest variation relative to intact, variable and notintact bark class. This is because once the condition of no bark is reached the tree is always described as a tree with no bark and therefore, a large variation in time since death arises. The same arguments could also be made for the all the other variables. This is a limitation in the measurement of these variables that cannot be adequately addressed due to the finite nature of the variables.

Due to the range in years since death encountered in this study, as well as the increasing variance in the error term (heteroscedasticity) in the explanatory variables, this model must be restricted to estimating death to about 70 years before present, which was the approximate range in years since death encountered at the Aleza Lake Research Forest. However even if the records at the ALRF did go back 100 years (or more), none of the current predictor variables would be reliable for estimation since they all will experience severe heteroscedasticity with increasing time since death. Radiocarbon dating, bulk density and nutrient flux functions like those used by Grier (1978), Graham and Cromack (1982), and Sollins (1982), could be used to extend the estimate.

This study's findings coincide with a few studies which have also examined morphological characteristics of decay and their relationship to years since death. It was found that about 97% of the trees sampled in the present study lose 99% of the fine branches and needles after 12 years. In the Sierra Nevada, Raphael and Morrison (1987) reported *Abies* (spp.) and *Pinus* (spp.) lose all needles and fine branches after 5 years. Graham and Cromack (1982) reported strong correlations between year of death and decay rate using a similar classification as the decay class variable in the present study for *Picea sitchensis* (R^2 = 0.421) and *Tsuga heterophylla* (R^2 = 0.227) in Olympic National Park in Washington, USA. The present study showed a similar strong correlation for spruce (R^2 = 0.581) and fir (R^2 = 0.690) (Table 1) for the qualitative measure of decay class.

This study's classification of decay class also corresponds to the decay class system of Daniels *et al.* (1997). The present study's results show both fir and spruce decay much quicker than *Thuja plicata* studied by Daniels *et al.* (1997) (Table 4). Both the larger tree size of coastal Thuja plicata, the cold, relatively dry climate of the sub-

boreal forest relative to coastal ecosystems and the acknowledged resistance of *Thuja plicata* to decay are likely responsible for these large discrepancies. For the present study it was noted that spruce seems to decay faster than fir (Table 4). The documented negative correlation for decay rate and tree size (Harmon *et al.* 1986) combined with the fact that larger snags usually stand longer than small snags (Raphael and Morrison 1987) suggests that fir should decay faster than spruce because spruce is generally a larger tree in this system and therefore should remain standing longer. Furthermore, published information about resistance to decay places both *Picea spp.* and *Abies spp.* as species with low resistance to decay. Therefore, it seems plausible that the faster decay rate of spruce could be attributed to different types of decay fungi rather than differences in the extractives found in the wood itself.

2.5 CONCLUSIONS

By accurately estimating the year of death for trees, the TSD models can be used as tools to quantify the date of tree mortality in forest stands. These data can then be used in disturbance studies to quantify spatiotemporal patterns of disturbance in wet-cool, SBSwk1 forests. Given the limitations of the range of estimation, disturbance studies in wet sub-boreal forests using this method alone should be restricted to 70 years before present. Although this period will not span the time since stand establishment in old forests, it can provide fine detail on disturbance dynamics over a short time and be used in forests where other methodologies are relatively ineffective. Combined with indirect techniques like those developed by Lorimer and Frelich (1989), Frelich and Lorimer (1991), Frelich and Graumlich (1994), Abrams *et al.* (1995), Frelich and Reich (1995), and Cherubini (1996), the TSD results can be used to quantify medium and fine-scaled disturbances and their interactions.

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2.7 APPENDIX

Data are presented here to provide the reader with the primary data collected from the

dead trees in the permanent sample plots. See section 2.2 METHODS for description of

categories.

Piot Tree Image of Branch Branch<	E.P.	Dead	Species	Position	Density	Depth	Primary	Primary	Fine	Fine	Bark	Bark	Year
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	Plot	Tree				of	Branch	Branch	Branch	Branch	Presence	Integrity	of
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	Number	Cumuna		5	Decay	Integrity	A	2	Presence	2	1	Death
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	2	Spruce	Down	5	14	3	4	2	2	2	4	1945
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	4		Down	1	0	 _1	2	3	3	2	4 2	1932
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	261	Fir	Down	2	10	1	2	2	3	3	2	1977
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	100	14	Spruce	Down	2	0.25	2	3	3	3	3	4	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	100	18	Fir	Down	4	8.25	2	3	3	3	3	4	1932
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	100	22	Spruce	Down	5	15	3	3	3	3	3	4	1932
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	100	25	Fir	Down	4	11	3	4	3	3	3	4	1932
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	100	26	Spruce	Down	4	12.05	3	4	3	3	3	4	1950
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	32	Spruce	Down	2	10	2	3	3	3	3	2	1960
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	268	Fir	Down	2	1.5	2	3	3	3	3	1	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	70	Spruce	Down	3	5.5	2	3	3	3	3	4	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	498	Fir	Standing	1	0	2	1	2	3	1	1	1995
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	72	Spruce	Down	3	13.8	1	4	3	1	3	4	1955
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	71	Spruce	Down	3	16	3	3	3	3	3	4	1950
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	497	Fir	Down	1	0	2	1	2	3	1	1	1995
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	76	Spruce	Down	2	1	1	3	3	1	3	4	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	474	Fir	Standing	1	0	2	1	1	3	1	1	1995
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	84	Spruce	Standing	1	0	1	1	2	2	1	1	1995
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	48	Fir	Down	3	15	1	3	3	1	3	4	1945
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	92	Spruce	Down	3	12.5	2	3	3	3	3	4	1977
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	106	99	Spruce	Down	2	9	1	3	3	3	3	4	1955
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	422	Fir	Standing	1	0	1	1	1	3	1	1	1995
$\begin{array}{ c c c c c c c c c c c c c c c c c c c$	106	423	Fir	Standing	1	0	1	1	1	3	1	1	1995
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	34	Spruce	Standing	1	0	1	1	2	3	1	1	1995
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	30	Fir	Standing	2	1	1	2	3	2	2	2	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	29	Spruce	Standing	2	24	1	4	3	3	2	2	1977
106 246 Spruce Standing 1 0 1 2 3 3 2 3 1977 106 278 Spruce Down 2 1 1 2 3 3 2 3 1990 106 45 Fir Down 2 1 1 2 3 3 2 3 1990 106 45 Fir Down 2 1 1 2 3 3 2 3 1977 106 88 Spruce Down 1 1 1 2 3 3 2 3 1990 106 288 Spruce Down 2 5 1 4 3 3 2 2 1977 106 255 Fir Standing 1 1 3 4 1955 106 79 Fir Down 3 12 2	106	409	Fir	Standing	1	0	3	1	1	3	1	1	1995
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	246	Spruce	Standing	1	0	1	2	3	3	2	3	1977
106 45 Fir Down 2 1 1 2 3 3 2 3 1977 106 88 Spruce Down 1 1 1 2 3 3 2 3 1990 106 288 Spruce Down 2 5 1 4 3 3 2 3 1990 106 288 Spruce Down 2 5 1 4 3 3 2 3 1990 106 255 Fir Standing 1 1 3 4 3 3 2 2 1977 106 65 Fir Down 3 12 2 3 3 3 3 4 1955 106 79 Fir Down 3 12 2 3 1 1 1995 106 5 Spruce Down 3 <td< td=""><td>106</td><td>278</td><td>Spruce</td><td>Down</td><td>2</td><td>1</td><td>1</td><td>2</td><td>3</td><td>3</td><td>2</td><td>3</td><td>1990</td></td<>	106	278	Spruce	Down	2	1	1	2	3	3	2	3	1990
106 88 Spruce Down 1 1 1 1 2 3 3 2 3 1990 106 288 Spruce Down 2 5 1 4 3 3 3 4 1977 106 255 Fir Standing 1 1 3 4 3 3 2 2 1977 106 255 Fir Standing 1 1 3 4 3 3 2 2 1977 106 65 Fir Down 3 2 3 3 3 3 4 1955 106 79 Fir Down 3 12 2 3 3 3 3 4 1950 106 15 Spruce Standing 1 0 2 1 2 3 1 1 1995 106 1 Spruce	106	45	Fir	Down	2	1	1	2	3	3	2	3	1977
106 288 Spruce Down 2 5 1 4 3 3 3 4 1977 106 255 Fir Standing 1 1 3 4 3 3 2 2 1977 106 65 Fir Down 3 2 3 3 3 3 4 1955 106 65 Fir Down 3 2 3 3 3 3 4 1955 106 79 Fir Down 3 12 2 3 3 3 3 4 1955 106 15 Spruce Standing 1 0 2 1 2 3 1 1 1995 106 5 Spruce Down 3 25 1 4 3 3 3 4 1977 106 12 Spruce Standing 1	106	88	Spruce	Down	1	1	1	2	3	3	2	3	1990
106 255 Fir Standing 1 1 3 4 3 3 2 2 1977 106 65 Fir Down 3 2 3 3 3 3 3 4 1955 106 65 Fir Down 3 12 2 3 3 3 3 4 1955 106 79 Fir Down 3 12 2 3 3 3 3 4 1955 106 15 Spruce Standing 1 0 2 1 2 3 1 1 1995 106 5 Spruce Down 3 25 1 4 3 3 3 4 1977 106 1 Spruce Standing 1 0 3 2 2 1 1 1995 106 12 Spruce Standing	106	288	Spruce	Down	2	5	1	4	3	3	3	4	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	255	Fir	Standing	1	1	3	4	3	3	2	2	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	65	Fir	Down	3	2	3	3	3	3	3	4	1955
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	79	Fir	Down	3	12	2	3	3	3	3	4	1950
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	15	Spruce	Standing	1	0	2	1	2	3	1	1	1995
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	5	Spruce	Down	3	25	1	4	3	3	3	4	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	1	Spruce	Standing	1	0	1	2	2	1	1	1	1995
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	12	Spruce	Standing	1	0	3	2	2	3	1	3	1990
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	20	Spruce	Down	2	2	1	4	3	3	3	4	1960
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	20	Spruce	Down	3	$\frac{1}{2}$	1	3	3	3	3	2	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	106	23	Fir	Down	1	0	3	1 1	1	3	2	2	1977
	106	46	Snruce	Standing	$\frac{1}{1}$	ŏ	3	$\frac{1}{1}$	2	3	1	1	1905

$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	420	Fir	Standing	1	0	1	1	2	3	1	1	1995
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	51	Fir	Down	2	1	1	4	3	1	3	2	1977
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	423	Fir	Down	1	0	1	1	1	1	1	1	1995
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	59	Spruce	Down	2	1	1	3	3	3	2	2	1977
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	63	Fir	Down	2	2	3	4	3	3	3	4	1960
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	60	Spruce	Standing	1	0	1	1	2	3	1	1	1990
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	306	Spruce	Standing	1	0	1	1	3	3	3	1	1977
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	61	Spruce	Down	1	0	3	2	3	3	3	2	1977
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	73	Spruce	Down	2	1	1	2	3	2	2	2	1977
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	106	73	Fir	Down	2	2	1	2	3	3	2	2	1955
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	112	422	Fir	Down	2	1	1	3	3	3	3	4	1977
112 18 Sprue Standing 1 0 2 1 3 3 3 3 1927 112 22 Sprue Standing 2 1 1 3 3 3 3 4 1955 112 30 Fir Down 4 25.9 1 3 3 3 3 4 1955 112 430 Fir Down 1 0 2 3 3 3 3 4 1977 112 430 Fir Down 5 4.7 2 4 3 3 3 4 1955 112 45 Spruce Down 3 3.5 3 3 3 3 4 1955 112 45 Spruce Down 5 6 1 4 3 3 3 3 3 3 2 1977 112 <t< td=""><td>112</td><td>7</td><td>Fir</td><td>Down</td><td>3</td><td>17</td><td>1</td><td>3</td><td>3</td><td>3</td><td>3</td><td>4</td><td>1950</td></t<>	112	7	Fir	Down	3	17	1	3	3	3	3	4	1950
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	112	19	<u>FII</u>	Standing	1	0	2	1	3	3	3	3	1077
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	112	10	Spruce	Standing	2	1	1	2	3	3	3	<u>л</u>	1977
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	112	22	Spruce	Standing		25.0	1	2	2	3	2	4	1935
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	112	30	<u>FIF</u>	Down	2	15		J	2	2	2	ч 	1955
112 131 177 Down 1 0 2 3 3 3 3 2 197 112 131 Spruce Down 5 4.7 2 4 3 3 3 4 1935 112 46 Fir Down 3 3.5 3 3 3 3 3 4 1935 112 46 Spruce Down 5 6 1 4 3 2 3 4 1935 112 45 Spruce Down 5 6 1 4 3 2 3 4 1945 112 50 Spruce Down 3 26 3 3 3 3 3 3 4 1977 112 51 Spruce Down 3 26 3 3 3 3 3 2 1960 112 55 Spruce Standing 1 1 2 3 3 3 3 4 <td< td=""><td>112</td><td>48</td><td>Spruce</td><td>Down</td><td><u> </u></td><td>13</td><td>1</td><td>2</td><td>2</td><td>3</td><td>3</td><td>2</td><td>1977</td></td<>	112	48	Spruce	Down	<u> </u>	13	1	2	2	3	3	2	1977
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	112	430	Fir	Down	1	0		3	3	2	5	2	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	131	Spruce	Down	2	1			2	3		2	1990
112 46 Fir Down 3 3.5 3 3 3 3 3 4 1977 112 50 Spruce Down 5 6 1 4 3 3 3 4 1976 112 50 Spruce Down 5 6 1 4 3 2 3 4 1977 112 55 Spruce Down 3 15 2 3 3 3 3 4 1977 112 51 Spruce Down 3 26 3 3 3 3 3 4 1977 112 56 Fir Standing 1 1 2 3 1 3 1 3 1077 112 36 Fir Standing 1 1 2 3 3 3 4 1977 112 36 Fir Standing 2 1 2 2 3 3 2 1970 112	112	95	Spruce	Down	3	4./	2	4	3	3	3	4	1935
112 45 Spruce Down 4 11 1 4 3 3 3 4 1950 112 50 Spruce Down 5 6 1 4 3 2 3 3 3 2 1977 112 55 Spruce Down 3 15 2 3 3 3 3 4 1977 112 56 Fir Standing 2 1.5 3 3 3 3 3 4 1977 112 60 Fir Standing 2 0 2 3 1 3 1 3 1960 112 60 Fir Standing 2 1 2 3 1 3 3 4 1977 112 412 Fir Standing 2 1 2 3 3 3 4 1977 112 43 Spruce Down 2 1 2 2 3 3 2 1977	112	46	Fir	Down	3	3.5	3	3	3	3	3	4	1977
112 50 Spruce Down 5 6 1 4 3 2 3 4 1947 112 55 Spruce Down 3 15 2 3 3 3 2 1977 112 51 Spruce Down 3 15 2 3 3 3 3 4 1977 112 56 Fir Standing 2 1.5 3 3 3 3 2 1960 112 60 Fir Standing 1 1 2 3 1 3 1 3 1977 112 36 Fir Down 2 5 2 3 1 3 3 4 1977 112 36 Fir Down 2 4 1 1 1 3 3 2 1990 112 412 Fir Standing 3 4 2 2 3 3 2 2 1977 112	112	45	Spruce	Down	4			4	3	3	3	4	1950
112 55 Spruce Standing 2 2.5 3 2 3 3 3 2 1977 112 44 Spruce Down 3 15 2 3 3 3 3 4 1977 112 51 Spruce Down 3 26 3 3 3 3 3 4 1977 112 56 Fir Standing 2 1.5 3 3 3 3 3 2 1960 112 60 Fir Standing 1 1 2 3 1 3 1 3 1977 112 46 Fir Down 2 5 2 3 1 3 3 2 1977 112 412 Fir Standing 3 4 2 2 3 3 3 2 1977 112 59 Fir Standing 1 0 1 3 3 3 2 2 1977		50	Spruce	Down	5	6		4	3	2	3	4	1945
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	55	Spruce	Standing	2	2.5	3	2	3	3	3	2	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	44	Spruce	Down	3	15	2	3	3	3	3	4	1977
112 56 Fir Standing 2 1.5 3	112	51	Spruce	Down	3	26	3	3	3	3	3	4	1977
112 60 Fir Standing 1 1 2 3 3 3 3 2 1960 112 15 Spruce Standing 1 1 2 3 1 3 1 3 1 3 1 3 1 3 1 177 112 36 Fir Down 2 5 2 3 1 3 3 4 1977 112 412 Fir Standing 2 1 2 2 3 3 3 4 1977 112 92 Spruce Down 2 2 1 2 2 3 3 2 1977 112 59 Fir Standing 1 0 1 3 3 3 2 2 1977 112 35 Spruce Standing 1 0 2 1 2 3 1 1 1977 112 379 Spruce Standing 1 0	112	56	Fir	Standing	2	1.5	3	3	3	3	3	2	1960
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	60	Fir	Standing	2	0	2	3	3	3	3	2	1960
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	15	Spruce	Standing	1	1	2	3	1	3	1	3	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	36	Fir	Down	2	5	2	3	1	3	3	4	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	412	Fir	Standing	2	1	2	2	3	3	3	4	1977
112 433 Spruce Down 2 2 1 2 2 3 3 2 1977 112 59 Fir Standing 3 4 2 2 3 3 3 4 1977 112 381 Fir Standing 1 0 1 3 3 2 2 1977 112 55 Spruce Down 2 3 1 2 3 3 2 2 1977 112 57 Spruce Standing 1 0 2 1 2 3 1 1 1990 112 62 Fir Standing 1 0 1 3 1 3 1 1 1990 112 384 Spruce Standing 1 0 1 2 3 1 1 1977 112 399 Spruce Standing 1 0 1 2 1 1 1990 107 1	112	92	Spruce	Down	2	4	1	1	1	3	3	2	1990
11259FirStanding342233341977112381FirStanding10133322197711255SpruceDown231233221977112379SpruceStanding10212311199011262FirStanding313333221977112384SpruceStanding101313111977112384SpruceStanding10231311197711267SpruceStanding10121211199711267SpruceStanding1012121119901071FirStanding10112331199010727FirStanding10112331199010728SpruceStanding10112331199010720FirStanding101233321971107 <td>112</td> <td>433</td> <td>Spruce</td> <td>Down</td> <td>2</td> <td>2</td> <td>1</td> <td>2</td> <td>2</td> <td>3</td> <td>3</td> <td>2</td> <td>1977</td>	112	433	Spruce	Down	2	2	1	2	2	3	3	2	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	59	Fir	Standing	3	4	2	2	3	3	3	4	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	381	Fir	Standing	1	0	1	3	3	3	2	2	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	55	Spruce	Down	2	3	1	2	3	3	2	2	1977
11262FirStanding313333221977112384SpruceStanding101313111977112399SpruceStanding10231311197711267SpruceDown1012121119901071FirStanding1012121119901071FirStanding10123311199010727FirStanding10112331199010728SpruceStanding10112331199010729SpruceStanding10111211199010710FirStanding10111211199010710FirStanding213133332197110720FirStanding101231119841072FirDown1012231119841072Fir	112	379	Spruce	Standing	1	0	2	1	2	3	1	1	1990
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	62	Fir	Standing	3	1	3	3	3	3	2	2	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	384	Spruce	Standing	1	0	1	3	1	3	1	1	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	399	Spruce	Standing	1	0	2	3	1	3	1	1	1977
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	112	67	Spruce	Down	1	0	1	2	1	2	1	1	1990
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	107	1	Fir	Standing	1	0	1	1	1	3	1	1	1995
10728SpruceStanding10112331199010729SpruceStanding10112331199010710FirStanding101112331199010710FirStanding1011112111199010719SpruceStanding10123111199010720FirStanding213133332197110721SpruceStanding10123223197110722FirDown1012231119841072FirDown33.513323419401078FirDown21.5133332195510710FirStanding10222312197110713FirStanding10122211197110716SpruceStanding3252333334193	107	27	Fir	Standing	1	0	1	2	3	3	1	1	1984
107 29 Spruce Standing 1 0 1 1 2 3 3 1 1990 107 10 Fir Standing 1 0 1 1 1 2 3 3 1 1990 107 10 Fir Standing 1 0 1 2 3 1 1 1 1990 107 19 Spruce Standing 1 0 1 2 3 1 1 1 1990 107 20 Fir Standing 2 13 1 3 3 3 3 2 1971 107 20 Fir Standing 1 0 1 2 3 2 2 3 1971 107 21 Spruce Standing 1 0 1 2 2 3 1 1984 107 2 Fir <td>107</td> <td>28</td> <td>Spruce</td> <td>Standing</td> <td>1</td> <td>0</td> <td>1</td> <td>1</td> <td>2</td> <td>3</td> <td>3</td> <td>1</td> <td>1990</td>	107	28	Spruce	Standing	1	0	1	1	2	3	3	1	1990
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	107	29	Spruce	Standing	1	0	1	1	2	3	3	1	1990
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	107	10	Fir	Standing	1	0	1	1	1	2	1	1	1990
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	107	19	Spruce	Standing	1	0	1	2	3	1	1	1	1990
$\begin{array}{c c c c c c c c c c c c c c c c c c c $	107	20	Fir	Standing	2	13	1	3	3	3	3	2	1971
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	107	21	Spruce	Standing	1	0	1	2	3	2	2	3	1971
$\begin{array}{c ccccccccccccccccccccccccccccccccccc$	107	22	Fir	Down	1	0	1	2	2	3	1	1	1984
107 8 Fir Down 2 1.5 1 3 3 3 3 2 1955 107 10 Fir Standing 1 0 2 2 2 3 1 2 1971 107 11 Fir Standing 2 1 1 2 3 3 1 2 1971 107 11 Fir Standing 2 1 1 2 3 3 1 3 1960 107 13 Fir Standing 1 0 1 2 2 2 1 1 1971 107 16 Spruce Standing 3 25 2 3 3 3 3 4 1930	107	2	Fir	Down	3	3.5	1	3	3	2	3	4	1940
107 10 Fir Standing 1 0 2 2 2 3 1 2 1971 107 11 Fir Standing 2 1 1 2 3 1 3 1960 107 13 Fir Standing 1 0 1 2 2 2 1 1 1971 107 16 Spruce Standing 3 25 2 3 3 3 3 4 1930	107	8	Fir	Down	2	1.5	1	3	3	3	3	2	1955
107 11 Fir Standing 2 1 1 2 3 3 1 3 1960 107 13 Fir Standing 1 0 1 2 2 2 1 1 1971 107 16 Spruce Standing 3 25 2 3 3 3 3 4 1930	107	10	Fir	Standing	1	0	2	2	2	3	1	2	1971
107 13 Fir Standing 1 0 1 2 2 2 1 1 1971 107 16 Spruce Standing 3 25 2 3 3 3 3 4 1930	107	11	Fir	Standing	2	1	1	2	3	3	1	3	1960
107 16 Spruce Standing 3 25 2 3 3 3 3 4 1930	107	13	Fir	Standing	1	0	1	2	2	2	1	1	1971
	107	16	Spruce	Standing	3	25	2	3	3	3	3	4	1930

107				2	22	1	4	2	2	2	1	1020
107	15	Fir	Down	2	23	1	4	3	3	3	4	1930
107	273	Fir	Down	1	0	1		1	3	1		1995
107	107	Spruce	Standing	1	0	2	1	2	3	1	1	1995
107	288	Fir	Standing	<u> </u>	0	1	1	2	3	1	1	1990
107	549	Fir	Standing	1	0	1	2	2	3	2	1	1995
107	81	Fir	Standing	5	6	2	4	3	3	3	4	1930
107	18	Fir	Standing	3	10	3	3	3	3	3	2	1971
107	536	Spruce	Standing	1	0	1	2	2	1	3	1	1995
107	22	Fir	Standing	2	1	1	3	2	3	1	2	1990
107	23	Fir	Down	2	1	1	4	3	3	3	4	1971
107	326	Spruce	Standing	1	0	1	2	3	3	3	4	1971
107	323	Fir	Down	1	0	3	3	3	3	3	2	1971
107	286	Fir	Standing	1	0	1	1	2	3	1	1	1990
107	200	Fir	Down	5	14	2	4	3	3	3	4	1930
107	20	Fir	Down	5	17	1	4	3	3	3	4	1030
107	21	FH Ein	Down	3	12	2		3	3	3		1020
107	31		Down	5	12		4	2	2	2		1930
107	32	Fir	Down	3	23		4	3	3	3	4	1930
107	293	Spruce	Standing	1	0		2	2	3		1	19/1
107	45	Fir	Down	5	16		4	3	3	3	4	1930
107	42	Fir	Down	5	13	3	4	3	3	3	4	1935
150	2	Fir	Standing	1	0	3	1	1	3	3	3	1990
150	340	Fir	Standing	2	1	2	1	1	1	3	2	1984
150	9	Fir	Down	2	1	3	3	3	3	3	2	1977
150	19	Fir	Down	1	0	3	3	3	3	1	1	1977
150	21	Fir	Down	1	0	1	3	3	3	3	2	1977
150	15	Fir	Standing	1	0	3	2	3	3	1	1	1977
150	22	Fir	Standing	1	0	3	1	1	3	1	1	1995
150	27	Fir	Down	3	11	1	4	3	1	3	4	1936
150	28	Fir	Down	4	10	1	4	3	2	3	4	1936
150	45	Spruce	Standing	1	0	1	2	2	3	1	1	1984
150	45	Fir	Standing	2	2	1	2	2	3	1	2	1000
150	40	FII Ein	Standing	1	1	1	2	2	3	1	1	1990
150	51	<u>[[]</u>	Standing	2	2	1	2	2	2	2	2	1990
150	08	Spruce	Down	2	2		2	3		3	2	1984
150	70	Spruce	Down	2	$\frac{2}{2}$	1	2	2	1		2	1960
150	73	Fir	Down	2	2	3	2	2	3		2	1977
150	75	Fir	Down	2	2	3	3	3	3		2	1984
150	82	Fir	Down	<u> </u>	0	<u> </u>	<u> </u>	2	3			1977
150	88	Fir	Down	1	0			2	3	3	2	1990
150	87	Spruce	Standing		0	1	1	2	3	1		1984
150	95	Fir	Standing	1	0	1	1	2	1	1	1	1990
150	106	Spruce	Standing	1	0	1	1	2	3	1	1	1990
150	345	Fir	Standing	1	0	2	1	1	2	1	1	1995
150	312	Fir	Down	1	0	2	1	1	3	3	2	1995
150	331	Fir	Down	1	0	1	3	1	3	3	4	1977
150	116	Fir	Standing	2	1.5	1	1	1	3	1	1	1995
150	119	Fir	Down	1	0	1	2	3	2	3	2	1990
150	118	Fir	Down	1	0	1	2	1	3	3	2	1995
150	120	Fir	Down	1	0	1	2	1	3	1	2	1990
150	122	Fir	Down	1	0	3	2	3	3	1	1	1990
150	125	Spruce	Down	5	17	1	3	3	3	3	4	1950
150	125	Fir	Standing		10	† .	1	$\frac{1}{2}$	3	1	$\frac{1}{1}$	1005
150	124	<u> </u>	Standing			1	$\frac{1}{1}$	2	2	<u> </u>	†;	1005
150	1.04	<u> </u>	Dame	1			2	1	2	1	12	1000
150	132		Down			1	2	12	1	1	12	1990
150	328	Fir	Down			1	2	2			13	19//
130	133	Fir	Down	2	2.5	<u> </u>	2	12	3	13	12	1984

150	137	Fir	Down	1	0	1	2	3	3	1	1	1977
150	138	Fir	Down	1	0	1	2	3	3	1	1	1984
150	140	Fir	Standing	2	1	1	3	3	3	3	3	1977
150	145	Spruce	Down	2	1	2	3	3	3	3	3	1960
150	147	Fir	Down	2	0	1	3	3	2	3	3	1955
150	149	Fir	Down	2	1.5	1	3	3	1	3	4	1960
149	153	Fir	Standing	2	0	1	1	1	3	3	1	1995
149	195	Spruce	Down	1	0	1	3	2	3	3	4	1971
149	169	Fir	Down	2	1	1	3	2	3	3	2	1960
149	198	Fir	Standing	1	0	1	2	2	3	3	2	1971
149	285	Fir	Standing	2	1.5	1	3	2	3	3	2	1984
149	255	Fir	Down	2	1	1	2	2	3	3	2	1984
149	316	Fir	Standing	1	0	1	1	1	3	1	1	1990
149	318	Fir	Down	3	8	1	3	2	3	3	4	1971
149	409	Fir	Standing	1	0	2	2	2	3	3	2	1984
149	385	Spruce	Standing	1	0	1	1	2	2	1	2	1971
149	28	Fir	Standing	1	0	1	2	2	3	1	1	1995
149	210	Fir	Standing	1	0	1	2	2	3	1	1	1971
149	220	Fir	Standing	3	4	1	2	2	3	3	2	1971
149	217	Fir	Standing	1	0	2	3	2	3	3	1	1971
149	284	Fir	Down	3	5	2	3	2	3	3	4	1971
149	258	Fir	Standing	1	0	1	3	2	1	3	3	1984
149	279	Spruce	Standing	1	0	2	1	2	3	1	1	1990
149	274	Fir	Standing	1	0	2	1	2	3	3	2	1984
149	303	Spruce	Standing	1	0	1	1	2	3	1	1	1990
149	302	Fir	Standing	1	0	2	1	2	3	1	1	1995
149	372	Spruce	Standing	1	0	1	1	2	3	1	1	1990
149	241	Fir	Standing	1	0	1	2	2	3	3	3	1984
149	186	Fir	Standing	2	1.5	1	2	2	3	3	3	1971
149	189	Fir	Down	2	1	1	2	2	3	3	3	1971

VARIABLE	Spruce	(n = 69)	Fir (n	= 114)
	\mathbb{R}^2	Р	R^2	Р
Decay Class	0.581	<0.001	0.690	< 0.001
Proportion of Decay	0.495	<0.001	0.612	<0.001
Bark Integrity	0.516	<0.001	0.594	<0.001
Bark Class	0.469	<0.001	0.582	<0.001
Branch Integrity	0.466	<0.001	0.639	<0.001
Fine Branch Flexibility	0.324	<0.001	0.424	<0.001
Position	0.179	<0.001	0.181	<0.001

Table 1. Bivariate regression statistics for each explanatory variable regressed (bivariate regression analysis) against years since death used in preliminary analysis to detect for linearity for each species.

Table 2. Correlation matrix for spruce and fir models. The number of correlations amongst explanatory variables that exceed r = 0.8 indicates the degree of multicollinearity in the overall model. Bold values indicate a combination of variables with significant multicollinearity.

Spruce	POSITION	DECAY CLASS	BRANCH	FINE BRANCH FLEXIBILITY	BARK CLASS	BARK INTEGRITY	PROPORTION OF DECAY
Position							
Decay Class	0.650						
Branch Integrity	0.072	0.264					
Fine Branch Flexibility	0.450	0.536	0.138				
Bark Class	0.605	0.684	0.179	0.671			
Bark Integrity	0.612	0.679	0.227	0.641	0.832		
Proportion of Decay	0.562	0.849	0.293	0.516	0.676	0.689	
Fir	POSITION	Decay Class	BRANCH INTEGRITY	FINE BRANCH FLEXIBILITY	BARK CLASS	BARK INTEGRITY	PROPORTION OF DECAY
Position							
Decay Class	0.324						
Branch Integrity	0.037	0.151					
Fine Branch Flexibility	0.305	0.489	0.157				
Bark Class	0.417	0.671	0.107	0.454			
Bark Integrity	0.460	0.727	0.088	0.447	0.840		
Proportion of Decay	0.327	0.835	0.127	0.422	0.609	0.664	

Table 3a. Summary of regression statistics for the spruce models. For both standing and down trees, both models were significant ($\infty = 0.05$), but many of the partial slope coefficients were not significant due to the heteroscedasticity and multicollinearity.

SUMMARY OF MODEL FIT: SPRUCE	STANDING	DOWN
R Square	0.873	0.753
R Square Adjusted	0.800	0.588
Root Mean Square Error	6.147	10.414
Mean of Response	14.636	28.472
Observations	33	36

ANALYSI	S OF VARIANC	Έ						
	DEGREES OF	FREEDOM	SUM OF	SQUARES	MEAN S	QUARE	F – R/	
Source	Standing	Down	Standing	Down	Standing	Down	Standing	Down
Model	12	14	5188.027	6945.666	432.336	496.119	11.443	4.575
Error	20	21	755.607	2277.306	37.780	108.443	<0.0001	0.0009
C Total	32	35	5943.634	9222.972				

EFFECT TEST

	DEGREES OF I	FREEDOM	SUM OF	SQUARES	F – RATIO		PROBABILITY > F	
Source	Standing	Down	Standing	Down	Standing	Down	Standing	Down
Decay Class	2	4	638.881	2359.423	8.455	5.439	0.002	0.004
Branch Integrity	2	2	158.324	63.657	2.095	0.294	0.149	0.749
Fine Branch Flexibility	2	2	305.934	358.263	4.049	1.652	0.033	0.216
Bark Class	2	2	10.943	194.782	0.145	0.898	0.866	0.422
Bark Integrity	2	2	298.367	54.536	3.949	0.252	0.036	0.780
Proportion of Decay	1	1	117.380	114.371	3.107	1.331	0.093	0.262

Table 3b. Summary of regression statistics for the fir models. For both standing and down trees, both models were significant ($\propto = 0.05$), but many of the partial slope coefficients were not significant due to the heteroscedasticity and multicollinearity.

SUMMARY OF MODEL FIT: FIR	STANDING	DOWN
R Square	0.768	0.847
R Square Adjusted	0.691	0.800
Root Mean Square Error	7.202	9.661
Mean of Response	14.302	31.230
Observations	53	61

ANALYS	IS OF VARIAN							
	DEGREES OF	FREEDOM	SUM OF SQUARES		MEAN	SQUARE	F – RATIO	
Source	Standing	Down	Standing	Down	Standing	Down	Standing	Down
Model	13	14	6704.430	23777.154	515.725	1693.370	9.444	18.196
Error	39	46	2022.734	4293.633	51.865	93.340	<0.0001	<0.0001
C Total	52	60	8727.167	28070.787				

EFFECT TEST

Source	DEGREES OF FREEDOM		SUM OF SQUARES		F – RATIO		PROBABILITY > F	
	Standing	Down	Standing	Down	Standing	Down	Standing	Down
Decay Class	3	4	1349.623	798.058	8.674	2.138	0.0002	0.091
Branch Integrity	2	2	9.642	263.915	0.093	1.414	0.911	0.254
Fine Branch Flexibility	2	2	1393.927	1015.112	13.430	5.438	<0.0001	0.008
Bark Class	2	2	345.451	208.686	3.331	1.118	0.040	0.336
Bark Integrity	2	2	378.869	271.540	2.435	0.9697	0.080	0.415
Proportion of Decay	11	1	64.156	792.044	1.237	8.486	0.273	0.006

Decay	Cedar		Spru	ıce	Fir		
Class	Standing	Down	Standing	Down	Standing	Down	-
1	-	3.5	12	15	10	13	
2	-	50	27	23	19	28	
3	276	279	67	24	23	45	
4	122	1200	-	47	67	63	
5	150	-	-	56	-	66	
	}						

Table 4. Comparison of mean years since death and Decay Class for *Thuja plicata* (Cedar) reported by Daniels *et al.*, (1997) and spruce and fir (this study).



Figure 1. Regression fit for spruce model with actual year of death taken from the Aleza Lake Research Forest permanent sample plot data and x-axis and predicted year of death from the TSDM.



Figure 2. Regression fit for fir model with actual year of death taken from the Aleza Lake Research Forest permanent sample plot data and x-axis and predicted year of death from the TSDM.


Figure 3. Plotted values of dates of tree mortality from the Times Since Death Model (y-axis) and from tree ring cores whose radial growth increased by 50% following tree mortality (x-axis). Linear regression line fitted to the data pairs indicates the two estimates are very close $R^2 = 0.924$.

CHAPTER 3. A METHODLOLOGY FOR ESTIMATING YEAR OF DEATH IN SUB-BOREAL FORESTS USING TREE RING GROWTH RATES

3.0 ABSTRACT

Tree ring growth rate criteria have been widely used to quantify disturbance regimes in forests of complex age structure but the methodology requires local calibration of growth rate parameters. This chapter summarizes the development of tree ring growth rate criteria for understory trees used to assign a canopy ascension date to canopy trees. Canopy ascension dates correspond to overhead mortality and this information can be used to quantify disturbance regimes. The criteria were developed in a wet, cool Sub-Boreal Spruce forest near Prince George, British Columbia. Two sampling methods were used. First in eight 10-meter radius plots, all dead and live trees (>30 cm tall) were stemmapped. Date of death in dead trees (n = 101) was estimated using a time since death model (Chapter 2). Increment cores or basal sections were then taken from all living trees in the plot and tree attributes were collected (species, diameter, crown class, live crown ratio). Year of death from the time since death model was then compared to year of death estimated from release patterns in nearby understory trees. When there was agreement between the two estimates of year of death (+/- 10 yrs), the understory tree was classified as a released tree. Trees not showing release were eliminated. From the remaining trees it was determined that only trees > 20 cm dbh when they died caused release in understory trees. Furthermore, understory trees were typically <5 meters from the dead tree, they were at least 5cm dbh < than the dead tree and they were of vigorous growth. Next, the relationships described above were used as criteria for selecting an independent population of understory trees (n = 428) subtending dead trees located at random. From these data growth rate criteria were developed to determine canopy ascension dates. The

criteria are as follows: 1) Gap origin growth rates is 1.50mm/yr, 1.72mm/yr and 1.07mm/yr for *Picea glauca* × *engelmannii*, *Abies lasiocarpa*, and *Betula papyrifera*. 2) Release criteria (for all species) is a 65% increase in growth sustained for 15 yrs following a 15 yr period of slow growth. 3) Other criteria used to assign canopy ascension dates were constant declining, parabolic or ambiguous tree ring patterns, which indicated gap origin trees that were growing slower than the gap-origin growth rate criterion. Criteria were also developed to assign release from suppression from the interpretation of irregular growth patterns.

3.1 INTRODUCTION

Analyses of tree ring growth patterns have been used to reconstruct disturbance regimes in forests of complex age structure (Frelich and Lorimer 1989). The method relies on the development of annual ring growth criteria that indicates the date a tree is released from suppression, or the date a seedling establishes in a gap, when a near-by canopy tree dies (*i.e.* canopy ascension dates). The location and timing of canopy ascension dates in a stand have to be analyzed to provide information on the spatial and temporal patterns of canopy level disturbance for eastern hardwood forests, eastern boreal forests, and western sub-alpine forests (Lorimer and Frelich 1989; Frelich and Lorimer 1991; Frelich and Graumlich 1994; Abrams *et al.* 1995; Frelich and Reich 1995; Cherubini 1996). However, the methodology has not been developed for sub-boreal systems in western North America, which are inherently challenging for this methodology due to the tall, narrow tree crowns which may not cause as substantial increases in understory light regimes after death as broad crowned hardwood forests.

Furthermore, growth rate criteria need to be developed locally in order to avoid over or under estimating disturbance intensity. For example, climatic effects, ontogenetic patterns, and stand development factors (such as canopy thinning) could all potentially cause release in a tree and be misinterpreted as a canopy disturbance. Thus specific criteria need to be developed that take into account these effects as well as the inherent variation in tree response due to species, type of disturbance and stand (species composition, age, height, canopy structure), and site factors (nutrient availability, moisture status, soil temperature).

The development of tree ring growth rate criteria in this study is assisted by multiple linear regression models that estimate the date of death for *Picea glauca* × *engelmannii* (Parry ex Engelm.) (hybrid spruce, hereafter referred to as spruce) and *Abies lasiocarpa* (Hook.) Nutt. (sub-alpine fir, hereafter referred to as fir) (Chapter 2). These models improved the process of developing tree ring growth rate criteria by providing an independent estimate of time since death for canopy trees. Therefore the objectives of this study are to determine the reliability of using tree ring release information to date tree mortality in SBS forests and develop criteria for estimating canopy ascension date using growth rate patterns contained within tree ring cores.

3.2 METHODS

3.21 Study Area and Site Selection

The research was conducted in two old-growth forests at the Aleza Lake Research Forest which is located at 54° 07' N, 122° 04' W, about 60 kilometers east of Prince George, British Columbia, Canada. Stand 1 is located on the north side of the Bear Road approximately 1 km east of the Bear Road and Aleza Road junction. Stand Two is located on the west side of the Aleza Road approximately 2.5kms south of the Bear Road and Aleza Road Junction. The elevation of the research forest is between 600 and 750 meters above sea level on the Nechako Plain of the Fraser River Basin in the Interior Plateau physiographic region (Holland 1976). The Aleza Lake Research Forest is located in wet, cool, sub-boreal spruce-fir forest. The region is classified as the Sub-Boreal Spruce, wetcool 1 (SBSwk1) biogeoclimatic zone according to a biogeoclimatic classification system in common usage in British Columbia (See Meidinger and Pojar (1991) for details). The SBS wk1 climate is characterized by cold, snowy winters and moist, cool summers. The climate is slightly less continental than typical for the SBS due to the orographic influence of the Northern Rocky Mountains to the east, resulting in higher precipitation than usual for the rest of the zone (Meidinger and Pojar 1991). The old-growth forests are mixtures of Picea glauca × engelmannii (spruce) and Abies lasiocarpa (fir) with scattered Pseudotsuga menziesii var. glauca (Douglas-fir), Pinus contorta var. latifolia (lodgepole pine) and Betula papyrifera (birch). Old-growth forests at the Aleza Lake Research Forest are uneven aged (Decie 1957). Sampling was conducted in three old-growth stands located on medium to good sites with minimal variation in soils and topography.

3.22 Sampling Design and Plot Measurements

Two sampling approaches were used in this study. First (Comprehensive Analysis), in eight 10 meter radius plots all dead trees $(n = 101) \ge 10$ cm dbh were located and decay characteristics used as predictor variables in the TSD model were collected (Chapter 2). Ten cm dbh was used as a minimum diameter since preliminary investigations revealed that trees smaller than this rarely caused release in nearby trees. Decay data were entered into the TSD model to estimate the date of death for each tree. All live trees ≥ 3.3 meters tall were cut down at 1.0m and a basal section was collected or, in larger trees, an increment core was taken (also at 1.0m). Tree ring cores were stored in plastic straws, mounted on 1 inch thick grooved Styrofoam strips. The tree ring samples and the basal samples were dried, sanded and scanned using a flatbed scanner. The scanned images were analyzed using Windendro® (Regent Instruments, Blaine, Quebec) which measures and records annual ring width growth (mm). In the second sampling approach (Selective Analysis), dead trees were located unsystematically (n = 176). Variables required for the TSD model (Chapter 2) were collected from these trees and a minimum of one gap-filling tree was selected for an increment core sample (based on criteria developed in the Comprehensive Analysis, see results).

3.23 Analysis

Comprehensive Analysis

In order to determine if a release (i.e. sustained increase in growth) event occurred following overstory mortality, ring width data for live trees was visually inspected for growth patterns that suggested release. Trees that did not show release were eliminated

(*i.e.* trees with constant declining growth or extremely flat incremental growth patterns). On the remaining trees, tree ring cores were inspected for growth increases that occurred within \pm 10 years of the TSD model estimate for year of death. Release events were eliminated which did not correspond to the date of death estimated from the TSD model (\pm 10 years) or were unlikely due to unrealistic distances from gap-maker to gap-filler, or due to the size relationship of the gap-maker to gap-filler. On the rest of the trees, a 15-year mean growth rate before and after the release date was calculated. Percent release was then calculated for each event as: 15 year growth after release / 15 year growth before release) \times 100. The 15-year average was used to eliminate the influence of short-term variations in growth rate on the chronology. Trees releasing after 1982 could not be averaged for a full 15 years. Releases after 1982 were only included if they were sustained until the year of sampling (1998). Trees releasing after 1990 were not included in the analysis because assumptions could not be made that the release would be sustained for 15 years.

Understory trees whose 'released' growth rates were 25% > than pre-release growth rates and within +/- 10 yrs of the TSD model estimates were used to examine several relationships. Dead-tree – understory-tree size relationships were used to determine the relative size difference necessary to cause a release and the minimum size required to cause release in a subordinate tree of any size. The diameters of dead trees and estimated diameter of the live trees (estimated as: present diameter – (2 × total ring width increment since release)) at the time of death provide evidence for how large a dead tree must be before it causes a growth increase in a given size of understory tree. Dead-tree – understory distance relationships were also quantified. The distribution of

distance data provided an estimate for the range in influence mortality has on the understory trees as measured from the base of the dead tree to the base of the released tree.

Selective Analysis

Interpretation of Growth Patterns

In the Selective Analysis, detailed annual growth criteria (early growth rate criteria, percent release criteria, and overall growth criteria) were developed to be used in future studies (Chapter 4 and 5). The objectives here were to: 1) Determine a gap-origin growth rate threshold (i.e. high rates of early growth indicate a tree was growing in a gap created by canopy mortality when it reached the coring height). 2) Determine a release threshold where slow growth followed by sustained high growth indicates a tree was initially suppressed by overstory competition then released following a gap-making event (Figure 1a). 3) Determine criteria to deal with trees that do not show either 1) or 2) but may have some pattern that may indicate a tree originated in a gap or was released, even though it did not meet the early growth rate or release criteria (Figure 1b-e). This approach generally followed the methods of Lorimer *et al.* (1988) and Lorimer and Frelich (1989) with modifications for this study's forests where necessary.

Early Growth Rate Criteria

Trees germinating in gaps should have faster annual radial growth rates than understory tree growth rates (Oliver and Larson 1996). Therefore, trees meeting a minimum growth rate threshold can then be used to judge the decade of an overhead mortality based on their total age at the coring height. Over 400 gap-filling trees were

classified as either gap-origin or initially suppressed in the following manner. Open grown trees have sigmoidal increases in cumulative diameter growth that results in an incremental annual growth pattern that peaks early on, usually around 20-30 years, followed by a generally declining pattern. Thus, if a tree is in the canopy and the past growth rate is equal to or greater than current growth, it can be assumed that the tree originated in a gap (Lorimer *et al.* 1988). A 10-year average growth rate was then determined for each tree for the first 10 years of growth from the pith. In total, 319 fir, 104 spruce, and five birch were sampled.

The growth rate data were then used to set the early growth rate criteria using Equation 1 (below) obtained from Lorimer *et al.* (1988). The formula was used in an iterative process until $P_{xi} = 95\%$ was obtained. This assures that 95% of the time, the growth rate threshold selected, correctly distinguishes true gap-origin trees from fast-growing suppressed trees. However, this strict (high) criteria will also prevent slow growing gap-origin trees from passing the criteria. Lorimer *et al.* (1988) suggest that it is preferable to maintain this high confidence in gap origin because other growth rate that fail to meet the threshold.

Probability of suppression (Lorimer et al. 1988):

Equation 1
$$Pxi = \frac{(Sxi \bullet Qsi)}{(Sxi \bullet Qsi) + (Gxi \bullet Qgi)}$$

Where:

 P_{xi} = probability of suppression for a sapling of size class *i* with growth rate x_i S_{xi} = proportion of suppressed (understory) trees of size class *i* exceeding growth rate x_i G_{xi} = proportion of gap saplings in size class *i* exceeding growth rate x_i Q_{si} = proportion of all saplings of size class *i* that are suppressed Q_{gi} = proportion of all saplings of size class *i* that are growing in gaps, such that $Q_{si}+Q_{gi}$ =1.0

Percent Release Criteria

Abrupt and sustained increases in incremental diameter growth (Figure 1a) may indicate that a tree was released from suppression by canopy mortality. In order to determine the growth response of understory trees to overhead tree mortality and evaluate these responses for release criteria, mortality dates of trees were estimated using a time since death model (Chapter 2). These dates of mortality were then compared to dates of release preserved in increment cores from the gap-filling trees. If the dates of release coincided within 10 years of the time since death model estimate, the tree was classified as a gap-filler and a percent release value was calculated from radial increment ((15-yr growth after release /15-year growth rate before release)× 100). The release criteria were then developed as follows.

To avoid classifying crown thinning responses and adjacent mortality as overhead canopy mortality a minimum release duration was implemented. Since trees already in the canopy fill in gaps through lateral expansion of the crown quickly, any growth increase in canopy trees will be short lived (Lorimer and Frelich 1991). Furthermore, since the gap will be quickly colonized, adjacent understory trees will also only receive short-term benefits. Therefore a 15-year sustained release criteria was selected.

To avoid classifying an increase in growth due to a period of slow growth caused by drought from being classified as a release, a minimum period of slow-growth before release was selected. Lorimer and Frelich (1989) found that the most severe drought of the 20th century only moderately affected diameter growth on the most sensitive sites in

eastern mixed forests. Decreases in growth due to drought occurred over 2-12 years and averaged 5.0 years. Therefore, a "15 year slow growth before release criteria" was proposed. The minimum slow growth criterion was used in this study to screen climatic variations, which are normally short lived from interpretation as release.

To avoid classifying crown thinning (*i.e.* trees in the canopy responding to the death of other trees in the canopy) and adjacent mortality as overhead mortality, two approaches were taken. First, threshold diameter limits, beyond which, trees would be too large to be candidates for understory release were established for each species. In this study < 5% of spruce were overtopped at greater than 40 cm dbh, while for fir and birch, < 5% were overtopped at greater than 30 cm dbh. Thus, trees greater than these diameters at the time of release were not counted as canopy ascensions even if they met the percent release criteria because a growth increase is likely due to canopy thinning and not a release from suppression. Secondly a relatively high percent release value was chosen (25%-quantile), since adjacent mortality usually cause weaker growth increases than overhead releases (Lorimer and Frelich 1989).

3.3 RESULTS AND DISCUSSION

3.31 Comprehensive Analysis

Of 101 dead trees in the pilot study 51 release events occurred within 10 years of the time since death model estimate. However, 29 dead trees were less than 20 cm DBH when they died, and only two of these 29 trees had an associated release event. The total number of release events associated with mortality of the 72 trees greater than 20 cm was 49 (68%). The rest of the mortalities either did not have any understory trees (n = 11) or the understory trees did not respond for reasons that could not be determined (n = 12). Since dead trees smaller than 20 cm DBH did not cause consistent or substantial increases in the growth of nearby understory trees, time since death model estimates of death provide the only reliable estimate available for smaller trees. Therefore when sampling potential gap-fillers for dead trees in the Selective Analysis, and in further studies only dead trees greater than 20 cm DBH should be expected to cause release in understory trees.

The mean percent release for the 49 release events was 80% with 95% of the releases falling between 66% and 94%. The maximum release was 246% and the minimum was 13%. Only 6% of release events were less than 25%. The time since death model increased the certainty that each release event was associated with tree mortality therefore, a fairly liberal threshold of 50% for release was established as the release criterion for the Comprehensive Analysis. Trees showing <50% release were eliminated and were not analyzed in the remainder of the relationships.

The mean distance from gap-maker to gap-filler was 2.84 meters, the minimum was 0.51 meters and the maximum was 6.67 meters. Ninety-five percent of the release

events occurred between 0.54 and 6.4 meters from the dead tree. There were no strong relationships, using linear or other functions between percent release (response) and distance from dead tree (p>0.05 in all cases). There was a weak trend for trees close to the dead tree (<1 meter) and far away (>5 meters) to exhibit less release than trees in the 2-4 meter range. There was also no difference in percent release when *I. tomentosus* caused mortality (gradual mortality) was compared to other – typically more punctuated gap-making events (p = 0.20).

There was no clear relationship between the percent release and the dead tree live tree diameter ratio, or the diameter of the dead tree, although in all cases the dead tree was at least 5 cm (dbh) larger than the understory tree. This suggests that understory trees which are at least 5 cm dbh smaller than the dead tree and within 5 meters of its base, have the potential to release. Thus, distance appears to be more important than dead tree: live tree size relationships as a sampling guideline. Therefore, sampling criteria for gap-filling trees replacing dead canopy trees was based on the following guidelines: less than 5 meters from the dead canopy tree, at least 5 cm less than the diameter of the dead tree at time of release and if possible in the 5-15 cm DBH range, in intermediate or suppressed canopy positions.

3.32 Selective Analysis

Gap-Origin Criteria

For birch the minimum gap-origin growth rate was 1.072mm/yr (n = 3) and the maximum suppressed growth rate was 0.552 mm/yr (n = 2) (Figure 2). Since the growth rate distributions were non-overlapping, the selection of the minimum growth rate

indicating gap-origin status for birch was 1.072 mm/yr. Although this value is based on a very small sample, birch is typically associated with gaps in sub-boreal spruce-fir forests since it is a relatively shade intolerant species (Archibold 1980; Krajina *et al.* 1982) thus the gap-origin growth rate criteria can be relatively liberal.

For fir, the distribution of ring widths overlapped considerably between suppressed and gap-origin trees (Figure 2) (n = 319). Since there were two other growth criteria (Figure 3) used to independently estimate disturbance date, an early growth rate threshold was selected which yielded a high confidence (95%) of gap-origin or alternatively, a low probability of mistakenly identifying a fast-growing suppressed sapling as a gap origin tree. Using a formula to determine gap-origin thresholds with 95% confidence level given in Lorimer *et al.* (1988), the threshold for fir was set at 1.72 mm/yr. The same guidelines were followed for spruce and the threshold was set at 1.5 mm/yr (n = 104).

Percent Release Criteria

Fifty percent of the observations for percent release fell between 65% and 129% with the median being 92% and there was no significant difference in percent release between species (p = 0.194). The distribution of percent release was not normal, but a median test also did not detect significant differences in percent release between species (Chi Square = 1.34,p=0.50). Therefore, the same release criteria were used for all species. The percent release criterion was based on supporting evidence from other studies and on the percent release data distribution in the present study. In most studies it was been shown that the typical release from suppression for *Picea* spp. and *Abies* spp. is less than

100%. For example, seventy-one year old *Picea glauca* in eastern Canada released about 67% (in diameter growth) following thinning (Fraser 1962). In a 16-year-old plantation Picea glauca diameter release was 37% following herbicide release (Balvinder et al. 2001). Sutton (1995) reported a 50-100% increase in diameter growth in a 30 year old Picea glauca stand following a weeding treatment and Biring et al. (1999) reported an 85% increase in growth in *Picea glauca* and *Abies balsamifera* over twelve years following herbicide treatments. Based on the evidence provided from these studies, a 65% increase in growth (which corresponds to the 25%-quantile in the percent release data distribution) was chosen. In comparison, Veblen (1986) used 150% as a release criterion for Picea glauca × engelmannii and Abies lasiocarpa, but only imposed a fiveyear sustainability requirement. In hemlock hardwood forests Lorimer and Frelich (1989), and Frelich and Graumlich (1994) used a minimum 50% growth increase for Acer saccharum and Betula allagheniensis sustained for a minimum of 10 years. Thus the criteria selected here is reasonable. The trees that do not pass the release threshold or the early growth rate threshold are recovered with overall growth rate interpretations (below) (Figure 3).

Overall Growth Rate Pattern Criteria

The relatively high thresholds for gap-origin and percent release were established in order to have high confidence in attributing a growth response to mortality and this inevitably results in some trees not passing the criteria. For these trees, lifetime incremental patterns were assigned to several groups and assumptions about these group patterns were used to assign the tree a date of canopy ascension (Figures 1b,c,d,e). The

first group was overall growth patterns that started out relatively high and remained consistent or had an increasing growth pattern followed by a flat or declining pattern (Figure 1b) (Frelich and Graumlich 1994). These patterns of growth are characteristic of dominant trees in even-aged stands (Assman 1970; Oliver and Larson 1996; Frelich and Graumlich 1994) and accordingly it is reasonable to assume that a similar pattern would result in gap origin trees (Lorimer and Frelich 1989). Therefore, the date of canopy ascension for these trees is equal to the year that the tree reached the coring height of 1.0m.

Another type of lifetime growth pattern used is a parabolic shape where tree growth increases gradually for a few decades, reaches a peak then gradually declines (Figure 1c). These patterns were considered indicative of gap-origin trees, growing at less than the gap-origin threshold if the peak growth rate was achieved within 25 years of the first ring in the chronology (Lorimer and Frelich 1989).

Ambiguous patterns are those that have a period of increasing growth lasting > 25 years but do not pass the percent release criteria (Figure 1d). An ambiguous zone was established beginning with the first ring of the increasing period to where 80% of the maximum growth rate was achieved (Lorimer and Frelich 1989). The decade of canopy ascension was determined to be the decade where the median growth rate was achieved during the ambiguous period. This interpretation is based on the assumption that ascension to the canopy in these trees would not coincide with a growth increase of less than 25% (Frelich and Lorimer 1989). Trees not meeting this criteria were treated as irregular patterns and the interpretations are described below.

Trees that have alternating high and low growth cycles or other random patterns, but do not meet the growth criteria described so far are considered to have irregular growth patterns (Figure 1e). Trees that have a declining arrangement of successive peaks with the first peak having the largest growth rate achieved within the first 25 years of growth are interpreted as gap-origin. Trees that have a peak growth later than 25 years from the earliest ring are treated as ambiguous patterns as described earlier (Lorimer and Frelich 1989).

3.4 CONCLUSIONS

Tree ring growth rate criteria can be used to indicate the year of canopy ascension for trees in western sub-boreal forests. This method had been previously untested in these forests. The method developed here shows that the technique can be used in humid forests in northerly latitudes and in forests dominated by trees with tall narrow crowns. This study provides a guide for tree ring growth rate criteria in studies in similar environments and provides criteria locally developed and tested that can be applied to disturbance regime investigations.

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Figure 1. Demonstration of various incremental growth patterns used to assess date of canopy ascension. Y-Axis = tree growth in mm/yr. X-axis = year the growth rate was recorded. Indicates the year of canopy ascension. The indicates the year of the ambiguous zone.



Figure 2. Box-plots showing the range (mean, standard deviation, minimum, maximum, and quartiles) in initial 10-year average growth rate for: gap-origin and suppressed *Betula* papyrifera (n = 3,2), Abies lasiocarpa (n = 104,215), and Picea glauca × engelmannii (n = 56,48).

1.) High Early Growth Rate Analysis:

Indication: Tree Originated in a Gap

Criteria:

Abies lasiocarpa = 1.72mm/yr

Picea glauca \times *engelmannii* = 1.5mm/yr

Betula papyrifera = 1.072mm/yr

2.) Rapid, Sustained Increases in Radial Growth Rates (Release) Analysis

Indication: Tree was suppressed for a period then, due to overhead mortality was released.

Criteria:

- a) 160% Release
- b) Sustained for 20 years
- c) < 40cm dbh for *Abies lasiocarpa* and < 30 cm for *Picea glauca* × *engelmannii*
- 3.) Overall Growth Pattern Analysis

Indication:

ion: I) Tree Originated in a Gap

Criteria:

- a) Consistently high or increasing growth followed by a decline.
- b) Parabolic growth pattern with peak growth occurring within first 25-years.
- c) Declining peaks with first peak indicating highest growth within first 25years.
- II) Tree was released from suppression

Criteria:

- a) Increasing growth lasting >25-years but peak growth achieved after 25 years.
- b) Peak growth later than first 25-years.

Figure 3. Decision set for determining year of canopy ascension. Each tree was assessed using each of the criteria. More than one year of canopy ascension per tree is possible.

CHAPTER 4. SPATIOTEMPORAL PATTERNS OF SMALL-SCALE DISTURBANCES IN SUB-BOREAL SPRUCE FORESTS: IMPLICATIONS FOR PARTIAL CUT HARVESTING AND *INONOTUS TOMENTOSUS* ROOT DISEASE

4.0 ABSTRACT

In a wet-cool sub-boreal forest east of Prince George, British Columbia, Canada, fine-scale, 70-year disturbance chronologies were compared for four forest types: oldgrowth and partially cut forests with and without Inonotus tomentosus Fr. (Teng) infection and mortality. In both old-growth and partially cut forests 46, 10 meter radius plots (92 total) were centered on dead or cut formerly dominant or codominant Picea glauca × engelmannii trees. Twenty-three plots for both old-growth and partial cut forests were centered on dead trees that showed evidence of past Inonotus tomentosus infection and 23 were centered on uninfected dead trees. Total P. glauca × engelmannii mortality was approximately 50% lower in the partial cut category since the decade of harvest (1950-1960), regardless of infection status. In all four forest types decadal mortality increased from the 1930's to the 1970's and then decreased since the 1980's. The functional gap size, averaged 16.76 m^2 and was independent of dead tree diameter, species, crown class or agent of mortality. Summed gap-size measures for all trees dying in a decade indicated that between 6.9 and 8.1% of stand area was made available to understory trees per decade but was also highly variable among decades. Mean decadal mortality was similar to estimates for similar forest ecosystems influenced by small-scale disturbances.

Due to high mortality rates of large individuals and low recruitment rates to the canopy for *P. glauca* \times *engelmannii*, the population structure of the old-growth forests

appears to be shifting from a *P. glauca* × *engelmannii* dominated canopy to an *A. lasiocarpa* dominated canopy, but *Inonotus tomentosus* does not appear to be the cause. Rather, higher *A. lasiocarpa* densities in the understory and more frequent *A. lasiocarpa* recruitment to the canopy combined with high rates of *P. glauca* × *engelmannii* mortality explain this shift. In partial cut plots, higher relative *P. glauca* × *engelmannii* recruitment and lower *P. glauca* × *engelmannii* mortality indicate that *P. glauca* x *engelmannii* populations may rise relative to its' present density.

4.1 INTRODUCTION

The Sub-Boreal Spruce (SBS) forest region of central interior British Columbia is a diverse forest region whose climax forests are mainly mixtures of *Picea glauca* × *engelmannii* (Parry ex Engelm.) (hybrid spruce, hereafter referred to as spruce) and *Abies lasiocarpa* (Hook.) Nutt. (sub-alpine fir, hereafter referred to as fir) (Meidinger and Pojar 1991). Mean fire return interval estimates in dry and wet SBS forests range from 150-250 years, and 227-6250 years, respectively (Parminter 1992; Hawkes et al. 1997). Long fire return intervals in wet areas of the SBS enable small-scale (i.e. gap) disturbances to become a predominant stand dynamics mechanism in these forests. Furthermore, smallscale disturbances may become increasingly important since fire suppression has excluded or reduced fire's influence on the ecosystem (Clark 1994; Frelich and Reich 1995; Andison 1996; Kneeshaw and Bergeron 1998).

Quantification of the patterns of small-scale disturbances and the stand dynamics they cause is important in both managed and unmanaged landscapes. The increasing scarcity of old-growth forests has inspired the preservation of their remnants (Welles *et al.* 1998) yet the long-range implications of gap dynamics on stand structure and composition are unknown. Secondly, in managed SBS landscapes, landscape ecology principles that suggest biodiversity can be maintained by mimicking natural disturbance patterns with harvesting patterns (DeLong and Tanner 1996). If this goal is to be met, partial cut harvesting systems that approximate small-scale natural disturbance patterns need to be designed for forests where small-scale disturbances are predominant. Ecologists are just beginning to realize that small-scale disturbance regimes are important

ecological processes in wet SBS forests and quantitative information of these regimes and how forests respond to them are lacking.

Agents of gap formation in SBS forests include root and stem rot fungi, phloem feeding insects (e.g. *Dendroctonus rufipennis)*, tree life spans, and abiotic factors such as windthrow and snow loading (Kneeshaw and Burton 1997; Kneeshaw and Bergeron 1998; Lewis and Lindgren 1999). Among these is the root rot pathogen *Inonotus tomentosus* (Fr.) Teng, which is common in most *Picea spp*. dominated forests worldwide (Whitney 1980; Merler *et al.* 1988; Lewis and Hansen 1991a; Lewis *et al.* 1992; Lewis 1997). In the SBS forests of central interior British Columbia, *I. tomentosus* primarily attacks spruce (Hunt and Unger 1994) and infected trees are subject to chronic declines in vigor. Eventually root dysfunction and structural weakening lead to standing mortality or windthrow of individual or small groups of trees (Lewis and Hansen 1991b; Lewis 1997). Following tree mortality, root colonization by the fungus increases due to the absence of active defense mechanisms in the sapwood and the fungal mycelium moves outward from the heartwood to the sapwood (Lewis *et al.* 1992).

The mycelium in the dead sapwood enables *I. tomentosus* to spread through rootto-root contact (Lewis *et al.* 1992). In this way the disease may spread from tree-to-tree (Lewis *et al.* 1992) potentially reducing spruce density in disease pockets. Due to the host preference of *I. tomentosus* and the ability to remain infectious for up to 40 years, gaps in the canopy formed by this pathogen may result in higher rates of spruce mortality and lower spruce populations in the gaps. Thus relative to some other small-scale disturbance agents *I. tomentosus* could lead to compositional shifts, due both to decreased density of

spruce in the overstory surrounding gaps, and a decreased probability that spruce recruits will fill the gaps.

It can be hypothesized that compared to the effects of *I. tomentosus* in old-growth forests, partial-cut silvicultural systems may exacerbate the effects of *I. tomentosus* on gap dynamics, and forest structure. Partial cutting may increase *I. tomentosus* virulence and this may increase spruce mortality as inoculum volumes are increased by harvesting relatively healthy infected spruce which, if left uncut, would be able to confine the fungus to the heartwood for a much longer period. This could mean increased contact frequency with new hosts and ultimately, increased mortality rates for spruce in partial cut silviculture applications.

This research addresses four specific questions about small-scale disturbance regimes and associated stand dynamics in wet SBS forests.

- 1. What is the temporal pattern of small-scale disturbance in *I. tomentosus* infected and uninfected old-growth forests and how do these compare to infected and uninfected partially cut forests?
- 2. Does the rate of spruce mortality differ between *I. tomentosus* infected and uninfected old-growth forests and how does partial cutting affect these rates?
- 3. How has current stand composition been affected by harvesting and/or infection status?
- 4. Is the future stand composition likely to change due to infection and/or harvesting status?

4.2 METHODS

4.21 Study Area

The research was conducted in two old-growth and two partially cut forests at the Aleza Lake Research Forest, located at 54° 07' N, 122° 04' W, about 60 kilometers east of Prince George, British Columbia, Canada. It lies between 600 and 750 meters above sea level on the Nechako Plain of the Fraser River Basin in the Interior Plateau physiographic region (Holland 1976). For the old growth forests, one stand was sampled on the north side of the Bear Road approximately 1 km east of the Bear Road and Aleza Road junction. A second stand was sampled on the west side of the Aleza Road approximately 2.5kms south of the Bear Road and Aleza Road Junction. For the partial cut forests one stand was sampled on the west side of the Aleza Road near the junction of the Aleza Road and the Upper Fraser Road. A second stand was sampled on the east side of the Aleza Road adjacent to the junction of the Aleza Road and the West Branch Road. The ALRF is located in the sub-boreal spruce, wet-cool 1 (SBSwk1) biogeoclimatic zone (See Meidinger and Pojar (1991) for details). The SBSwk1 climate is characterized by cold, snowy winters and moist, cool summers. The climate is slightly wetter and more moderate than central SBS sub-zones due to the orographic influence of the Northern Rocky Mountains to the east, resulting in higher precipitation than usual for the rest of the zone (Meidinger and Pojar 1991). The old-growth forests are mixtures of spruce and fir with scattered Pseudotsuga menziesii var. glauca (Douglas-fir), Pinus contorta var. latifolia (lodgepole pine) and Betula papyrifera (paper birch). Old-growth forests at the Aleza Lake Research Forest are thought to be uneven aged (Decie 1957). The dominant spruce, perhaps members of the initial fire origin cohort, are possibly 300 years old or

more. The oldest fir are about 200 – 250 years and are probably members of a post-fire establishment cohort. The scattered Douglas-fir component can be as many as 500 years old (Decie 1957) and may be survivors of the last fire. A well-developed understory layer is mainly comprised of fir (80%) and spruce (20%). Spot fires, spruce beetle (*Dendroctonus rufipennis*), various diseases including *I. tomentosus* and timber harvesting in some stands have been the main disturbance agents at the Aleza Lake Research Forest since the last wildfire (Decie 1957).

The partial cut forests at the Aleza Lake Research Forest have the same site characteristics as those described for old-growth forests. Partial cutting was designed to improve spruce regeneration success and overall stand structure and quality through selective harvests conducted during the winters of 1952-1956 (TSX 42765, 774118). These systems implemented forest management concepts typical of uneven aged selection systems (e.g. management of species composition, stand structure, and residual growing-stock) (Jull and Farnden *unpublished data*). The following guidelines were followed by trained crews prior to harvesting: defective trees were identified for felling; larger trees were removed where possible; vigorous trees were left; uniform spacing of residual spruce was attempted with removal of fir where possible; and sufficient volume was removed to insure an economic operation (DeGrace et al. 1952). The residual basal area was approximately 50% of initial basal area.

4.22 Site Selection

Forest cover and contour maps were initially used to locate 30 candidate stands (15 old-growth and 15 partial cut) that were relatively uniform in composition on

medium to good sites with minimal variation in soils and topography. The old-growth stands were undisturbed by human activities and the partial cut sites were selectively logged between 1952 and 1954. Each of the 30 candidate stands were ground checked for appropriate characteristics and a number were eliminated because they didn't meet the initial criteria. Each stand was also checked for the presence of *I. tomentosus* using standard field techniques (Finck *et al.* 1989). From the original 30 stands, four were selected (two old-growth and two partial cut) that were most similar amongst themselves, and best met the criteria above. The stands selected also had low to moderate (5-10%) incidence of *I. tomentosus* infection.

4.23 Sampling Design and Measurements

Plots were established in the four selected stands systematically with a 50 x 50 meter spaced grid. Four forest types were sampled. Old-growth without tomentosus (OGNT), and partial cut without tomentosus (PCNT) plots were free of any evidence of *I. tomentosus* mortality or infection in living or dead trees. OGNT and old-growth with *I. tomentosus* (OGT) plots were centered on the nearest dead tree (dead for approximately 40 years) that was a canopy dominant or codominant tree at the time of its death. This was done to provide similar mortality rate estimates between the old-growth plots and the partial cut plots which were logged about 40 years before sampling. PCNT plots were centered on the nearest cut stump to the grid point with no evidence of *I. tomentosus* infection or mortality with in the plot boundary. OGT plots were centered on a canopy tree that died approximately 40 years ago and had *I. tomentosus*. PCT plots were established on a cut stump that had evidence of past infection by *I. tomentosus* in the roots or the stump surface. In the OGT and PCT forest types all living trees were

inspected for *I. tomentosus* infection and this information was used to determine the incidence of infection in these forest types. For each forest type, 23, 10 meter radius (0.314 ha), plots were established.

To quantify the disturbance regime, the location of all dead trees in the plot (> 10 cm dbh), the tree decomposition characteristics required as input for the time since death model (TSD model) (Chapter 2) and, if possible, the cause of death were collected. For most disturbance agents, post-hoc classification of mortality is difficult beyond a few years. However, *I. tomentosus* causes diagnostic pitting in large roots and stem bases that can be identified with confidence for at least 40 years after mortality occurs (Lewis and Hansen 1991a). For several trees it was impossible to determine either the species or the cause of death. In these cases "unknown" was recorded and time since death was determined using canopy ascension date (Chapter 3).

Two potential gap-fillers were selected from among the trees subtending each dead canopy tree and one increment core was taken from each at 1.0 m. These trees were stem-mapped, assessed for crown class, live crown ratio, diameter, and species. Tree ring cores were stored in plastic straws, and later mounted on 1 inch thick grooved Styrofoam strips, dried, sanded and scanned using a flatbed scanner. The scanned images were analyzed using Windendro® (Regent Instruments, Blaine, Quebec) which measures and records annual ring width growth (mm). Canopy ascension criteria and the TSD model were used in combination to estimate a date of death for each dead tree (below).

4.24 Data Analysis Disturbance Chronology

Disturbance chronologies (mortality by decade) were prepared for each forest type. Chronologies are only presented since 1930, which is the limit of the TSD model capability and is approximately the limit for including smaller trees due to tree decomposition. The disturbance chronologies were developed by averaging year of death estimates from the TSD model (Chapter 2) and canopy ascension dates (Chapter 3), in potential gap-fillers. When there were no adequate gap-filling trees for the dead canopy tree only the TSD model was used. When the species of the dead tree could not be determined or was of a species that could not be modeled by the TSD model, only tree ring cores were used to date the mortality. Disturbance chronologies were divided into 10-year intervals from the beginning to end of each decade (Frelich and Graumlich 1994). For the partial cut plots, all cut stems were included in the disturbance chronology and mortality dates for these coincide with the 1950-1960 decade.

Functional Gap Size

Functional gap size is an estimate of the growing space (m²) that a canopy tree's mortality (*i.e.* gap-maker) makes available to the understory trees most likely to attain canopy status after it dies (*i.e.* gap-filler). The mean of the distance from gap-maker to gap-filler data was used as a proxy for the radius of a circle to calculate the average area a dead tree makes available to understory trees when it dies. Gap size estimates for each tree dying in a given decade were summed to determine the area made available to understory trees per decade. This data was then transformed to a percentage of stand area converted to gaps per decade (sensu Frelich and Graumlich 1994; Yamamoto 1995).

Accumulated mortality (stems/ha and basal area)

The total mortality since 1930 for all plots in each forest type was used to compare differences in accumulated mortality and spruce mortality. Plot level accumulated mortality was converted to accumulated basal area mortality because basal area comparisons may show differences in stand mortality dynamics beyond the population level (i.e. growth effects). The proportion of spruce basal area mortality over total basal area mortality and the proportion of spruce mortality caused by *I. tomentosus* in infected forests were also determined and compared using the Tukey-Kramer, Honestly Significant Difference test (Toothaker 1993) ($\alpha = 0.05$).

Stand Composition

The species tally by diameter class was used to compare compositional differences in regeneration (trees < 10 cm diameter at breast height), and canopy layers (trees > 10 cm diameter at breast height). Density by species were calculated as both a proportion of and as a total stems/ha and basal area (m^2 /ha). Mean treatment (i.e. OGT, OGNT, PCT, PCNT) values were compared using the Tukey-Kramer HSD test.

Transition Probabilities

Potential gap-fillers are defined as the two chosen trees subtending each dead canopy tree that showed the best potential of replacing the dead tree in the canopy relative to the total pool of regenerating trees (Lertzman 1992). Criteria for selection included a marked release in annual radial growth, vigorous with a good live crown, subordinate to the dead tree in the canopy at the time of death, and within close proximity to the dead tree (<5m) (Chapter 3). One most likely gap-filler was selected from the two

potential gap-fillers based on their ability to assert dominance over potential gap-fillers due to their vigor, growth response and proximity to the dead tree. In cases where no single tree showed clear dominance over other potential gap-fillers, both were taken.

The sum of the gap-maker/gap-filler transitions was used to develop transition probabilities for each species in the four forest types. Dead trees without any gap-fillers (e.g. recent mortality or microsite limitations) were not included in the matrix (approximately 9% of all dead trees). Gap-fillers associated with more than one gapmaker were assigned a fractional probability of transition based on the number of gapmakers it was replacing (Lertzman 1992). Gap-makers that could not be identified to species were recorded as 'other'. Transition probabilities were determined from 1930-1950, 1950-1970, and 1970-1997 to examine variation in transition probabilities with time and due to harvest operations.

Simulation of Future Stand Composition

Predicted future stand composition was modeled using the 1970-1997 transition matrix and the average annual rates of mortality for each species for the same period. A constant annual mortality rate, constant transition probability, constant stand density, and the absence of catastrophic or wide-spread canopy level disturbance were assumed for the model. The current species composition for each forest type for trees ≥ 0 cm DBH was taken, then the annual mortality from the current density for each species was subtracted. Each annual mortality was then multiplied by the transition probability for each gap-filling species. These results were added to a running total of density for each species to provide estimates of population dynamics for a period of 200 years.
4.3 RESULTS

4.31 Stand Composition

Eighty-five % of the *I. tomentosus* infected forest types had less than 6% infection incidence in living trees. The remaining 15% had between 6% and 15% infection incidence. Average understory density (trees >30 cm tall and <10cm dbh) for the four forest types was 3305 stems per hectare (p>0.05) (Table 1). Spruce density was significantly lower in both old-growth forest types than the PCNT forest type and in the OGT forest type than the PCT forest (Tukey-Kramer HSD, p = 0.0006) (Table 1). In the canopy layer (trees \geq 10cm dbh), average stand density was 765, 813, 641 and 760 stems/ha for the OGNT, OGT, PCNT, and PCT forest types, respectively (Table 1). The canopy density for the PCNT forest type was significantly lower than all other forest types (p = 0.011) but there were no other significant differences between any other forest type. This may indicate more intense partial cutting in this forest type relative to the other PCT forest type. Spruce density in the canopy layer was significantly lower in both the OGT, OGNT and PCT forest types relative to the PCNT forest types, but only when *I. tomentosus* is not present.

Average basal area was similar for the four forest types (p = 0.825) (Table 1). However, the percent spruce basal area of total basal area was highest in the OGNT forest type compared to the OGT and PCT forest types (p = 0.0132) (Table 1). The PCT forest type also had a significantly lower percent spruce basal area than in the OGT forest type. These results indicate that spruce basal area is higher in forest types not infected by *I*. *tomentosus* and is higher in old-growth than partial cut forests. The latter result is likely due to the removal of large diameter-high basal area trees in partial cut stands.

4.32 Disturbance

Disturbance Chronology

Since 1930, mortality has occurred in all decades in all four forest types (Figure 1). Average decadal mortality by decade since 1930 for the OGT, OGNT, PCT and PCNT forests was 48.07, 44.40, 32.91, 35.25 stems>10cm dbh/ha/decade (not shown). Average decadal spruce mortality in the 1960's was 30.12, 28.73, 11.22, and 11.42 stems/decade for the OGT, OGNT, PCT and PCNT forests, respectively. Thus spruce mortality was more than halved following the harvest in both uninfected and infected partial cut forests relative to the old-growth forests. In contrast, fir mortality increased since the harvest in the partial cut forest types but not in the old-growth forest types (Figure 1). For the partial cut sites and the old-growth sites, spruce mortality, not including cut trees, was highest in all forests during the 1970's. Fir mortality was highest during the 1960's for the old-growth forests and highest during the 1980's for the partial cut forests and highest during the 1980's for the partial cut forests had declining total mortality rates and the same trend was evident during the 1990's for the partial cut forests.

4.33 Accumulated Mortality

Mean accumulated mortality (less cut trees) was significantly higher in the OGT forest type compared to both partial cut types (p = 0.0068) (Table 1). Mean accumulated spruce mortality was also significantly higher for both old-growth forest types compared

to both partial cut forest types (p<0.0001). Average accumulated basal area mortality was similarly significantly higher for both old-growth forest types compared to both partial cut forest types (p<0.0001), as was the proportion of spruce mortality of total basal area mortality (p<0.0001). The proportion of spruce basal area mortality killed by *I. tomentosus* was 0.312, and 0.150 in the OGT and PCT forest types, respectively (p = 0.025). Total mortality, total spruce mortality, total basal area mortality, and total and proportional spruce basal area mortality were all therefore generally reduced by partial cutting but there is no evidence to suggest that *I. tomentosus* caused significantly higher spruce mortality in this study.

4.34 Functional Gap Size

Most likely gap fillers averaged 2.35 m from dead spruce (N = 380) and 2.29 m from dead fir (N = 490) and species differences were only marginally significant (p =0.052). Since gap fillers respond to the two gap making species similarly, analyses presented hereafter are for species pooled. The maximum distance from a gap-maker to a gap-filler was 5.6 meters and the minimum was 0.05 meters. Ninety-five % of the releases occurred between 0.55m and 4.44m. There was no significant relationship between the distance of gap-maker to gap-filler and the diameter of the gap-maker (p = 0.068).

The average gap size was $16.76m^2$. The 97.5^{th} quantile (r = 4.44m) gap area was $61.90m^2$ indicating that only 2.5% of the single tree gaps have a functional gap size larger than $62 m^2$. The product of mortality rate estimates and mean gap size, indicates that the

percentage of stand area made available to new recruits per decade is 8.1%, 7.4%, 7% and 6.9% for the OGT, OGNT, PCT, and PCNT forest types, respectively.

4.35 Transition Probabilities

In general, transition probabilities indicate that fir gap-fillers outnumber all other gap-filler species by about 2:1 except in cases where the sample size of a particular gap maker is small. In old-growth forest types, spruce recruitment does not appear to be strongly affected by infection status since, in some cases spruce recruitment was greater in the OGT forest types than in the OGNT forest types (Figures 2,3,4). Furthermore there were no temporal changes in transition probability over the last 70 years in either old-growth or partial cut forest types. In general partial cut forest types had higher spruce recruitment than old-growth forest types in all cases but the fir to spruce transition in 1970-1997. Furthermore, the spruce recruitment was not predictably higher in the PCNT forest type relative to the PCT forest type. Therefore spruce recruitment was increased by partial cutting but was unaffected by *I. tomentosus*. No interaction of partial cutting and *I. tomentosus* was found.

4.36 Simulations of Future Stand Compositions

Two hundred year stand composition projections indicate that fir density may increase from its current proportion of 65-70% to about 80% while spruce density may decline from 28-30% to about 15% (Table 2). These projections also suggest that birch, Douglas-fir and western hemlock will continue to be maintained in low densities in these forests.

Assuming no further harvests in the partial cut forest types in the next 200 years in the PCNT forest type (Table 2), spruce may increase from current relative density of approximately 33% to 38% and fir may decline from 63% to 57%. Other species should also be maintained as minor components. In the PCT treatment spruce density will not rise as it did in the PCNT forest types but will be 7-10% higher than in the old-growth forest types.

4.4 DISCUSSION

Disturbance Chronology

Disturbance chronologies indicate that old-growth, sub-boreal forests are influenced by continuous low intensity disturbances. It also appears that *I. tomentosus* infected and uninfected forests have similar disturbance dynamics. Therefore, at the low infection levels observed in these stands (typically <6%) (British Columbia Ministry of Forests 1995), *I. tomentosus* appears to contribute to the general pattern of low intensity disturbance by working in concert with other agents to cause single tree to small group tree mortality. However, it does not increase spruce mortality compared to uninfected forests. Partial cut forests generally have lower rates of disturbance than old-growth forests and spruce mortality has been reduced. The effect of higher disease incidence, and therefore more inoculum, was not tested in this study. However, spruce mortality due to *I. tomentosus* could increase with moderate to high infection incidence which may explain the apparent species shifts observed in stands with higher infection rates (Lewis and Trummer 2000).

Estimates of disturbance intensity (~7-8% of stand area) by decade in these oldgrowth spruce-fir forests are similar to several other forest types dominated by small disturbances. In an old-growth hemlock-hardwood forest in western upper Michigan, Frelich and Graumlich (1994) reported mean decadal disturbance rates of 5.4%. They noted many small gaps created in each decade contributed to the low disturbance rate, which is indicative of individual to small group tree mortality. Yamamoto (1995) reported that current stand area in gaps for an old-growth sub-alpine coniferous forest in

central Japan was 7.3%. Frelich and Lorimer (1991) reported 5.7 to 6.9% mortality in a hemlock-hardwood forest moderated by light intensity disturbances.

Disturbance rates were highly variable over time ranging from virtually no disturbance to nearly 15% of stand area. For example, the 1970's and 1980's were the decades of peak disturbance for all forest types. During these decades disturbance was approximately 13.5%, 14.2%, 7.8% and 9.7% for the OGT, OGNT, PCT, and PCNT forests respectively. Even these upper estimates of disturbance intensity for the study area do not approach the levels of disturbance reported for medium to heavy intensity disturbances caused by wide-spread canopy level mortality caused by insects or catastrophic windthrow (Frelich and Graumlich 1994; Veblen *et al.* 1994; Kneeshaw and Bergeron 1998). Therefore the timing and intensity of gap formation at the Aleza Lake Research Forest corresponds to continuous, small-scale gap formation consisting of individual trees or small groups of trees.

Accumulated Mortality

Total accumulated mortality, total spruce mortality and the proportion of spruce mortality were all significantly lower in partial cut forest types compared to old-growth forest types. Thus, the partial cut harvest probably captured potential mortality that would have occurred if the stands were not cut and also has subsequently improved resource availability for residual trees and improved survivorship. If spruce mortality was lower in OGT forest types compared to PCT or PCT and PCNT forest types, there may have been evidence for an interaction with partial cutting and *I. tomentosus*. The results here are opposite, with spruce mortality lower in PCT forest types relative to OGT forest types,

and no difference between PCT and PCNT forest types. Therefore it can be concluded that partial cutting in *I. tomentosus* infected areas does not increase the spread rate of the root disease. Further, the evidence shows that spruce mortality can actually be lowered (~15%) by partial cutting in infected forest types (Table 1). The results of thinning in a *Picea glauca* plantation affected by *I. tomentosus* by Whitney (1993) indicated lower mortality of *Picea glauca* in the thinned plantations relative to unthinned controls. Whitney suggested that thinning increased discontinuity of roots leading to fewer subsequent infections, and to increased vigor in residual trees that would prolong a trees' life even if infected by *I. tomentosus*. In a detailed study on changes in inoculum volume following harvest, Lewis (unpublished data) did not find a significant increase in total inoculum volume with age of stump although the root disease did appear to move radially from the heartwood into the sapwood following harvest.

Stand Composition

Documented understory tree recruitment to the canopy began as early as 1930, but many gap-filling trees indicated releases occurring much earlier than this. The evidence of recruitment in this study supports DeGrace (1952), who using permanent sample plot data, reported that the forests at the Aleza Lake Research Forest were changing from even to uneven aged during the 1940's and 1950's. In a similar spruce-fir forest type near Smithers and Houston, British Columbia, Kneeshaw and Burton (1997) reported that older forests also appeared to be successfully maintaining themselves through understory recruitment in the absence of fire. Stand composition analyses indicate that spruce populations in the understory are similar for the two old-growth forest types and for the two partial cut forest types (Table 1). These comparisons suggest that *I. tomentosus* does not affect understory spruce populations in either old-growth or partial cut stands. In general, partial cutting increased spruce populations by creating an understory environment more suitable for spruce colonization and survivorship. This more suitable environment appears to benefit spruce germination even in *I. tomentosus* infected forest types.

In the canopy layer, it was evident that *I. tomentosus* had no effect on spruce populations for old-growth stands. However, when spruce basal area was considered it was noted that the OGT forest types had lower spruce basal area than the OGNT forest types. Similarly, spruce densities in OGT and PCT forest types were not significantly different but spruce basal area was higher in OGT forest types compared to PCT forest types (Table 1). Since mortality rates were not substantially different between these forests and populations were similar, the result may be due to decreased growth rates in residual *P. glauca* × *engelmannii*. Thus there does not appear to be an impact of applying partial cutting to infected stands on spruce populations but there may be an effect on spruce volumes. Other studies have reported decreased growth rates of *Picea spp*. due to *I. tomentosus* infections (e.g. Whitney 1980, Merler 1984, Lewis 1997).

Transition Probability and Simulations of Future Stand Composition

Based on the assumptions in the model used here, in the old-growth forests, spruce density may decline from its current abundance of about 28-30% to around 10% after 200 years (Table 2). This is due to lower current mortality rates for fir and its high

success as a transition species. This projection corresponds with Kneeshaw and Burton (1997) who noted mixed spruce-fir forests may become dominated by fir. In these forests as well as the forests of the present study, a period of low spruce regeneration, high spruce mortality and reduced spruce recruitment to the canopy contribute to the eventual dominance of fir. However since spruce is a longer lived species than fir, the long-term decline in spruce populations may not be as significant as modeled here. Furthermore other undefined terms in the model may effect the predictions presented. For example, higher than modeled sub-alpine fir mortality due to abiotic or biotic factors would open the canopy and potentially increase spruce regeneration and recruitment to the canopy. However the model does provide a base-line estimate of stand development based on a 70 year average of mortality/recruitment dynamics and is useful as a point-of-comparison.

In the old-growth forest types recent spruce mortality has been higher than fir mortality. Given this result and the high rate of fir recruitment over time (Figures 2,3,4) it is reasonable to assume that fir density has been on the rise over the last 70 years in the old-growth forests and spruce density has been decreasing. These stand dynamics may characterize the current seral stage of these old-growth forests where the fire-origin cohort of spruce has experienced high mortality rates as they approach the end of their life-span and are replaced by prolific fir regeneration.

In the partial cut forests the combination of lower spruce mortality, following the harvest, and generally higher spruce canopy recruitment rates relative to the old-growth forests should mean that current spruce density is markedly higher in the partial cut forests relative to the old-growth forests. This is clearly the case for the regeneration

layer (Table 1) but not for the canopy layer where spruce density was similar for both old-growth and partial cut forest types.

However, since the stand improvement harvest specifications were to cut large diameter stems, spruce density in the canopy would have been dramatically reduced immediately following the harvest. Even moderate annual diameter growth rates of 2.0 to 3.0 mm/yr (Newbery, *unpublished data*), in advanced spruce regeneration would take between 20-25 yrs to reach 10 cm dbh if they were 5 cm dbh at the time of harvest. If the current old-growth stand composition is indicative of pre-harvest partial cut stand composition, relative regeneration layer spruce density would only have been around 8-13% (Table 3). Since current relative regeneration spruce density in the partial cut forests is 18-21% (Table 3) many of the existing spruce in these forests have germinated since the harvest. At the same moderate growth rate mentioned above they would take at least 50 years to reach 10 cm dbh and thus were still not counted in the canopy layer tally conducted in 1997 (about 42 years after harvest). Therefore, there is biological evidence that suggests spruce density in this layer will also rise because of the harvest over the long term as modeled by the simulations.

4.5 CONCLUSIONS

Overall, the disturbance regime in old-growth forests is one of low intensity single tree to small group tree mortality which does not differ between *I. tomentosus* infected and uninfected gaps. The application of partial cutting to mixed spruce-fir forests has decreased mortality rates in general and of particular importance, spruce mortality rates have been decreased in partial cut forests regardless of infection status. However growth rates of spruce may be reduced in *I. tomentosus* infected forests. Transition matrices indicate increasing dominance of fir at the expense of spruce assuming disturbance regimes and transition success remain consistent in the old-growth forests. In partial cut forests, spruce populations will generally increase in density.

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Layer	Stand Attribute	OGT (n = 21)	OGNT (n = 23)	PCT (n = 22)	PCNT (n = 23)
	Average Density (stems/ha: Mean/SD)	3704/ 782.51	3236/ 943.98	3317/ 859.10	2997/ 1141.86
Regeneration Layer	Percent Spruce Density: Mean/SD	12/ 5.84	17/ 6.93	21/ 11.42	23/ 10.04
	Percent Fir Density: Mean/SD	92/ 6.49	86/ 7.93	78/ 12.02	77/ 10.78
Canopy Layer	Average Density (stems/ha): Mean/SD	813/ 210.49	813/ 765/ 210.49 147.57		641/ 131.87
	Percent Spruce Density: Mean/SD	26/ 11.14	26/ 30/ 11.14 8.26		33/ 13.85
	Average Basal Area (m²/ha): Mean/SD	36.23/ 2.21	36.53/ 2.10	38.25/ 2.10	38.51/ 2.06
	Percent Spruce Basal Area: Mean/SD	47/ 0.16	57/ 0.06	41 /0.16	50/ 0.18
	Average Total Mortality (stems/ha): Mean/SD	355.9/ 114.7	340.70/ 96.72	253.41/ 100.48	292.44/ 117.39
	Average Spruce Mortality (stems/ha): Mean/SD	148.17/ 72.89	142.63/ 71.87	59.55/ 50.18	55.01/ 40.74
	Average Basal Area Mortality (m2/ha): Mean/SD	26.52/ 9.80	29.33/ 9.80	17.16/ 8.99	18.28/ 9.18
	Percent Spruce Mortality of Total Mortality: Mean/SD	51/ 0.19	56/ 0.19	31/ 0.26	27/ 0.29
	Percent Spruce Mortality Caused by Inonotus tomentosus: Mean/SD	31/ 0.28	N/A	15/ 0.19	N/A

Table 1. Summary of stand composition and mortality data. For the partial cut forest types, the mortality data do not include cut stems.

Table 2. Species composition dynamic over the next 200 years for each forest type based on the average annual mortality rates for each species since 1930 and the transition probability for each gap-maker obtained from the transition matrices since 1970. The illustrations assume no catastrophic or high intensity disturbance occurs during the modeling horizon. OGNT = old-growth without *I. tomentosus* caused mortality, OGT = old with *I. tomentosus* caused mortality, PCNT = partial cut forests without *I. tomentosus* caused mortality.

Treat- ment	Current Composition		+ 50 years		+100 years		+ 200 years					
	Spruce	Fir	Other	Spruce	Fir	Other	Spruce	Fir	Other	Spruce	Fir	Other
OGNT	0.30	0.65	0.05	0.27	0.68	0.05	0.24	0.71	0.05	0.17	0.77	0.06
OGT	0.26	0.70	0.04	0.23	0.73	0.04	0.20	0.76	0.04	0.14	0.81	0.05
PCNT	0.33	0.63	0,04	0.34	0.62	0.04	0.36	0.60	0.04	0.38	0.57	0.05
РСТ	0.23	0.72	0.05	0.23	0.73	0.04	0.23	0.73	0.04	0.24	0.74	0.02



Figure 1. Disturbance chronologies for the four forest types. Each bar represents the average mortality (stems/ha) occurring in each decade for spruce and fir species and total mortality which includes other species (never exceeds more than 22 stems/ha).



Figure 2. Transition probability data from 1930-1950 for: OGNT = old-growth without *I. tomentosus* caused mortality, OGT = old with *I. tomentosus* caused mortality, PCT = partial cut forests without *I. tomentosus* caused mortality, PCT = partial cut forests with *I. tomentosus* caused mortality. In all cases the transitions are in the form of gap-maker : gap-filler. For example the Spruce:Fir transition indicates a Spruce mortality being replaced by an Fir gap-filler. Data are presented in triads such that each gap-making species has three possible transition outcomes and there are three possible gap-making species. Thus, for each forest type, transition probabilities total one for each species of gap-maker. (N < 5 for Spruce gap makers in the PCNT forest type).



Figure 3. Transition probability data from 1950-1970 for: OGNT = old-growth without *I. tomentosus* caused mortality, OGT = old with *I. tomentosus* caused mortality, PCT = partial cut forests without *I. tomentosus* caused mortality, PCT = partial cut forests with *I. tomentosus* caused mortality. In all cases the transitions are in the form of gap-maker : gap-filler. For example the Spruce:Fir transition indicates a Spruce mortality being replaced by an Fir gap-filler. Data are presented in triads such that each gap-making species has three possible transition outcomes and there are three possible gap-making species. Thus, for each forest type, transition probabilities total one for each species of gap-maker. (N < 5 for Other gap makers in the PCNT forest type).



Figure 4. Transition probability data from 1970-1997 for: OGNT = old-growth without *I. tomentosus* caused mortality, OGT = old with *I. tomentosus* caused mortality, PCNT = partial cut forests without *I. tomentosus* caused mortality, PCT = partial cut forests with *I. tomentosus* caused mortality. In all cases the transitions are in the form of gap-maker : gap-filler. For example the Spruce:Fir transition indicates a Spruce mortality being replaced by an Fir gap-filler. Data are presented in triads such that each gap-making species has three possible transition outcomes and there are three possible gap-making species. Thus, for each forest type, transition probabilities total one for each species of gap-maker. (N < 5 for Other gap makers in all forest types).

CHAPTER 5. STAND LEVEL SPATIO-TEMPORAL DISTURBANCE PATTERNS CAUSED BY *INONOTUS TOMENTOSUS* AND OTHER AGENTS IN SUB-BOREAL SPRUCE-FIR FORESTS

5.0 ABSTRACT

The small-scale canopy level disturbance regime in old-growth sub-boreal forests was compared for three stands with Inonotus tomentosus (Fr.) Teng caused mortality (5-10% infection incidence of infection) and three stands without any evidence of the root pathogen. The spatial and temporal patterns of canopy disturbance and the patch structure of trees were quantified from 0.49ha stem-mapped plots using spatial autocorrelation analysis (Moran's I and Standard Normal Deviates). Spatio-temporal patterns of canopy disturbance and canopy composition were similar for *I. tomentosus* infected and uninfected stands. For infected and uninfected stand types pooled, canopy disturbance per decade ranged from a maximum of 6.0% to a minimum of 5.09%. Canopy gaps averaged <7m in diameter but larger gaps up to about 28m in diameter also were found. Gaps were irregularly distributed throughout the plots over the last 250 years. Species patch structure analysis indicated that *Picea glauca* × *engelmannii* (Parry ex Engelm.) was more likely to be spatially associated with itself than with other species, whereas Abies lasiocarpa (hook.) Nutt. had neither positive nor negative spatial associations with itself or with *Picea glauca* × *engelmannii*. These results show that small-scale disturbances are important successional mechanisms in sub-boreal spruce forests and that small scaledisturbance characteristics do not differ between forests with and without *I. tomentosus* infection.

5.1 INTRODUCTION

Across the landscape of British Columbia's central interior, sub-boreal forest regions were historically characterized by mature forests dominated by *Picea glauca* × *engelmannii* (Parry ex Engelm.) (hybrid spruce, hereafter referred to as spruce), *Abies lasiocarpa* (Hook.) Nutt. (sub-alpine fir hereafter referred to as fir), and *Pinus contorta* (Hawkes *et al* 1997). The prevailing disturbance regime notion is that catastrophic fire came at intervals about equal to tree longevity (80-200 years) in this forest type, resetting succession over large areas before small disturbances had much effect on stand structure (Johnson 1992). This view of historical disturbance frequency maintains that forests were dominated by even aged, single storied stands, and had few uneven-aged, old-growth forests (Oliver and Larson 1996).

However, the sub-boreal forest region in central British Columbia is climatically and topographically diverse and this diversity strongly affects disturbance regimes. For example, in wet montane, sub-boreal and sub-alpine spruce-fir forests, catastrophic stand replacing disturbances occur between 227-6250 years whereas in dry forests of the same types, mean fire return intervals are about 200 years (Hawkes *et al.* 1997; DeLong and Tanner 1996). Small-scale disturbances may be major factors influencing succession and stand development in areas with long fire return intervals.

The contemporary dominance of clear-cut silviculture systems in both dry and wet spruce-fir forests in British Columbia has caused an increase in early seral, even aged stands across the landscape over the last 60 years. In many managed landscapes, these young forest types are overwhelmingly abundant relative to their pre-settlement occurrence (Alverson *et al.* 1988; Mladenoff *et al.* 1993; Parminter and Daigle 1997).

Concern over this alteration of natural landscape characteristics and stand level structure has lead to the demand for silvicultural approaches that maintain the natural landscape mosaic of stand types and structures whilst maintaining timber supplies in resource dependent communities. Therefore ecologists have been challenged to characterize the small-scale disturbance regime as a prerequisite for the development of appropriate silvicultural methods.

In sub-boreal spruce forests, several agents are responsible for small to mediumsized disturbances including: root diseases, phloem-feeding insects, wind, snow, ice and edaphic conditions. *Inonotus tomentosus* (Fr.) Teng is a common and economically significant root disease pathogen in these forests (Lewis 1997). *I. tomentosus* primarily attacks spruce, and infected trees are subject to chronic declines in vigor (Hunt and Unger 1994). Eventually tree mortality occurs due to dysfunctional roots, or windthrow due to weakened root systems (Lewis and Hansen 1991; Lewis 1997).

Due to its ability to spread from tree to tree via root-to-root contact, its preference for spruce as a host, and a high rate of blow-down in trees infected with *I. tomentosus*, the disease may cause aggregated disturbance patterns rather than randomly dispersed patterns in a stand. This aggregated pattern of disturbance may have implications for gap arrangement and demography (Qi and Wu 1996; Bellehumeur *et al.* 1997). For example, aggregation of *I. tomentosus* disease pockets may allow species of trees to occupy the gaps that are resistant to infection (*i.e.* fir). Thus the spatial pattern of *I. tomentosus* caused disturbance may lead to clusters of fir forming the canopy in *I. tomentosus* infection centers, and spruce persisting only outside the centers. Over time as the

infection centers coalesce, spruce populations may be diminished significantly compared to uninfected forests.

In a companion study (Chapter 4), 10 meter fixed radius plots were established in both infected and uninfected old-growth forests in order to assess fine-scale patterns of tree mortality and subsequent tree replacement tendencies. Disturbance affected an average of approximately 8.1% and 7.4% of stand area per decade for *I. tomentosus* infected and uninfected old-growth stands, respectively. This study found that I. tomentosus, at low (<6%) incidence, did not affect spruce mortality rates or subsequent gap-maker - gap-filler transition probabilities relative to the remaining array of disturbance agents affecting the stands at Aleza Lake. However, this gap-level study did not address the spatial pattern (*i.e.* gap dispersion) of the gaps themselves or subsequent species patch structure at larger scales. Therefore the objectives of this paper are to describe and compare the spatial and temporal patterns of natural disturbance and species patch structure for three, 0.49 hectare I. tomentosus infected stands and three uninfected old-growth spruce-fir stands located in wet-cool, sub-boreal forests in east central British Columbia. These objectives are addressed by developing canopy tree stem-maps and then analyzing spatio-temporal patterns of disturbance and species spatial patterns with Moran's I and Standard Normal Deviates. This approach focuses on the cumulative effects of gap formation at the stand level. Therefore this approach provides information on the small-scale disturbance regime at a higher scale than in gap-phase studies but at lower scale than in landscape studies.

5.2 METHODS

5.21 Study Area

The research was conducted in old-growth stands at the 10 235 hectare Aleza Lake Research Forest, located at 54° 07' N, 122° 04' W, about 60 kilometers east of Prince George, British Columbia, Canada. It lies between 600 and 750 meters above sea level on the Nechako Plain of the Fraser River basin in the Interior Plateau physiographic region (Holland 1976). The Aleza Lake Research Forest is located in a wet, cool subzone of the sub-boreal forest and is classified as the Sub-Boreal Spruce, wet-cool subzone (SBSwk1) according to a biogeoclimatic system commonly used in British Columbia (Meidinger and Pojar 1991). The sub-zone is characterized by cold, snowy winters and moist, cool summers. The climate is slightly wetter and more moderate than typical for other sub-boreal spruce sub-zones due to the orographic influence of the Northern Rocky Mountains to the east, resulting in higher precipitation than usual for the rest of the zone (Meidinger and Pojar 1991).

The old forests are mixtures of spruce and fir with scattered *Pseudotsuga menziesii* var. *glauca, Pinus contorta* var. *latifolia* and *Betula papyrifera*. Old forests at the Aleza Lake Research Forest are thought to be uneven aged (Decie 1957). The dominant spruce, perhaps members of an initial fire origin cohort, are as many as 300 years old. The oldest fir are about 200 – 250 years old and are probably members of a post-fire establishment cohort. The scattered *P. menziesii* component can be as many as 500 years old (Decie 1957) and may be survivors of the last fire as well as some younger individuals which successfully regenerated in the understory. The well developed

understory layer is mainly comprised of fir (80%) and spruce (20%) (Chapter 4). Spot fires, insects (*Dendroctonus rufipennis*), various diseases, (including *I. tomentosus*), timber harvesting, windthrow, and snow or ice damage have been the main disturbance agents at the Aleza Lake Research Forest since the last wildfire (Decie 1957).

5.22 Site Selection

Forest cover stratification: Forest cover maps were initially used to locate 12 stands that were large (*i.e.* > $\frac{1}{2}$ hectare) and relatively homogeneous mixtures of spruce and fir on medium to good sites, undisturbed by human activities, with minimal variation in soils and topography. Each of the 12 stands was ground checked for appropriate characteristics and a number were dropped because they didn't meet the initial criteria. Each stand was checked for the presence of *I. tomentosus* using standard field techniques (Finck *et al.* 1989). In living trees, the primary diagnostic of *I. tomentosus* are large, longitudinal pits formed in roots with advanced decay and the presence of dark reddishbrown stain in the roots with relatively recent infection (Finck *et al.* 1989). After a tree dies, the longitudinal pits can be used to confirm *I. tomentosus* for 30-40 years before decomposition makes diagnosis less reliable.

Three stands were selected with relatively abundant *I. tomentosus* infection (5-10%) and mortality throughout and three stands were selected without any apparent *I. tomentosus* infection. Plot 1 was located in a stand on the west side of the Aleza Road approximately 2.5kms south of the junction of the Bear Road and the Aleza Road. Plot 2 was located in a stand on the north side of the Bear Road approximately 1km east of the junction of the Bear Road approximately 1km east of the junction of the Bear Road and the Aleza Road. Plot 3 was located on the south side of the

East Loop Road approximately 500m east of the junction of the Old Ranger Road and the East Loop Road. Plot 4 was located in a stand on the East side of the Aleza Road about 1.5kms south of the switchback approaching Camp Creek. Plot 5 was located in a stand on the south east side of the Bear Road (near an secondary access road) about 3.5kms south-west of the Aleza Road and Bear Road junction. Plot 6 was located in a stand on the east side of the Aleza Road about 700m south of the Aleza Road and Upper Fraser Road junction.

In all cases, the plots were established on flat areas, with well-drained loamy soils. Indicator plant species present on the plots suggested that the sites were broadly mesic in moisture status and medium to rich in nutrient status (DeLong 1996). Soil moisture and nutrient status were not determined quantitatively because qualitative assessments of edaphic characteristics provide acceptable means of characterizing relative soil moisture and nutrient status within the same biogeoclimatic sub-zone (Klinka *et al.* 1989).

5.23 Sampling design and plot measurements

Within each of the six identified stands, one 70×70 meter plot (0.49 ha) was established. This plot size was selected because it was large enough to include many gaps. Each plot was sub-divided into a grid network with 7×7 meter spacing along each axis using a laser-surveying instrument (Criterion 400, Laser Technology Inc.). The seven meter spacing was chosen to sample at least 100 trees in each plot. There were 11 lines along each axis for a total of 121 grid points located at the intersection of each line.

At each grid point a wooden stake was labeled according to its location on the grid (*i.e. x*,*y* coordinates) and driven into the ground.

The canopy tree (defined as any tree whose crown receives direct sunlight from above) whose stem was closest to each grid point was then mapped relative to the grid point and was coded according to species, diameter, and live crown ratio (Frelich and Graumlich 1994). This canopy criteria was used because trees whose crowns receive direct light from above may have been released due to a gap-making event. Trees whose crowns do not receive direct light from above are assumed to be suppressed by the crown of neighboring trees. Selection of the nearest stem, rather than using the nearest crown results in the best estimate of original gap area before lateral crown expansion of bordering trees into the gap (Frelich and Martin 1988; Lorimer and Frelich 1989). From each canopy tree, one increment core was taken at 1.0 m to avoid, as much as possible, losses in core information due to butt rot. Cores terminating within 2 cm of the estimated location of the pith were considered complete and the total age was extrapolated from the earliest five years growth to the pith (Frelich and Graumlich 1994; Frelich and Reich 1995). If a complete core could not be taken from a tree after several attempts, the next closest tree was selected. The cores were labeled according to the grid point location, stored in plastic straws, dried, mounted on grooved rigid foam strips, sanded, and scanned. Ring width increments were digitally scanned and analyzed with Windendro® (Regent Instruments, Blaine, Quebec). Increment data was graphed for visual inspection of radial growth patterns.

5.24 Interpretation of Growth Patterns

Three general criteria were used to relate growth rate patterns to canopy mortality (Chapter 3). The tree criteria were: 1) High rates of early growth (1.5mm/yr for spruce, 1.7mm/yr for fir, and 1.07mm/yr for birch) indicate a tree was growing in a gap (created by a disturbance) when it was very young. 2) Tree release (>65%, sustained for 15 years, preceded by 15yrs of slow growth, for spruce <40cm dbh and for fir and birch <30cm dbh) indicates a tree was suppressed in the understory and then released by an overhead mortality. 3) Interpretations of overall growth patterns (see Chapter 3) indicating either gap origin status or release were used to determine the decade of canopy ascension for canopy trees not meeting gap-origin or release criteria.

5.25 Analysis for Spatial Patterns of Disturbance

The spatial patterns of canopy ascension dates were used to describe the spatial patterns of small-scale disturbance in the 70×70 meter grid plots. This approach does not require knowledge of locations of canopy trees when they died, but rather assumes that canopy ascension dates coincide with overhead mortalities in the vicinity. Spatial autocorrelation analysis using Moran's I is used to test for spatial independence in canopy ascension date at one locality relative to adjacent localities. Adjacency is specified for the analysis depending on the inter-tree distance and the lag distance set for the analysis (Sokal and Oden 1978a; Sokal and Oden 1978b; Legendre and Fortin 1989; Frelich *et al.* 1993; Frelich and Reich 1995). Thus, trees within the set distance lag are considered adjacent and those outside the lag are ignored. For this analysis a cumulative distance lag is employed and the analysis determines the Moran's I statistic for the decade of canopy

ascension for any tree within 7 meters of another. Each additional lag includes the previous lag distance plus 7 meters.

Interpreting Moran's I is similar to interpretations for the standard correlation coefficient (Sokal and Oden 1978a; Sokal and Rohlf 1995; Frelich et al. 1993; Frelich and Reich 1995). This statistic represents the strength of spatial association for canopy ascension dates for a defined distance lag (Frelich and Graumlich 1994). Moran's I was determined for each distance lag (i.e. 0-7m 0-14m, 0-21m, etc.) and a correlogram was constructed for each plot up to 70 meters. Each correlogram plots the Moran's I statistic for each distance lag on the ordinate axis and the distance lag on the abscissa. High positive values of Moran's I at short distances indicate that canopy ascension date is strongly correlated with canopy ascension dates in neighboring trees. Values of Moran's I will gradually decrease as distance increases in uneven-aged forests because date of release will not be reliably predicted by a neighbor's date of release. Significance testing of the correlograms was done first at the global level by determining if at least one pvalue for individual Moran's I coefficients was significant at the global level. This was done by using the Bonferroni correction method for multiple tests (e.g. $\alpha = 0.05$ /number of distance lags (11)) (Sokal and Oden 1978a). If the global test is has at least one significant Moran's I coefficient then the point at which Moran's I becomes no longer significant ($\alpha = 0.05$) can be interpreted as the average patch size diameter created by disturbance (Frelich et al. 1993; Frelich and Reich 1995). Globally insignificant correlograms are interpreted that average patch size diameter is less than the distance lag.

Spatial autocorrelation analysis was also used to determine the tendency towards association or disassociation between pairs of unlike or like species. (Sokal and Oden 1978a; Frelich *et al.* 1993; Frelich and Reich 1995). With species data, a join-counts statistic was calculated for spruce-fir joins, spruce – spruce joins, and fir-fir joins. The join-counts calculation is done between one sampled canopy tree at a given location and each remaining canopy tree immediately surrounding it on the grid in all directions within 7 meters. This connection scheme is a queens connection matrix (Sokal and Oden 1978a). Significance testing ($\alpha = 0.05$) is performed by calculating a standard normal deviate (S.N.D) for each join possibility. Significant positive spatial autocorrelation for a joinpair is indicated by S.N.D's > 2.0. Significant autocorrelation (p>0.05) of species is indicated by S.N.D's <-2.0 and 2.0 (Moran 1948; Sokal and Oden 1978a; Reed and Burkhart 1985; Frelich and Reich 1995).

5.30 RESULTS

5.31 Canopy Composition

Spruce canopy composition averaged 29.9% for the three *I. tomentosus* infected plots (n = 345), while fir canopy composition was 66.1%. *I. tomentosus* incidence was estimated at between 5-10%. For the three uninfected plots (n = 344), spruce density was 32.6%, while fir density was 58.7%. No significant difference (χ^2 (1,634) = 0.0957) (α = 0.05) was found for the proportion of spruce in the canopy between the two forest types.

5.32 Canopy Ascension Type by Species

From the 334 canopy trees sampled in the *I. tomentosus* plots, there were 369 canopy ascensions and for the uninfected plots there were 401 canopy ascensions recorded from 336 increment cores (Table 1). No significant difference (χ^2 (1,243) = 0.1523) was found between infected and uninfected forest types in the proportion of gap origin verses release events for spruce or fir (Table 1).

5.33 Canopy Ascension by Decade

In each forest type, canopy ascensions were recorded as early as 1675 (Figure 1 and 2). For plot one (Figure 1) the species ascending to the canopy between 1670 and 1680 was a spruce and for plot four (Figure 2) the species was a Douglas-fir. Very little mortality was recorded before 1795, which is likely because trees which would have responded to the mortality prior to that have died and because the criteria used for canopy ascension are vigorous enough to avoid detecting canopy thinning events in when the stand was younger.

With the exception of plot 2 and 6 (Figure 1), the highest rate of canopy ascension occurred between 1960 and 1970. For plots and 6 the highest rate of canopy ascension occurred between 1970 and 1980. The maximum canopy ascension in these decades ranged from a high of 52.50% of stand area in plot 3 to a low of 14.05% in plot one. Since the canopy ascensions recorded before 1800 were sporadic, average estimates of stand area converted to gaps in each decade (canopy turnover) were calculated from 1800 to 1998. Average canopy turnover rates were fairly consistent for all six plots, ranging from a maximum of 6.00% in plot 3 to a minimum of 5.09% in plots 2,5 and 6.

5.34 Spatial Patterns of Canopy Disturbance

Figures 3 and 4 show some degree of clumping in ascension cohorts. The spatial pattern of canopy ascension since about 1750 is generally characterized by small gaps created in a given decade or couple of decades interspersed with canopy ascension dates separated by a few decades or more. A global significance test for the correlograms using the Bonferroni correction method indicted that at least one p-value for a Moran's I coefficient in a correlogram must be <0.005. Only Plot 3 (Figure 6) had any significant Moran's I coefficients at the global level. However, the significant Moran's I coefficients were close to zero which indicate there was no similarity in disturbance date. Therefore, all six correlograms indicate that average gap size caused by disturbance is less than 7 meters in diameter. No differences in correlogram structure between *I. tomentosus* plots and uninfected plots were evident indicating that the pattern of disturbance in *I. tomentosus* stands is similar to uninfected stands.

5.35 Spatial Patterns of Species Patches

Standard normal deviates (S.N.D's) (Table 2) indicate that: 1) positive spatial autocorrelation (*i.e.* clumping) generally exists for spruce; 2) Fir-spruce spatial patterns are random and; 3) there is a weak trend for fir to be negatively associated with itself. There does not appear to be an effect of *I. tomentosus* on the species patch structure since fir has a random arrangement, as evidenced by the not statistically significant (α >0.05), low-order negative values of the indicated S.N.D's (Table 2).

5.4 DISCUSSION

5.41 Spatial Patterns of Disturbance

Fir was the most frequent species entering the canopy in all six plots since canopy replacement began at about 1750. However, fir was associated with canopy ascensions occurring in more recent decades than in earlier decades where spruce was more common. The same trend was reported in Chapter 4 where transition probability data suggested that fir has become the dominant species of understory tree currently replacing canopy trees (regardless of species) for the last 50 years. It is evident then that canopy composition of fir has been increasing in recent decades. It can be speculated that ultimately a shift from a spruce and fir mixed forest to a fir dominated forest is likely. Since the incidence of infection in these stands was low to moderate (5-10%), small patches of disturbance irregularly distributed were noted. Given a higher (>15%) incidence of infection it is possible that gaps created would be larger due to coalescence of infection centers (Lewis *et al.* 1992).

Gap size averages <7m in diameter but varies from small (<7m diameter) to fairly large (28m diameter) openings created in the canopy (Figures 3, 4, 5, and 6). The openings are irregularly distributed over the stands. This type of spatio-temporal pattern of disturbance suggests that windthrow or windsnap, ice and snow damage, root diseases, senescence and endemic populations of spruce bark beetle have been the predominant disturbances in these stands since the last catastrophic disturbance. The result is a patchwork pattern of disturbance which has enabled understory recruitment to the canopy. Note that the locations of canopy ascension dates (Figures 3 and 4) clearly show larger gaps than the Moran's I analysis indicates. Moran's I analysis only interprets average gap
size. Thus, the larger patches of disturbance especially during the 1960-1980 (Figures 3 and 4) period represent variation in the disturbance regime, but the higher frequency of smaller gaps than larger gaps in these forests bring average gap-size diameter below 7m. The discrepancy between correlogram structures (Figures 5 and 6) and the physical representation of the data (Figures 3 and 4) suggests that larger scale disturbances, possibly caused by more wide spread bark beetle, snow, ice or windthrow occasionally influenced stands but overall the disturbance regime is one of single tree mortality dispersed irregularly throughout the forests.

5.42 Species Patch Structure

Spruce was 28.4% and 32.6% of canopy density (stems/hectare) for the infected and uninfected stands respectively, was significantly positively correlated with itself. Therefore spruce is more likely to be associated with itself than other species. Fir:Fir joins were not statistically significant as were Spruce:Fir joins. Several ecological explanations are plausible for the statistical grouping of spruce as shown. Spruce grouping may be linked to a combination of the following: 1) the establishment of spruce regeneration on nurse logs, 2) exposed mineral soil caused by root tip-ups due to windthrow, or 3) the grouping of a residual old spruce cohort.

5.5 CONCLUSIONS

Based on spatial-autocorrelation analysis of release dates in understory trees, canopy gaps are small and irregularly located in the wet Sub-Boreal Spruce forests at Aleza Lake. These forests are affected by a variety of disturbance agents. While *I. tomentosus* is a significant cause of tree mortality in some stands, its pattern of disturbance was not found to be unlike other disturbance patterns based on this analysis.

The combined impacts of all the disturbances have enabled understory recruitment to the canopy as early as the late 1600's. In recent decades significant mortality (as high as 52.5%) has occurred and although this rate happened in only one plot, disturbances over 10% of stand area occurred quite often. This rate of canopy mortality suggests that the forests may be changing from a multi-aged old-growth stand to an uneven-aged old-growth forest, defined here as a forest in which all of the original cohort has died and has since been replaced by understory species.

Current fir canopy composition is 66% in *I. tomentosus* infected stands versus 59% in uninfected stands. However, much of the replacement that has been occurring over the last 50 years, consists of fir. Therefore spruce composition in the canopy has been declining and will likely continue to decline due to the small gap disturbance regime which suites fir shade tolerance and seed germination strategies better than spruce. However greater life-spans for spruce will help to maintain it in the canopy (Lewis and Lindgren 1999), particularly in these stands with low *I. tomentosus* incidence. Species patch analysis indicated that spruce was positively associated with itself which is probably due to clumping of spruce on nurse logs or exposed mineral soil cause by root tip-ups and the grouping of a residual old spruce cohort. The decline of spruce due to a

variety of disturbance mechanisms suggests that over time the old-growth forests will be dominated by fir in canopy composition and spruce may decline to about 10% of stand composition (Chapter 4).

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		Type of ascension			
Treatment	Species	Release	Gap	Tota	
Infected	Spruce	0.44	0.56	113	
Infected	Fir	0.59	0.41	242	
Infected	Birch	0.38	0.62	13	
Infected	Hemlock	0.00	0.00	0	
Infected	Douglas-fir	0.00	1.00	1	
Uninfected	Spruce	0.53	0.47	131	
Uninfected	Fir	0.54	0.46	235	
Uninfected	Birch	0.57	0.43	21	
Uninfected	Hemlock	0.55	0.45	11	
Uninfected	Douglas-fir	0.33	0.67	3	
	Total	414	356	770	

Table 1. Proportion of canopy ascension types by treatment type, and species.

Treatment	Plot	Fir-Spruce Joins	S.N.D.	Fir-Fir Joins	S.N.D.	Spruce- Spruce Joins	S.N.D.
Infected	1	59	1.0520	59	-1.2310	12	1.7860
Infected	2	61	1.1137	60	-1.3227	13	2.0256
Infected	6	43	0.7450	74	-1.0703	13	2.9002
Not Infected	3	42	0.5949	46	-1.0879	21	3.2140
Not Infected	4	56	0.8433	36	-1.3081	24	2.7775
Not Infected	5	49	1.0009	78	-1.2248	10	2.4557

Table 2. Summary of spatial autocorrelation of species association using joins-count statistics. Standard Normal Deviates greater than 2.0 indicate a higher than expected number of like joins which is interpreted as significant spatial autocorrelation.

■ Spruce ■ Fir □ Other



Figure 1. Canopy ascension by decade and by species for *Inonotus tomentosus* infected plots (Plots 1,2, and 6). The ordinal axis shows the percentage of stand area affected by disturbance in each decade.

Spruce Fir D Other



Figure 2. Canopy ascension by decade and by species for *Inonotus tomentosus* uninfected plots (Plots 3,4, and 5).





Figure 3. Locations of canopy ascension dates for trees in the three infected plots. Numbers on the axis are in meters. Blank squares indicate that no canopy tree was found within seven meters of the sampling location on the 7 by 7 meter grid.



Plot 5



Figure 4. Locations of canopy ascension dates for trees in the three uninfected plots. Numbers on the axis are in meters. Blank squares indicate that no canopy tree was found within seven meters of the sampling location on the 7 by 7 meter grid.



Figure 5. Correlogram showing Moran's I statistic on the ordinate axis and distance lag on the abscissa for plots 1,2 and 6 (plots with *Inonotus tomentosus*). Open symbols represent statistically significant Moran's I coefficients.



Figure 6. Correlogram showing Moran's I statistic on the ordinate axis and distance lag on the abscissa for plots 3,4, and 5 (plots free of *Inonotus tomentosus*). Open symbols represent statistically significant Moran's I coefficients.

CHAPTER 6. SUMMARY OF FINDINGS, MANAGEMENT RECOMMENDATIONS AND CONCLUSIONS

6.0 STUDY RATIONALE

Ecosystems cross a hierarchy of scales. A downed log on the forest floor is an ecosystem with its own biophysical attributes. This log is part of a larger ecosystem, perhaps an old spruce-fir stand. The spruce-fir stand is part of a watershed or a landscape ecosystem, and the landscape part of a regional ecosystem. The large regional ecosystem fits into an even larger biome such as the boreal forest in this example. At each successive level in the hierarchy, more species are involved; there is more variation in physical characteristics; and, the interactions, function, structure, and dynamics become more complex and variable. At each stage in the hierarchy forest ecosystems have unique structure, specialized functions, complex interactions and are continually changing. Individual ecosystems vary in their own complexity over time and the level of complexity between ecosystems also varies. However, the resiliency and stability of ecosystems are greatest when their complexity is maximized (Kimmins 1997).

Human influence on ecosystems has generally caused a decrease in complexity and therefore a reduction in their resilience and stability. Forests have been cleared throughout the world and are replaced with agricultural ecosystems. The orchard, corn or wheat field is managed for one species and increasingly genetically identical individuals. Wetlands have been drained to support agriculture or urban development. Natural forests are being cleared to make way for managed forests, converting a landscape with astonishing biological diversity to a landscape where only a few species are managed to optimize timber production on short economic rotations.

Knowledge about ecosystem structure, function, complexity, interactions and change is crucial in order to understand the impact of human influence on the environment. This knowledge may be critical for the survival of our species because accumulated effects of ecosystem degradation may affect the entire biosphere, the atmosphere and the hydrosphere. Together these define the biophysical characteristics of the ultimate ecosystem, Earth. Evidence of these global consequences of ecosystem mismanagement are already evident: global warming, desertification, extinctions, soil erosion, and stream siltation.

As natural ecosystems are lost and the integrity of remaining ones compromised, the concept of ecosystem management has crept into the dialogue of land and resource management. Ecosystem management adopts principles that are entrenched in 'landscape ecology' and 'natural disturbance ecology' (Parminter and Daigle 1997). One of the concepts of landscape ecology in the forestry context is that if forest management mimics natural disturbances, inherent ecosystem attributes will be preserved and important ecological processes will be maintained (Parminter and Daigle 1997). It follows from this principle that if natural disturbances are large and catastrophic then large clearcuts of the same size, pattern and concentration would be the appropriate harvesting method to mimic this disturbance. Similarly if small-scale disturbances are predominant then, partial cut harvesting methods would be most appropriate. Most often landscapes are not dominated by one disturbance pattern or type. Landscapes are shaped due to a variety of disturbances operating at a variety of scales and intensities (White 1987; Engelmark *et al.* 1993). Forest management should therefore employ variation when planning land-use activities to reflect the variation in pattern caused by natural processes.

In boreal forests considerable effort has been directed towards studying landscape level disturbance patterns and stand dynamics. Much of the work has concentrated on characterizing the fire return interval, patch size of fire disturbances and the resultant landscape level age-class mosaic (Bergeron *et al.* 1993). For example, much of the subboreal, montane forests in central interior of British Columbia are composed of fireorigin forests whose climax species composition on upland sites are dominated by spruce (*Picea glauca, Picea engelmannii* or *Picea glauca* × *engelmannii*), *Abies lasiocarpa*, *Pinus contorta, Populus tremuloides, Pseudotsuga menziesii*, and *Betula papyrifera*. Although dryer parts of the region were burned by wildfire at intervals ranging from 150-250 years (British Columbia Ministry of Forests and B.C. Ministry of Environment, Lands, and Parks 1995), wetter parts, particularly those in the foot-hills and sub-alpine elevations historically had fire return intervals ranging from 227-6250 years (Hawkes *et. al.* 1997). Within these wet, mountainous areas, information is lacking about the spatiotemporal pattern of small-scale disturbances and on subsequent stand dynamics (succession).

Small-scale disturbances have been shown to be important processes in many forested ecosystems including boreal forest ecosystems. However, studying the patterns and processes of small-scale disturbances have typically been neglected in boreal forests simply because fire was conventionally thought to be the main disturbance agent in this forest type (Bergeron *et. al.* 1993). In wet boreal and sub-boreal forests, fire return intervals have been shown to be quite long, often approaching intervals that are characteristic of more humid environments such as west-coast temperate rainforests, and sub-alpine forests. Given the long fire return intervals that are possible in these wet, cool

boreal forests, small-scale disturbances have been identified as a factor in modifying the forest community (population structure and demographics) and the physical environment (light regimes, temperature, moisture regimes and nutrient availability and dynamics) (Bergeron *et al.* 1993). The extent of their influence is related to the length of time between catastrophic disturbances.

Windthrow, insect attacks, and root diseases, are important types of small-scale disturbance agents in these forests (Hofgaard 1993; Kneeshaw and Burton; 1997; Kneeshaw and Bergeron 1998). One of the most important small-scale disturbances in boreal forests is *Inonotus tomentosus*. This root disease pathogen is ubiquitous in *Picea spp.* forests and is responsible for significant mortality especially in mature forest ecosystems dominated by *Picea spp.* (Lewis 1997). Therefore understanding the role of *I. tomentosus* in stand disturbances is necessary in order to understand its impact on *Picea spp.* forest communities which make up a significant component of boreal and sub-boreal forest landscapes. Secondly, the patterns of disturbance in general are useful in designing forest harvesting activities that mimic natural disturbance patterns. And, lastly in order to confidently prescribe partial cut harvesting systems, potentially adverse or undesirable impacts on stand composition and structure that occur because of potential interactions between partial cutting and *I. tomentosus* need to be understood or ruled out.

In order to contribute to the knowledge and understanding of disturbance ecology and stand dynamics of wet, natural and unmanaged sub-boreal spruce forests in central British Columbia, this thesis raised three basic questions:

1. What are the spatial and temporal patterns of disturbance for old-growth forests with and without the influence of *I. tomentosus*?

- 2. How does stand composition and structure differ between *I. tomentosus* infected and non-infected old-growth forests?
- 3. How does partial cutting influence stand development in *I. tomentosus* infected and non-infected forests?

The remainder of this chapter summarizes the findings of the thesis research, discusses potential applications of the methodology developed for this research and discusses future research needs.

6.1 SUMMARY OF RESEARCH

6.11 Canopy Disturbance

1) *Disturbance History*: Mortality of canopy trees was indicated by tree ring information sporadically as early as the 1670's and was consistently evident since the late 1700's. The oldest individuals in the stands were well over 300 years old and did not appear to have fire scars. Therefore, these indirect results show it has been at least 300 years since the last stand-replacing disturbance at Aleza Lake. If the last large scale fire occurred roughly 300 years ago, then mortality evident in the late 1700's began approximately 100 after the fire. This would correspond to the timing of the understory re-initiation stage where mortality of canopy trees creates canopy gaps that allow understory species to regenerate and recruit to canopy positions.

2) *Canopy Disturbance Rates:* Two independent studies (Chapter 4 and Chapter 5) indicated similar levels of canopy mortality in natural forests (un-harvested forests) as expressed by the percentage of canopy disturbance per decade. In a fine scale study (fixed radius plots, Chapter 4), average percent canopy disturbance was between 6.9% and 8.1% per decade. In a coarser-scale study (grid plots, Chapter 5), canopy disturbance averaged 5.09% and 6.0% per decade. Therefore based on widespread sampling in four different stands, using two independent approaches, canopy disturbance at Aleza Lake ranges on average from 5% to 8% per decade.

6.12 Gap Size

Gap size was also determined using two independent and distinct methodologies developed in Chapter 4 and Chapter 5. In Chapter 4, the estimate of average singe-tree gap-size was $16.76m^2$. In Chapter 5, it was determined that patch diameter averaged <7mwhich corresponds to an gap area of about $38.5m^2$. Note that the $38.5m^2$ gap size estimate was limited to the lag distance specified in the spatial autocorrelation analysis (7m). Based on these two approaches, it is evident that average gap size is typically $<38.5m^2$ indicating that the vast majority of gaps are due to single tree mortality. Larger gaps do form in these forests but with lower frequency than single tree gaps.

6.13 Canopy Mortality by Species

In Chapter 3 it was determined that spruce accounted for 42% of total accumulated mortality and (because of its generally larger size) over 50% of accumulated basal area mortality. This high percentage of total mortality in old forests is likely due to the fact that a uniform cohort predominately composed of spruce, has been suffering high rates of mortality due to a variety of mechanisms.

6.14 Stand Composition, Canopy Replacement and Future Stand Composition

Results from Chapter 4 and Chapter 5 indicate that canopy composition is dominated by fir at about 65-70% of canopy by stems per hectare for all size classes combined. Spruce represents about 25-30% of stand density and about 47-57% of basal area. Understory composition was also dominated by fir at 86%-92% of stand density. Due to the high density of fir in the understory, canopy tree replacement by this species outnumbers all other understory species by at least 2:1. Due to high rates of spruce mortality over the last 50 years or more, and high proportion of fir replacing dead canopy trees of any species, the spruce component of the canopy has been on the decline for the past several decades. Fir composition has been increasing over the same period. Given the current combination of high canopy recruitment rates of fir, high spruce mortality and the overwhelming abundance of fir in the understory layer, fir populations will continue to increase over the next 200 years.

6.15 Impacts of *Inonotus tomentosus* and Partial Cutting on Disturbance and Stand Composition

In old-growth forests with low to moderate infection incidence (<15%), specific differences in disturbance regime caused by *Inonotus tomentosus* are not apparent. Disturbance history, disturbance rates, gap size, spatial patterns of disturbance and accumulated spruce mortality are not significantly different in old-growth stands with *I. tomentosus* compared to old-growth stands without the root disease.

Partial cutting has increased the density of spruce in the understory, and decreased subsequent mortality rates in both infected and uninfected stands relative to old-growth forests. Since most of the understory spruce has regenerated post-harvest they have not yet moved into the canopy layer. Given time, canopy layer spruce populations should also rise. Reductions in mortality are most likely due to captured mortality of older and larger individuals and upgrading the vigor of remaining spruce. Although spruce populations were not significantly lower in *I. tomentosus* infected stands compared to uninfected old-growth and partially cut stands, spruce volumes are significantly lower (6-10%).

6.2 MANAGEMENT APPLICATIONS

6.21 Prescribed Harvest Intensity for Partial Cut Harvesting in Wet-Cool SBS Forests

Disturbance chronologies presented in this thesis indicated that over a period of 70 years (Chapter 4) and 200+ years (Chapter 5), average canopy disturbance averaged between 7.4 and 8.1% per decade. From the accumulated mortality data (Chapter 4), this level of canopy disturbance corresponds to approximately 44-48 mortalities/hectare/ decade. Diameter class distributions of dead trees (Figure 1) indicates that the average diameter of trees dying is 29.9cm dbh. Species composition of dead trees is 41-42% spruce (stems/ha) and 51-56% (basal area). All of this evidence suggests that partial-cut harvesting if conducted every 10 years in these old spruce-fir forests should remove 44-48 stems/ha/decade with an average diameter of 29.9cm and approximately 51-56% of the basal area should be spruce.

6.22 Harvest Dispersion

Harvests should create a variety of gap sizes but the average gap diameter should be 7m or less. This suggests that single tree selection silviculture systems combined with small group tree selection systems would be the most appropriate combination of silviculture systems for these forests to maintain natural forest structure. The gaps themselves should be irregularly distributed across a landscape or stand.

6.23 Harvest Timing

Due to the continuous low intensity disturbance that prevails in these forests, it would not be advisable to "bank" harvests for 3 or more decades and then triple or more harvest intensity, especially if the objective is to maintain "old-forest" values (*i.e.* more intense harvests may increase spruce regeneration – as it did in the partial cut forests – which is contrary to natural stand-dynamics where fir recruits to the canopy). However if the objectives are to maintain spruce as a component in the stands for timber supply, more intense harvests on less frequent intervals would provide conditions necessary for spruce recruitment and survival.

6.24 Development of Methodology

This research has advanced two important retrospective methodologies that have made possible the quantification of disturbance regimes for this area: The Time Since Death model (TSD model) (Chapter 2), and the Growth Rate/Percent Release criteria (Chapter 3). Both methodologies could be used in similar studies so long as regional climate and latitude are similar. The methods should be tested and calibrated for local conditions before studies begin.

The TSD model probably has the most potential for widespread immediate use with only minor calibrations necessary so long as the species are limited to spruce and fir. This model allows for very quick and accurate estimates of year of mortality which allows for large areas to be sampled and many tree deaths to be calculated. Climate has been shown to play a major role in tree decomposition, therefore calibration of this model should be performed before studies begin.

The simplest and most efficient means of calibrating the TSD model would be to compare death estimates from the TSD model to year of death estimates calculated from increment cores in understory trees. An error factor built into the time since death

prediction from the TSD model developed in the present study could be either added (for slower rates of decomposition) or subtracted (for faster rates of decomposition) by comparing the two dates. For example, if the TSD model consistently indicates mortality dates 10 years earlier than tree ring core estimates then an error factor of + 10 years would need to be added to the TSD model estimate.

The TSD model allows research of the mortality dynamics for forests of any age as long as tree diameters exceed 10cm dbh. Furthermore, because it is efficient and accurate the disturbance regime over a very large area or in many areas can be determined. The main disadvantage of the TSD model is that it is only accurate in predicting time since death up to about 70 years. Therefore when a longer term in disturbance regime study is needed, tree growth pattern analysis is the still the best method.

Until now, growth/release criteria of understory trees that enable the interpretation of the disturbance regime has been lacking in the sub-boreal and boreal forests of British Columbia. This thesis developed release and growth rate criteria for understory spruce, fir, and *B. papyrifera* responding to the death of an overstory tree. Although this information may not be precisely applied to other ecosystems in the boreal and subboreal forests, it should provide a guide for ecosystems with similar physical (latitude, soils, temperature, and moisture) and biological characteristics (species composition, crown shape/form, and tree height).

6.25 Future Research

Research concerned with the role of small-scale disturbances in boreal and subboreal forests has only just begun. Furthermore, disturbances operate at many different scales, they interact with physical and biological ecosystem components and with other disturbance agents, and disturbances are stochastic. All this variation combined with the developing understanding means that research into small scale disturbance regimes must continue over large areas, and in many different stands before adequate information is gained. Thus, an efficient yet comprehensive approach needs to be adopted in order to characterize the natural disturbance regime before too much of the landscape is managed using harvest patterns that are not compatible with the natural disturbance regime.

A general approach is suggested here to expedite the investigation:

- Stratify the land base: The boreal and sub-boreal forests in British Columbia should be stratified into units that tend to have the longest stand replacing disturbance interval. This work has already been done by the biogeoclimatic ecosystem classification (Meidinger and Pojar 1991) and the natural disturbance type classification system (British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands and Parks 1995).
- 2) Prioritize the land base: Determine where partial cut harvesting systems should be implemented based on ecological, or social values. Much of this work has also been done in the Land and Resource Management Planning Process or the Timber Supply Review.
- 3) Develop methodology and sample the land base: Using the TSD model developed in this thesis, calibrating the model for climactic conditions, and linking time since death

estimates to the wildlife tree class system (British Columbia Ministry of Forests and British Columbia Ministry of Environment, Lands, and Parks 1995) would provide for a easily developed, widely applicable and easily used tool for determining time since death. Sampling could be done in conjunction with operational timber cruising. This could make the sampling quite inexpensive and cover many stands.

- 4) Compile information and develop harvesting patterns: The data from the sampling should then complied and compared. Broadly similar disturbance regimes should be identified at this point and incorporated into specific management guidelines.
- 5) Apply and monitor: once the guidelines are in place and operational harvests are using the guidelines, a monitoring program should be followed. Monitoring should include an assessment of whether the system is providing similar stand structure, and composition and dynamics compared to natural stands.

6.3 CONCLUSIONS

This thesis has indicated that small-scale disturbances are important ecological processes in sub-boreal forest ecosystems. The information presented in this thesis can now be added to a small but growing body of literature concerned with investigating the patterns and processes of small-scale disturbance across the circumpolar boreal forest. In such a large biome, and in a relatively new discipline much work still needs to be done. It is hoped that this thesis will play a small but significant role in supporting related research and in advancing management applications related to disturbance ecology.

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Figure 1. Diameter class distribution (dbh) of dead trees in old-growth forests (n = 509). Mean dbh = 29.9cm.