NATURAL DISTURBANCE AND STRUCTURE IN TWO PRIMARY BOREAL FORESTS OF WESTERN NEWFOUNDLAND

by

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A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

in

THE FACULTY OF GRADUATE STUDIES

Department of Forest Sciences
Faculty of Forestry

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

April, 2004

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ABSTRACT

It was long assumed that small-scale gap disturbance did not figure predominantly in boreal forests. Attention has focused, instead, on the role of stand-replacing fire and insect outbreaks in structuring the boreal forest landscape. Recent work, however, beginning principally in Scandinavian boreal forests, has highlighted the primary role of small-scale canopy gap disturbance in old-growth boreal forests.

To examine the role of gap dynamics in boreal forests of western Newfoundland, two primary forest landscapes were compared: (1) a 225 km² Main River study area located at the southern base of the Great Northern Peninsula, and (2) a 106 km² Little Grand Lake study area in western Newfoundland, Canada. It was hypothesized that the size and age structure, on both the stand- and landscape-level, were determined by distinctly different disturbance regimes, namely, fungal-mediated gap dynamics in the Main River forests and insect-mediated patch dynamics in the Little Grand Lake forests. The contrast between the cool, short-growing season of the Main River watershed and the warmer, longer-growing season of the Little Grand Lake area probably determine the different disturbance regimes.

The hypothesis was tested by comparing the size and age structure of two primary forests and inferring disturbance process from stand and landscape patterns. In the Little Grand Lake study area, a chronosequence of naturally regenerated stands also permitted the examination of post-disturbance stand development.
Results confirmed that the structure of both forest landscapes is determined by radically different disturbance regimes. The Main River landscape is a natural disturbance type (NDT) 1 ecosystem in which stand-initiating disturbance is rare. The Little Grand Lake landscape, however, is an NDT 3 ecosystem in which stand-initiating disturbances are frequent.

The old-growth stage of stand development dominates the Main River landscape. Stands are structurally complex with well-developed rotated sigmoidal diameter distributions (semi-logarithm), heterogeneous canopies, and reverse-J age class distribution with trees at maximal known ages. The seedling bank is old (up to 100+ years) and characterized as well by a reverse-J size and age distribution. Stand and landscape structure are reflective of a disturbance regime dominated by small-scale (< 100 to 200 m²) canopy disturbance mediated by fungal root and butt rots.

The Little Grand Lake forests are a fine patch mosaic composed of approximately 0.5 to 150 ha even-aged or irregular stands comprising all age classes from 0-20 to 120 + years. All stages of stand development (stand initiation to transition/true old-growth) are present and form a well-developed chronosequence. Stands and seedling banks are generally modal or near modal in terms of tree diameter at breast height (dbh), height, and age distributions. Stands of edaphic or stochastic old-growth further complexify the mosaic landscape. Stand and landscape structure are reflective of a disturbance regime dominated by large-scale patch mortality and partial mortality mediated by recurrent hemlock looper (Lambdina fiscellaria fiscellaria (Guen.)) and spruce budworm (Choristoneura fumiferana (Clem.)) herbivory.
Sustainable forest management of these forest landscapes is called to develop appropriate strategies, goals and objectives that are congruent with differences in disturbance regime and stand and forest structure.
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ACKNOWLEDGEMENTS

The writing of a dissertation is a solitary affair. Only the lone writer is able to sift through, ferret out, and distinguish among the mass of data, ideas, observations and insights gleaned over the years. The collection of data, the crafting of analysis and the development of ideas are, however, anything but a solitary affair. Such activities are impossible without others, many others, in fact. This dissertation is no exception. If it were left to me alone, who knows what would have emerged. This work is the fruit of the labour of many people, their ideas, their generosity and support, their unfailing love. All mistakes, dead-ends, and fallacious reasoning are mine.

To Gordon Weetman, my mentor and advisor, who agreed to take me on in the golden years of his career, and who assumed emeritus status long before his final doctoral student finished. I have appreciated his indefatigable support and his clear commitment to scholarship. His trips to Newfoundland, twice to my study sites and once to Labrador, were appreciated.

My heartfelt thanks to Charles John and Monte Osmond, both formerly of the Newfoundland and Labrador Forest Service, for their kindness and unfailing support that permitted me to begin my field research in Newfoundland. Without their generosity, much would have remained simply in potentia.

I would not have been able to do very much without the support of the Newfoundland and Labrador Forest Service. At all levels of the organization, no door was
left closed and no request ill-considered. I thank Mohammed Nazir (Assistant Deputy Minister), Alan Masters (Deputy Minister), Ivan Downton (Director, Forest Ecosystem Management), and Len Moores (Director, Ecosystem Health) for their support. Apart from the generous financial support, in-kind support was significant and included helicopter time, field lodging, truck rental, field and lab equipment, tree-ring scanner and computer, maps, aerial photographs and countless other items. Mention must be made as well of the many salaried hours offered by field personnel in support of my field research.

Comfortable field accommodation in both study areas was provided by the Newfoundland and Labrador Forest Service.

The Atlantic Forestry Centre (Canadian Forest Service) provided significant support in the way of trucks, all-terrain vehicles, trailers, wood preparation facilities, and lab and office space. I thank Wade Bowers, former director of the Corner Brook lab, for his generosity. I thank Doyle Wells, who was always ready to help in whatever manner possible and whose warm generosity never waned.

Glen Knee and Glen Payne of the College of the North Atlantic (Corner Brook campus) provided tree ring scanning equipment and lab space.

Financial and logistical support were generously provided by the Newfoundland and Labrador Forest Service (Len Moores), Canadian Forest Service (Wade Bowers), Western Newfoundland Model Forest (Jim Taylor), Corner Pulp and Paper Limited (George van Dusen), Parks Canada-Gros Morne National Park (Stephen Flemming), the Natural Sciences and Engineering Council of Canada, the Sisters of Mercy, the Presentation Sisters of Newfoundland, and William and Annerose Sims of Vancouver. Scholarships were
provided by the University of British Columbia. The Upper Canada Province of the Society of Jesus provided generous financial support throughout the entire period of study.

My field and lab assistants proved to be exemplary and patient in all kinds of weather and field conditions; Andrew Basha, Paul Tipple, Justin Basha, Paul Sinyard, and Chris Curnew. Andy Connors’ technical skills, which he shared so generously, proved to be invaluable in keeping me on the road and in the field.

My work took me from the west coast of Canada to the west coast of Newfoundland. The Basilian Fathers at St. Mark’s College, University of British Columbia, graciously provided a home in Vancouver. In Corner Brook, it was the staff of the Cathedral parish of the Immaculate Conception and Bishop Raymond Lahey, former bishop of the Diocese of St. Georges’s, who welcomed me. My thanks to the successive pastors of the Cathedral who welcomed a Jesuit amongst their midst: Rev. Joe Gash, Rev. John Peddle, and Rev. Ed Gale.

Darrell Harris and Boyd Pittman opened the data banks of the Newfoundland forest inventory. Terry Hynes and Steve Hooper carried out the photo-interpretation of the Little Grand Lake study area. Scott Payne, Doug Jewer, Todd Strickland and Perry Benoit produced the Geographic Information Systems (GIS) database for both study areas. Scott Taylor (Gros Morne National Park) produced impressive maps of both study areas. Jim Gosse’s field experience was welcome during the early helicopter reconnaissance of both the Main River and Little Grand Lake study areas. Bruce Nicholl, former Ecosystem Manager for Forest Management District 15 and 16, and Kevin Sutton, Regional Ecosystem Director, were very generous and supportive of my field research. I thank Leo Hynes, for allowing the rental of his cabin in the Main River watershed.
Christine Ducharme never tired of my myriad of questions, helped in numerous ways and produced some of the graphics. Her joy-filled patience and professionalism are deeply appreciated. Brent Ducharme's skill with CorelDraw produced the marvelous stand development graphics. For statistical advice I thank Prof. Val LeMay (University of British Columbia), Prof. Toni Kozak (University of British Columbia), Pal Varga, and Viviane Lima. Joseph Chen and Joseph Pathakamuri provided valuable technical computer assistance.

The following people also provided significant help and advice over the years of my doctoral work: Bill Alexander, Winston Anstey, Bram Avery, Bruce Boland, Chris Cohlmeyer, Hubert Crummey, Basil English, Gordon Fifield, Bill Green, Brent Humphries, Derek Innis, Wayne Kelly, Gerard Leonard, Lem Mayo, Brian McLaren, Alex Murley, Hubert Smith, Clarence Strowbridge, John Thomas, Bill Wells and Paul White (Newfoundland and Labrador Forest Service); Bruce Armstrong, Matt Churchill and Faron Knott (Corner Brook Pulp and Paper Limited); Bill Bonnell, Bill Curran, Louis DeGrandpré, Brian Hearn, Joan Luther, Joanne MacDonald, Peter Newton, and Gary Warren (Canadian Forest Service); Sean Dolter and Glenda Garnier (Western Newfoundland Model Forest); Retired Prof. Colin Banfield, Prof. Emeritus Joyce MacPherson, and Prof. Bill Montevuechi (Memorial University of Newfoundland), Prof. Lori Daniels, Prof. Hamish Kimmins, and Prof. Bart van der Kamp (University of British Columbia), Prof. Alan White (University of Maine), Prof. Fangliang He (University of Alberta), Prof. Pierre Legendre (Université de Montréal), Prof. Craig Lorimer (University of Wisconsin-Madison), Prof. Marie-Josée Fortin (University of Toronto), Prof. Peter Macdonald (McMaster University), Prof. Ken Lertzman and Prof. Rolf Mathewes (Simon
Fraser University), Prof. Bruce McCure (Oregon State University), Prof. Hubert Morin
(Université du Québec à Chicoutimi), Prof. Serge Payette (Université Laval), Prof. Lianjun
Zhang (State University of New York – Syracuse), Lee Frelich (University of Minnesota),
Chip Bird (Parks Canada), Ed Berg (United States Fish and Wildlife Service), Melinda
Moeur, Paul Hennon, Gregory Nowacki, and Brian Sturtevant (United States Forest
Service), Ian Knight (Newfoundland and Labrador Dept. Mines Energy), Ken Rollings
(Newfoundland and Labrador Dept. Environment), Roberta Parish (British Columbia
Ministry of Forests), Paolo Cherubini and Fritz Schweingruber (Swiss Federal Institute for
Forest, Snow, and Landscape Research), Yves Jardon (Institut Québécois D’Aménagement
de la Forêt Feuillue), Geneviève Brunet, Al Connors, Paul Deal, Jary Dobry, Valérie
Levasseur, Charles McCarthy, Fred McCarthy and Ed Woodrow. As well, I especially
thank the helicopter pilots of both Universal Helicopters and Canadian Helicopters for their
humour, professionalism and guidance.

I thank my committee (Prof. Gordon Weetman, Prof. Karel Klinka, Prof. Valerie
LeMay, and Dr. Bill Meades (Canadian Forest Service)) for their formative support over
the years, and for critically reading the rather long opus. Prof. Bruce Larson (University of
British Columbia), Prof. Gary Bradfield (University of British Columbia) and Prof. Louis
Bélanger (Université Laval) proved to be excellent readers and defense examiners. Prof.
Michael Bovis (University of British Columbia) chaired the doctoral defense.

Finally, I thank my Jesuit brothers. My Jesuit community blessed my dream, sent
me to UBC for doctoral studies, paid for much, and never relinquished hope that I would
one day finish what I had started. May what God has started within me be for His glory and
for the life of the world. Ad majorem Dei gloriam.
DEDICATION

To my parents
Tom and Carmel McCarthy
who rooted my life
in
Grace and Nature
I have discovered that you will find far
more in the forests than in books;
trees and stones will teach you that which
you cannot learn from any master.

St. Bernard of Clairveaux, 12th century
Letter to Abbot Heinrich Murdach

Celui qui croirait que la connaissance des bois
peut être acquise sans beaucoup
de peines et d'études préliminaires,
se tromperait grossièrement.

Jean-Henri Jaume Saint-Hilaire
Traité des arbres forestiers, 1824

Glory be to God for dappled things –
For skies of couple-colour as a brinded cow;
For rose-moles all in stipple upon trout that swim;
Fresh-charcoal chestnut-falls; finches’ wings;
Landscape plotted and pieced – fold, fallow, and plough;
And all trades, their gear and tackle and trim.

All things counter, original, spare, strange;
Whatever is fickle, freckled (who knows how?)
With swift, slow; sweet, sour; adazzle, dim;
He fathers-forth whose beauty is past change;
Praise him.

Gerard Manley Hopkins, S.J.
Pied Beauty
Poems 1918
CHAPTER 1
INTRODUCTION

1.1 OBJECTIVE OF STUDY

A comparison is made of the stand- and forest-level size and age structure of two primary balsam fir (*Abies balsamea* (L.) Mill.)–black spruce (*Picea mariana* (Mill.). B.S.P.)–white spruce (*Picea glauca* (Moench) Voss)–white birch (*Betula papyrifera* Marsh.) forest landscapes in western Newfoundland. The study sites are located in the Main River watershed on the Great Northern Peninsula and in the Little Grand Lake area, western Newfoundland. Initial reconnaissance indicated the existence of distinct structural differences between the two forest landscapes. The Main River forests are high elevation (to 600 m) old-growth, generally open forests with contiguous forest cover. In contrast, the Little Grand Lake forests of higher site quality represent a naturally fragmented mosaic forest landscape. Stand and forest structure were used as proxy indicators of differential disturbance in forests of similar species composition and successional development.

This study examines how herbivorous insects and wood-decaying fungi differentially structure primary boreal forests. The primary hypothesis tested was the following: On both a stand- and forest-level, the size and age structure of the Main River and Little Grand Lake forests are determined by distinctly different disturbance regimes. The structure of the Main River forests is regulated by small-scale, gap-phase disturbance mediated by fungal pathogens, whereas the structure of the Little Grand Lake forests is
controlled by large-scale patch mortality mediated by recurrent insect herbivory. This hypothesis was tested by analyzing stand- and forest-level tree species composition, size structure and age characteristics. The Main River stands are considered to be true old-growth (sensu Oliver and Larson 1996), with small-scale (< approximately 200 m$^2$) gap disturbance mediated by fungal pathogens. For the most part, such stands are hypothesized to be all-aged, multi-sized and multi-storied. On the other hand, the recurrent stand-replacing insect disturbance of the Little Grand Lake forests should produce a chronosequence of stands characterized by modal or near-modal height, diameter and age distributions. The landscape should be characterized by a patch mosaic of stands of various ages and developmental stages. This structural dichotomy should hold for both the tree layer (> 1.3 m) and the regeneration layer (≤ 1.3 m). Comparative studies of the effect of temporal and spatial patterns of natural disturbances on stand and forest structural characteristics do not exist for Newfoundland boreal forests.

1.2 STUDY RATIONALE

There were several reasons for conducting this study.

1.2.1 Paucity of Forest Ecology Research in Newfoundland Boreal Forests

Despite the fact that the forests of Newfoundland have been commercially exploited for over 110 years, surprisingly little research has been carried out on the structure, stand dynamics, and disturbance regimes of primary forests. Exceptional in this regard was the pioneering forest phytosociological and successional work of A.W.H. Damman who provided the first ecological classification of Newfoundland’s forests (Damman 1964,
1967, 1971, 1983). Damman's student, William Meades, classified the forests of eastern Newfoundland (Meades 1986) and the Island's forest-associated heathlands (Meades 1983a). Their combined work has been published as a forest site classification manual for forest practitioners (Meades and Moores 1994).

Associated research relevant to an understanding of forest structure and dynamics include forest mensurational studies (Bajzak 1962; van Nostrand 1964; Bajzak et al. 1968; Page 1968; Page et al. 1970; Page and van Nostrand 1970; Newton and Smith 1988; Newton 1992), post-disturbance regeneration surveys (Richardson 1974, 1975), and research on stand structure and competition in density-stressed regenerating black spruce (Newton and Jolliffe 1993, 1998a, 1998b, 1998c), and coarse woody debris in second-growth and primary forests (Sturtevant et al. 1996; Sturtevant et al. 1997). Jardon and Doyon (in review) were the first to document historic forest insect outbreaks using dendrochronological techniques.

1.2.2 Structure and Dynamics of Old-Growth Boreal Forests

It has long been accepted that boreal forest structure and functioning are determined primarily by catastrophic, stand-replacing disturbances such as fire, windthrow and insect herbivory (Blais 1983; Johnson 1995; Ruel 2000). Less attention has been given to the role of small-scale disturbance in Canadian boreal forests (but see Kneeshaw and Bergeron 1998). However, recent work has shown that gap dynamics in boreal forests or near-boreal forests are more important than previously thought (White et al. 1985b; Hytteborn et al. 1991; Liu and Hytteborn 1991; Yamamoto 1993; Kuuluvainen 1994; Battles et al. 1995; McCarthy 2001; Bartemucci et al. 2002).
This study focuses on a poorly-known part of the Canadian boreal forest, the slow-growing, old-growth balsam fir–spruce forests of Newfoundland dominated by a wet, maritime climate. Climatic conditions and the general absence of a fire or insect disturbance regime have created conditions favourable to the development of old-growth.

1.2.3 Structure and Dynamics of Insect-Disturbed Forests

Newfoundland forests have a long history of insect herbivory by both the spruce budworm (*Choristoneura fumiferana* (Clem.)) and the hemlock looper (*Lambdina fiscellaria fiscellaria* (Guen.)). The vast majority of forest insect research has focused on insect population biology, chemical or biological control, remote sensing, and the economic and wood supply impacts of periodic outbreaks (Otvos et al. 1971; Otvos and Moody 1978; Munro et al. 1979; Crummey and Otvos 1980; Hudak and Raske 1981; Crummey 1995; Bowers and West 1996; Hudak 1996; Luther et al. 1997; Li et al. 2003; Parsons et al. 2003). Except for the work of Jardon and Doyon (*in review*), the role of insect herbivores as disturbance factors governing the natural stand- and forest-level structure and dynamics of chronically insect-mediated forest landscapes has not been examined.

1.2.4 Sustainable Forest Ecosystem Management

The Government of Newfoundland and Labrador has committed itself to sustainable forest ecosystem management (Government of Newfoundland and Labrador n.d.). Contemporary understanding of sustainable forest management is predicated on the assumption that the historic range of productivity, resilience and biodiversity developed within the context of specific disturbance regimes. An ecosystem management approach
attempts to choose those management activities that somehow “mimic” or “emulate” the spatial and temporal characteristics, specificity, magnitude and synergisms associated with historic natural disturbance events (White et al. 1999).

For the most part, however, commercial forestry in Newfoundland is currently pursued under the assumption that large-scale, stand-replacing disturbance determine forest dynamics. This assumption is prevalent in the areas of forest, wildlife and natural areas management. It justifies extensive and progressive clearcutting as the dominant silvicultural system and is the fundamental assumption underlying established stand growth and yield models. The variations in the types, extent and internal dynamics of the disturbances regimes are not fully appreciated.

Growth and yield models of old forests are little understood. It was not until the early 1990s that the Newfoundland and Labrador Forest Service established permanent sample plots in old forests. Assumptions about the process of stand breakup are often based on rules of thumb with little or no empirical data. For example, current yield models assume catastrophic stand breakup of “overmature” balsam fir forests at 150 years. This has not been empirically tested for different forest sites or disturbance regimes.

Both study areas have features of high conservation value. The endangered Newfoundland marten (Martes americana atrata) lives in both study areas. Furthermore, the Main River has recently been proclaimed a Canadian Heritage River and the boundaries of a proposed ecological reserve encompass the Little Grand Lake study area. A greater understanding of the natural structural and stand dynamic diversity characteristic to each study area would enhance the development of protected areas management plans.
The comparative study will provide forest managers with a greater understanding of
the range of natural stand structure and dynamics in Newfoundland boreal forests. This
understanding may significantly impact resource management decisions and promote more
sustainable forest practices.

1.3 METHODOLOGY

A central goal of ecology is the explanation of observed patterns in nature (Tilman
1988). Levin (1992) considered that “understanding patterns in terms of the processes that
produce them” to be “the essence of science, and ... the key to the development of
principles for management.” In other words, one strives to account for the range of
variation observed in nature.

The natural stand- and forest-level variation of the Main River and Little Grand lake
forests were compared. This study employed mensurative and not manipulative
experiments (Hurlbert 1984). No imposed changes in specific factors or experimental units
were carried out. Instead, the goal was to infer ecological process from a close description
and comparison of stand and landscape structural patterns (Leps 1990).

Inference about ecological process is no doubt stronger in the case of manipulative
experiments (Leps 1990; McPherson and DeStefano 2003), given that pattern and process
are not necessarily isomorphic (Cale et al. 1989). However, the use of short-term
manipulative experiments is often not amenable to the study of long-term forest disturbance
dynamics. Tilman (1989) alerts us to a number of concerns in the interpretation of short-
term ecological experiments; the impact of transient dynamics, multiple indirect effects on
the interaction of interest, temporal environmental variability, and the confounding effects of alternative stable states in ecosystems.

The use of pattern analysis is part of a long-standing tradition in ecological research, and if used properly can provide defensible insight into ecological systems. In fact, the temporal and spatial scales of ecological research are often only amenable to multiple techniques of investigation, including experiments, surveys, field descriptions or analysis of pattern in existing data (Ford 2000, p. 18). In this study, three investigative methods were employed to study the role of disturbance regime and stand development processes on stand and forest structure: (1) contrast of two landscapes, (2) substitution of space for time using a stand developmental chronosequence, and (3) retrospective reconstruction of stand dynamics using dendrochronological and spatial data. The use of different methods strengthens the level of scientific inference. Detailed methodologies for each section of inquiry are given in Chapter 5.

1.3.1 Contrast of Two Forest Landscapes

The differences in stand- and forest-level structure were attributed to differences in disturbance regimes. While it is true that forest structural differences are a product of the biogeoclimatic context, the over-arching structural imprint of the respective disturbance regimes was of primary interest.

Of significance is the difference in the frequency of outbreaks of both the spruce budworm and the hemlock looper in the two study areas. In the upper reaches of the Main River watershed, insect herbivory is rare and no record exists of stand-replacing insect disturbance (Corner Brook Pulp and Paper Limited 2000). The forests of the Little Grand
Lake area, however, have experienced recurrent, stand-replacing mortality caused by both the spruce budworm (Otvos and Moody 1978; Hudak and Raske 1981) and the hemlock looper (Otvos et al. 1971; Otvos et al. 1979; Hudak 1996).

Fire disturbance is rare in both study areas. The forests of northern and western Newfoundland are dominated by extensive, non-pyrogenic balsam fir-dominated forests influenced by a maritime climate (Wilton and Evans 1974). Actual fire cycles are unknown, but are certainly much longer than the approximate fire cycle of 100 years for the continental boreal forest (Heinselman 1981; Foster 1983).

1.3.2 Chronosequence

The long-lived nature of forests often prevents direct experimental testing of stand developmental processes. Given that long-term data sets from permanent sample plots are rare in forest studies, recourse is often made to a “substitution of space for time” through the use of chronosequences (Cole and van Miegroet 1989; Pickett 1989; Bakker et al. 1996). While the use of chronosequences promises special advantages to the study of long-term stand dynamics, care must be taken to minimize the confounding effects of site heterogeneity and disturbance history. Furthermore, sampled sites must cover the full range of the chronosequence for adequate interpretation of dynamics. The use of chronosequences assumes that all stands were of similar condition at the same age. Whether or not this condition has been fulfilled is often unknown. However, this may be less of a problem where the focus is less on successional change than on stand development, as was the case in this study.
1.3.3 Retrospective Studies

Commonly accepted retrospective techniques include palynology (Davis 1989; Payette 1993; Ritchie 1995), dendrochronology (Swetnam et al. 1988; Fritts and Swetnam 1989; Banks 1991) and stand structural information (Lorimer 1985; Frelich 2002). Each technique has its own strengths and limitations, but when used in combination can reveal significant insight into forest dynamics (Foster et al. 1996). This thesis focused on the use of both stand structural data and dendrochronological data.

1.3.4 Focus of Thesis

Of necessity, this thesis is limited in scope. This thesis focuses on the presentation and interpretation of size and age structure for trees and regeneration on both the stand and forest level. Tree spatial data (amenable to both point pattern and geostatistical analysis) and extensive dendrochronological and stem analysis data for both study sites were collected but are not presented. Regeneration–microsite data and old-growth coarse woody debris data will also be presented at a later date.
CHAPTER 2

GAP DYNAMICS OF FOREST TREES: A REVIEW WITH PARTICULAR ATTENTION TO BOREAL FORESTS

This chapter has already been published in (Environmental Reviews 9(1), pp. 1-59, 2001)

2.1 INTRODUCTION

The main objective of this review will be to focus on increasing evidence which points to the importance of small-scale gap dynamics in boreal forests. This will be accomplished by a general review of research on gap dynamics in tropical and temperate forests. Such research has confirmed the prevalence of gap dynamics in these forests. Insights on gap dynamics gained from this research will permit a focus on boreal forests. It is hoped that a review of this literature, as well as a consideration of the research conducted in boreal forests and the subalpine spruce (Picea)–fir (Abies) forests of Canada, the United States and Japan, will serve to underline the general importance of gap dynamics in boreal forests. Given the prevalence of large-scale disturbance in boreal forests, it has been assumed that small-scale gap dynamics were not important in determining the structure and function of boreal forests. It is the intention of this review to question this assumption.

This review will focus on a particular type of forest disturbance termed “gap dynamics.” Gap dynamics is characterized by small- or micro-scale disturbance of the mature forest canopy. Trees die standing, snap off, or are blown to the ground, creating a “hole” in the canopy. The death of a single stem or a few stems releases available growing
space (sensu Oliver and Larson 1996). In time, this growing space is occupied by tree regeneration, usually a result of released advance regeneration or recruitment from buried or dispersed seed propagules. Considered as a key process in autogenic succession (Kimmins 1997), gap dynamics in forest ecosystems have become the focus of much investigation over the last three decades, particularly in tropical and temperate systems (Yamamoto 1992a).

Investigation of forest gap dynamics dates from the late 1970s. This research has underlined the ubiquity and importance of small-scale canopy disturbance in forests not subject to extensive, large-scale, catastrophic disturbance. The vast majority of research on tree fall and gap dynamics has been conducted in tropical forests and in the temperate hardwood forests of the United States (Pickett 1983; White and Pickett 1985; Brokaw 1985a; Runkle 1985a; Denslow 1987; Platt and Strong 1989; Denslow and Spies 1990; Whitmore 1995). Significant work on gap disturbance has also been initiated in the Nothofagus forests of the southern Hemisphere (Veblen 1985a, 1985b, 1989a; Steward et al. 1991; Heinemann et al. 2000), temperate coniferous forests (Spies et al. 1990; Lertzman and Krebs 1991), subalpine spruce-fir forests of both the United States (Foster and Reiners 1986; Battles et al. 1996; Battles and Fahey 2000) and Japan (Yamamoto 1993, 1995), as well as in Japanese temperate forests (Yamamoto 1989, 1992b).

Except for recent work in Scandinavian and Russian forests (Liu and Hytteborn 1991; Kuuluvainen et al. 1998; Drobyshev 1999), little research has been conducted on gap dynamics in boreal forests. In the Canadian boreal forest, gap dynamics have been studied in spruce budworm-mediated balsam fir forests (Kneeshaw and Bergeron 1998) and in old, uneven-aged aspen (Populus tremuloides Michx.) forests of northeastern Alberta.
Papers dedicated to gap dynamics in special issues of both *Ecology* (Platt and Strong 1989) and the *Canadian Journal of Forest Research* (Denslow and Spies 1990) did not address boreal forests. The same is true for published reviews which focus exclusively on temperate (Runkle 1985a; Veblen 1985b) and tropical forests (Hartshorn 1978; Whitmore 1978; Brokaw 1985a; Denslow 1987). The single, known review of boreal forest gap dynamics (Kuuluvainen 1994) focuses solely on Scots pine (*Pinus sylvestris* L.)- and Norway spruce (*Picea abies* (L.) Karst.)-dominated forests of Finland. The current review attempts a more detailed analysis of gap dynamics in global boreal forests.

For purposes of this review, the geographical boundaries of the circumpolar boreal forest will be expanded to include the subalpine spruce–fir forests of both the Appalachians (Oosting and Billings 1951; McIntosh and Hurley 1964) and the northern islands of Japan (Kojima 1991, 1995). These “outlier” forests, dominated by the spruce–fir association, possess a physiognomy and floristics similar to the boreal forest of the northern latitudes. The high-altitude forests of Englemann spruce (*Picea engelmannii* Parry)–subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) found in western Canada (Coates et al. 1994) and the United States (Alexander 1987) will also be examined. While not considered boreal forests in the strict sense, these spruce–fir forests possess ecological characteristics similar to those found in the boreal forest.

This review will focus, for the most part, on gap dynamics of forest trees and the response of tree regeneration to canopy disturbance. Understory and gap vegetation other than trees will be considered only in terms of their effects on tree recruitment. For a
consideration of canopy gaps and organisms other than trees, the reader is referred to Schemske and Brokaw (1981), Collins et al. (1985), Levey (1988), and Fuller (2000).

At this point, it is important to distinguish difference between the terms “gap” and “patch” in this discussion of forest dynamics. The size of canopy openings obviously ranges from small openings created by the fall of individual trees or large branches to disturbances covering thousands or millions of hectares. Such a range of spatial scales will necessarily provoke changes in resource allocation and species response of a radically different nature. Unfortunately, both of the terms “gap” and “patch” have been used in a synonymous or inconsistent manner in the forest ecology literature despite an explicit, if not implicit, recognition of their difference (White and Pickett 1985; Peterken 1996; van der Maarel 1996; Barnes et al. 1998). A distinction is important, for it is evident that patches resulting from large-scale fires or insect outbreaks in the boreal forest are certainly not “gaps” in the same sense as “gaps” created by treefalls in tropical and temperate forests.

For the purposes of this review, gaps are defined as canopy openings not generally exceeding 200 m$^2$ in area. Tree death, normally on a single-tree or small group level, is caused by stem breakage due to root and butt diseases or windthrow in some instances. The continual production and filling-in of these small gaps may be termed a “matrix” process which dominates the disturbance regime in self-perpetuating, climax or near-climax, old-growth forests (Lewis and Lindgren 2000). Patches are larger openings in the canopy caused by rapid, at times catastrophic, biotic and abiotic disturbances and may be described as a “relatively discrete spatial pattern” (White and Pickett 1985) which exhibits sufficient structural and behaviour differences from the surrounding matrix. See Figure 2-1 for a conceptual differentiation of gap and patch processes. Figure 2-2 provides a spatial
<table>
<thead>
<tr>
<th>Attribute or Process</th>
<th>Gap dynamics</th>
<th>Patch modifying</th>
<th>Patch dynamics</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spatial scale of change</strong></td>
<td>Individual tree</td>
<td>←</td>
<td>Stand or portion thereof</td>
</tr>
<tr>
<td><strong>Size of canopy opening</strong></td>
<td>≤ 200 m²</td>
<td>←</td>
<td>&gt;200 m²</td>
</tr>
<tr>
<td><strong>Temporal scale of change</strong></td>
<td>Slow change (10 to 100s years)</td>
<td>←</td>
<td>Rapid, often catastrophic change</td>
</tr>
<tr>
<td><strong>Type of change</strong></td>
<td>Modification of original stand (quasi-constant tree recruitment and mortality)</td>
<td>←</td>
<td>Initiation of new cohorts (episodic tree recruitment and mortality)</td>
</tr>
<tr>
<td><strong>Change in resource availability</strong></td>
<td>Little change</td>
<td>←</td>
<td>Major change</td>
</tr>
<tr>
<td><strong>Forest development</strong></td>
<td>&quot;Climax&quot;, old-growth in quasi-equilibrium</td>
<td>←</td>
<td>&quot;Pioneer&quot;, early successional or stand-initiation (sensu Oliver and Larsen, 1996)</td>
</tr>
<tr>
<td><strong>Type of disturbance</strong></td>
<td>Decay (root and butt rots) or single-tree windthrow</td>
<td>←</td>
<td>Epidemic insect, fire, wind, avalanches, volcanoes</td>
</tr>
<tr>
<td><strong>Stand structure</strong></td>
<td>Often all-aged, reverse-J diameter distribution</td>
<td>←</td>
<td>Even-aged or multi-cohort, normal diameter distribution</td>
</tr>
<tr>
<td><strong>Regeneration strategies</strong></td>
<td>Release of advance regeneration</td>
<td>←</td>
<td>Seed propagule dispersal, seedbanks, vegetative propagation, as well as seedling bank release.</td>
</tr>
<tr>
<td><strong>Forest structure</strong></td>
<td>&quot;Homogeneous&quot; old-growth</td>
<td>←</td>
<td>Mosaic of seral stages</td>
</tr>
</tbody>
</table>

Figure 2-1. Conceptual model of gap (matrix) and patch processes and attributes (modified after K. J. Lewis and B. S. Lindgren, *The Forestry Chronicle*, 76(3): 433–443, 2000, Figure 1.)
Figure 2-2. Conceptual spatial (A) and temporal (B) models of mortality rate and patch appearance with various types of disturbance (from K. J. Lewis and B. S. Lindgren, *The Forestry Chronicle*, 76 (3): 433–443, 2000, Figure 2).
and temporal conceptual model of tree mortality effected by both gap and patch disturbance.

The conceptual model begins with a homogeneous time-zero forest, the disturbance regime of which is characterized by small-scale gap or matrix processes. At a point in time, an exogenous disturbance produces large-scale mortality which creates a patch. Processes operative within the patch are a combination of successional and stand developmental processes which effect gradual change over time. With time, the disturbance regime of the patch becomes more and more similar to that operative in the matrix (Lewis and Lindgren 2000). Forests dominated by patch disturbance are usually characterized, on the landscape level, by a mosaic of seral stages in various stages of stand development (sensu Oliver and Larson 1996).

No claim will be made for a review *in toto*. The already burgeoning and prolific literature on gap research in temperate and tropical systems continues to expand. After an initial historical overview of disturbance ecology, the review considers the reasons why there have been so few studies on gap dynamics in boreal forests. Subsequent sections review the investigations on gap dynamics carried out in tropical and temperate forests as well as in boreal forests. After a review of the etiology of gaps, research methodology will be considered. Gap size and geometry and the consequent differential fluxes of above- and below-ground resources that impact tree recruitment are subsequently covered. Final sections focus on characteristics of gap specialists and the feasibility of a gap-based silviculture. The review concludes with a presentation of some possible future research priorities (Figure 2-3).
Figure 2-3. Review of outline showing relationship among topics.
The purpose of such a synthesis is twofold: (1) an examination of the occurrence and relative importance of gap dynamics in global forests, including the boreal forest, and (2) the provision of an incentive for further work on boreal gap dynamics, particularly in the North American boreal forest.

2.2 HISTORICAL PERSPECTIVE

2.2.1 Disturbance Ecology

Disturbance is ubiquitous in forest ecosystems (Attiwill 1994; Rogers 1996). Defined as "any relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985), disturbance determines forest species composition, structure and process. Furthermore, disturbances exert their influence over a wide range of temporal and spatial scales. This disturbance, in turn, promotes changes in resource fluxes, changes that lead to some form of reorganization of the disturbed patch or gap at structural and functional levels which may be similar or dissimilar to predisturbance levels. Resource levels and inputs are changed and species respond accordingly.

The notion that disturbances are prevalent and even pandemic in all ecosystems was by no means always universally accepted. It is generally acknowledged that the pioneering work of Cowles (Cowles 1899, 1911) did much to enhance the understanding of plant communities as essentially dynamic in nature (Cooper 1926). Succeeding decades would find researchers intent on describing identifiable temporal sequences of vegetation, a process that would eventually lead to the development of the theory of ecological
succession. Of prime interest would be the amassing of evidence for the existence of a vegetation climax, a stable, self-reproducing plant community, whose species composition was determined solely by the local climate (Clements 1916). Using organismic terminology, Clements (1916) likened the sequence of successional stages to the developmental stages of an organism; just as an organism grows and passes from one stage towards another more advanced stage, the same with plant communities. Succession was clearly perceived as developmental in nature, with the stable climax phase considered as the ultimate adult stage of the embryonic successional stages.

Due to this preoccupation with the climatically-controlled climax, there existed relatively little appreciation for the role of natural disturbance in fashioning plant communities. Early dissenters of the strict view of climax as a final stage of plant community development included Tansley (1935), who proposed that certain ecosystems failed to attain a climatic climax because of the mitigating effects of edaphic and physiographic influences and disturbance events such as fire. In this case, climax is simply the culmination of the development of a system determined more directly by factors other than the regional climate. It was not that Clements and the early proponents of the classical monoclimax theory were not unaware of disturbance (i.e. proclimax, subclimax, (Clements 1936)), but that the theoretical framework was definitely dominated by the quintessential climax. Eventually, though, as communications grew among scientists, a consensus regarding the prevalence of ecological disturbance slowly developed. Jones (1945) questioned whether the term "climax forest" may exist only as a concept, never existing in reality due to the constant influence of catastrophic disturbance.
Recent commentators have gone so far as to describe the abandonment of the classical notion of a regional climax by modern ecologists (Pickett 1976), or citing the notion of climax as having been a "rather oppressive influence on the minds of many ecologists" (Sprugel 1976). On the other hand, White (1979), while acknowledging the problematic nature of the term "climax," did not advocate its complete abandonment. Instead, he accepted the concept's utility only if it was explicitly defined in terms of the disturbance dynamics and other dynamic properties of the particular ecosystem under investigation. For example, because of the preponderance of extensive areas of long-lived forests that have escaped catastrophic disturbance for extended periods (Pojar et al. 1987), the biogeoclimatic ecosystem classification of British Columbia accepts the polyclimax concept. However one may view the term "climax," research in disturbance ecology has repeatedly underlined the fact that attention to the intensity, scale and frequency of disturbance events must always be maintained in any study of ecosystem structure and function (Mooney and Godron 1983; Pickett et al. 1989; Sprugel 1991; Rogers 1996; Parminter 1998). Various disturbance events such as fire, insect and disease, windthrow and herbivory are subjects of studies which attempt to comprehend ways in which disturbance determines species composition, reproductive strategies, stand development, physiognomy and evolutionary changes in ecosystems.

2.2.2 Gap Dynamics

Alex Watt, in his 1947 presidential address to the British Ecological Society (Watt 1947), is generally credited with the first attempt to reconcile the notions of process and pattern in contemporary plant ecology (van der Maarel 1996). He attempted to move plant
ecology beyond the purely descriptive stage by injecting dynamic principles into the study of plant communities. This new level of explanatory knowledge allowed a more comprehensive understanding of inter- and intra-specific interactions and the forces which determine the maintenance and regeneration dynamics of particular plant communities.

Watt (1947) thought it best to understand plant communities in terms of patches or phases. Considered as a developmental sequence of a particular plant community, each patch or phase is joined together in a mosaic and dynamically related to each other in such a manner that the community patterns persist through time. In other words, the community passes through a series of developmental stages that repeat themselves in a cyclic fashion. This cycle is in turn determined by the extent, frequency and magnitude of various disturbances that impact the plant community. Using the terminology of Watt (1947), we may say that both process and pattern influence each other in a dynamic manner.

Watt (1947) used seven different plant communities to develop his thoughts on pattern and process. Germaine to my review is his description of gap-phase regeneration in European beech (Fagus sylvatica L.) forests. He defined the gap phase as that part of the forest developmental cycle dominated by the presence of tree regeneration, it being excluded from other phases. The gap phase may be initiated by small-scale disturbance such as tree-falls or by large-scale disturbance such as fire, insect or disease epidemics and extensive windstorms. It is during the gap phase, when the mature canopy experiences sufficient disturbance, that the site is opened up, permitting the release of either advance regeneration or the recruitment of new regeneration. It should be noted that, for Watt (1947), phases were synonymous with patches and that gap-phase could be of widely varying spatial dimensions, defined simply as the stage of forest development in which
regeneration was confined. As emphasized earlier, I will use the term gap in a more restrictive sense than was used by Watt (1947). Watt (1947) noted that regeneration may happen during the actual gap phase or during the phase corresponding to the mature phase. This distinction is important, for it is well known that many shade tolerant species are able to establish themselves as advance regeneration under a mature–overmature closed canopy which may be “losing its competitive hold” on the site’s growing space (Oliver 1981; Oliver and Larson 1996). An early confirmation of Watt’s gap-phase dynamics was given by Bray (1956) for sugar maple-basswood (*Acer saccharum* Marsh.–*Tilia americana* L.) forests of Minnesota.

Watt’s (1947) seminal idea of patch dynamics in vegetation ecology has subsequently been developed and promoted as workers have come to appreciate the degree of patchiness in ecological systems. Constituting a grille de lecture, the concept of patch dynamics has emerged as an intellectually satisfying and fruitful paradigm by which to understand plant community dynamics. Contemporary manifestations of Watt’s original insight have taken shape: dynamic landscape–succession model (Pickett 1976), mosaic phenomena of communities (Whittaker and Levin 1977), non-equilibrium coexistence hypothesis (Pickett 1980), shifting mosaic steady state (Bormann and Likens 1981), patch dynamics and disturbance (Souza 1984; Pickett and White 1985), forest gap models (Shugart and Seagle 1985), mosaic-cycle concept (Remmert 1991), and hierarchical patch dynamics (Wu and Loucks 1995). Regardless of the accepted nomenclature and theoretical perspective, it is evident that the paradigm of “patch dynamics” has provided significant insight into ecosystem structure and dynamics.
2.3 GAP DISTURBANCE AND BOREAL FORESTS

Why have boreal gap dynamics not been researched to the same extent that we witness in temperate and tropical forests? A prime reason is the generally felt assumption that gap dynamics cannot explain the initiation and maintenance of boreal forests. Instructive is the comment by Lorimer (1989), who stated that “while small gaps are not unknown in the boreal forest, it is unlikely that the origin of a sizable percentage of trees can be traced to such events.” Except for a single study of spruce budworm-mediated gap dynamics (more correctly termed “patch dynamics”) in Quebec’s southern boreal forest (Kneeshaw and Bergeron 1998) and gap dynamics in Albertan boreal aspen stands (Cumming et al. 2000), research on the actual prevalence of gap dynamics as a significant disturbance event in the Canadian boreal forest is non-existent.

This lacuna is understandable for the simple reason that boreal forest scientists have been preoccupied with the obvious large-scale, stand-initiating disturbances that dominate boreal systems, particularly fire, insect and wind disturbances. Viewed from a perspective of “natural disturbance types” (NDT), the boreal forest is assumed to exemplify what is termed a natural disturbance type 3 that is defined as “ecosystems with frequent stand-initiating events” (Province of British Columbia 1995). At the opposite end of the disturbance spectrum are natural disturbance type 1 ecosystems that are characterized by “rare stand-initiating events” in which small-scale gap dynamics are the predominant disturbance events (Province of British Columbia 1995). Rarely, however, have boreal forests been considered as NDT 1-type ecosystems. In the 1999 Canadian Sustainable Forest Management-sponsored conference entitled “Sustaining the Boreal Forest”, all of the nine papers devoted to natural disturbance in the boreal forest featured fire and insect
herbivory, with fire clearly continuing to garner the most attention (Veeman et al. 1999). This is understandable given the fact that the boreal forest, particularly the vast tracts of relatively uninhabited Canadian and Russian boreal forest, are periodically disturbed by extensive landscape-level fires.

Wildfire is considered of paramount importance in controlling the dynamics of the boreal forest (Heinselman 1973; Rowe and Scotter 1973; Wein and MacLean 1983; Cogbill 1985; Dyrness et al. 1986; Payette et al. 1989; Payette 1992; Dansereau and Bergeron 1993; Johnson et al. 1998). Johnson (1995) noted four characteristics of boreal fires which especially impact forest composition and successional dynamics: (1) the occurrence of intense crown fires, (2) the vast areas burnt, (2) the frequency of occurrence and, (4) the degree of forest floor combustion. Fires greater than 100,000 hectares are common, with fires affecting over 1 million hectares not unknown. Average fire rotations (Heinselman 1973) or fire cycles (van Wagner 1978) (defined as the time period required to burn an area equivalent to the area under study) differ depending on climate, lightening occurrence and tree species. Fire rotation estimates of 50–100 years are given for the drier continental boreal forests of western Canada and Alaska (Heinselman 1981; Yarie 1981). Fire cycles of approximately 100 years are cited for Quebec’s boreal forest (Payette et al. 1989; Bergeron 1991) and for the boreal forests of northern Sweden (Zackrisson 1977).

Insect disturbance in the boreal forest, especially by defoliators and bark beetles, is common and widespread (Holling 1992). Periodic insect outbreaks, especially by the spruce budworm and hemlock looper, have caused extensive defoliation and stand mortality across the range of balsam fir in the eastern Canadian boreal (Carroll 1956; Blais 1965; Brown 1970; Otvos and Moody 1978; Otvos et al. 1979; Blais 1983; Kettela 1983;

Starting about 1910, 1940, and 1970, three successive spruce budworm outbreaks in eastern Canada affected about 10, 25 and 57 million hectares of forest, respectively (Blais 1983; Morin and Laprise 1990). Recent work on spruce budworm-balsam fir dynamics has shown that spruce budworm outbreaks and balsam fir forests form a self-regulating system that perpetuates itself through time (Baskerville 1975; MacLean 1984, 1988; Morin 1994; Leblanc and Bélanger 2000). In the boreal forests of western Canada, particularly those dominated by white spruce, epidemic outbreaks of the spruce beetle (*Dendroctonus rufipennis* Kirby) are common and promote significant stand-initiating events (Werner et al. 1977; Werner and Holsten 1983; Holsten et al. 1995; Safranyik 1995; Werner 1996).

The forest tent caterpillar (*Malacosoma disstria* Hbn.) and the jack pine budworm (*Choristoneura pinus pinus* Free.) act as significant defoliators throughout the boreal forests of central and western Canada (Simpson and Coy 1999).

Given the ubiquity and intensity of fires and insect outbreaks and the common occurrence of fire-adapted species such as jack pine (*Pinus banksiana* Lamb.), black spruce and trembling aspen, all of which may reach ages greater than the average fire rotation of 100 years, it is easy to understand why gap dynamics would not be considered an important disturbance factor in the Canadian boreal forest. Most of the forest would experience catastrophic stand-replacing fires and insect outbreaks before the onset of any old-growth stage, thus preventing the conditions conducive for gap-phase regeneration. The prevalence of large-scale disturbance would minimize the development of a self-replacing, steady-state forest.
An appreciation of the role of micro-scale disturbance in high latitude boreal forests is, however, slowly growing. Notable are the comments made by the organizing committee of the 1996 Second International Workshop on Disturbance Dynamics in Boreal Forests. They noted that “the role of fire may be overemphasized in boreal systems, and old-growth forests controlled by alternating disturbances may be more abundant that has been generally considered” (Bergeron et al. 1996). In fact, publication of the conference papers two years later confirmed that gap disturbance appears to be common in boreal forests and, in some forests, is probably more important than fire (Bergeron et al. 1998).

Even before Watt (1947) developed his theory of patch dynamics, Sernander (1936) presented what he termed the “storm gap structure.” Working in old-growth Norway spruce (Picea abies (L.) Karst.) forests of central Sweden, Sernander (1936) understood the regeneration dynamics and mosaic structure of these forests to be determined by periodic gap-phase disturbance caused by treefalls. Recruitment in the gaps is facilitated by the release of suppressed advance spruce regeneration (“dwarf trees” according to Sernander) to form the future canopy, which in turn is prone to gap formation. Sernander’s storm-gap theory of spruce forest regeneration has been confirmed by contemporary quantitative studies of gap dynamics in the primeval forest reserve of Fiby urskog (Hytteborn and Packham 1985, 1987; Leemans and Prentice 1987; Leemans 1990; Hytteborn et al. 1991; Leemans 1991; Liu and Hytteborn 1991). Sernander’s work has also been confirmed by research on gap dynamics carried out in both northern Sweden (Hytteborn et al. 1987), Finland (Kuuluvainen 1994) and Russia (Kuuluvainen et al. 1998).

In the Canadian boreal forest, conditions exist which would promote the frequency of small-scale canopy disturbance. This is particularly true in areas of the boreal forest that
have escaped large-scale disturbance for long periods of time. Specific climatic or edaphic conditions may prevent the periodic occurrence of fire or insect infestation. In the humid maritime boreal forests of eastern Canada, for example, fire frequency is much less than that documented for the continental boreal. Forest fires are relatively uncommon in southeast Labrador where Foster (1983) determined a fire rotation of approximately 500 years, a fire cycle much greater than the 200 years suggested by Heinselman (1981) for the high precipitation areas of eastern Canada. Although fire cycles are unknown, Meades and Moores (1994) considered the extensive balsam fir forests of western and northern Newfoundland to have had very little fire history (Wilton and Evans 1974). Despite a natural fire cycle of 80 to 100 years in northern Sweden (Zackrisson 1977), areas of Norway spruce-dominated fire-free refugia or areas of very low fire frequency do occur (Hansson 1992; Segerström et al. 1994; Segerström et al. 1996). Using charcoal and pollen analysis, Ohlson and Tryterud (1999) documented long-term continuity (1700 years) in Norway spruce landscapes in southeastern Norway. Regeneration dynamics in these forests are characterized by small-scale gap dynamics (Steijlen and Zackrisson 1987; Liu and Hytteborn 1991; Hörmberg et al. 1995). Bergeron and Dubuc (1989), in a study of succession in the southern Quebec boreal, concluded that in the absence of fire, gap dynamics could emerge as a driving force determining successional patterns. This trend was confirmed by Kneeshaw and Bergeron (1998) who documented spruce budworm-mediated gap dynamics in old balsam fir forests in Quebec. A reassessment of the dominance of fire in the boreal is also emerging from research in the Russian taiga where Syrjänen et al. (1994) suggested that in extensive mesic areas dominated by Norway spruce, small-scale gap dynamics determine regeneration patterns.
In the Canadian boreal forest, conditions which promote the maintenance of self-perpetuating forests through long-term gap dynamics certainly exist. Theoretically, boreal forests not disturbed by fire or insect herbivory for long periods of time will revert to multi-cohort, self-perpetuating, gap-driven forests. The boreal forests of eastern Canada, particularly those of Newfoundland influenced by a humid, maritime climate, are dominated by late succession balsam fir in the absence of periodic fires. The forests of western Newfoundland, for example, are dominated by balsam fir, with black spruce and white spruce being of lesser importance, their occurrence depending for the most part on topographic and edaphic influences. The predominance of balsam fir in this region indicates a fire rotation longer than the average of 100–150 years normally cited for the Canadian boreal forest. Balsam fir will not reproduce after fire, only becoming established in late successional, nonpyrogenic forests (Damman 1964; Furyaev et al. 1983; Viereck 1983). The increase in moisture gradient from western to eastern Canada is paralleled by a significant decline in forest fire frequency as one moves from the western to the eastern boreal (Johnson 1995). Therefore, eastern Canadian boreal forests that experience both significant oceanic influence and an absence of insect infestations are prime candidates for gap dynamics. Furthermore, balsam fir’s ability to regenerate well on a variety of microsites, high shade tolerance and rapid growth after years of suppression (Ghent 1958) further enable the species to grow well in gap-driven forests.

Uneven-aged forests may even occur in forest areas traditionally assumed to be characterized by high fire frequencies. In both Saskatchewan (Dix and Swan 1971) and northwestern Ontario (Zoladeski and Maycock 1990), balsam fir forests were considered to be late successional forests capable of self-perpetuation in the absence of fire. On old burns
in southeastern Labrador, Foster (1985) identified uneven-aged forests that developed through slow and progressive post-fire establishment of black spruce and balsam fir over a period of 70 to 100 years. Furthermore, the extremely long intervals between fires (500 years) documented for southeastern Labrador have produced a landscape dominated by old, multi-aged spruce–fir forests with individuals exceeding 250–300 years in age (Foster 1983, 1984). Even fire-prone lichen–spruce forests in central Labrador–Ungava may escape fire to produce multi-cohort stands exceeding 300 years in age and regenerating via gap dynamics (Treter 1995). Early studies in Labrador (Wilton 1959, 1965) and neighbouring Quebec (Hatcher 1963) confirmed the presence of old, uneven-aged black spruce forests with a high proportion of balsam fir, or late successional undisturbed forests dominated by balsam fir with minor components of white spruce and white birch. Recent work by Groot and Horton (1994) in the Clay Belt of northeastern Ontario has identified old, uneven-aged black spruce forests characterized by age classes that span two to three centuries. Such forests, considered by Groot and Horton (1994) as a rarity in the boreal forest, were deemed able to perpetuate themselves in the absence of catastrophic disturbance. Harper et al. 2003 estimated that old-growth forests are extensive in the Clay Belt of Quebec and Ontario, covering some 30% to 50% of the forested landscape. Gap dynamics of shade tolerant spruce and fir combined with the ability of both spruce and fir to layer, could certainly account for self-perpetuation in these forests.

In summary, evidence is mounting which indicates that, despite the ubiquitous nature of catastrophic disturbance in the boreal forest, such disturbances do not fully explain the range of observed structural and compositional patterns found in the boreal
forest. Micro-scale gap dynamics seem to be a significant and often overlooked disturbance factor in boreal forests.

2.4 CAUSES OF CANOPY GAP DISTURBANCE

Gap disturbance is driven by treefalls and the production of standing dead trees. Trees die from insect, disease, and meteorological vectors, remain standing as snags or fall to the ground to create a canopy gap. This single or multi-tree gap may initiate a new period of recruitment depending on the presence of seed or advance reproduction and the degree to which site resources are released.

Trees either die standing, snap off, or uproot. The particular process of death affects not only the spatial characteristics of gap formation, but also the type of microsite produced and the potential resources available to gap regeneration. Table 2-1 provides a summary of the mode of tree mortality for gapmakers in different forest ecosystems.

Despite the wide variability in forest types studied, consistent patterns are evident. Tree mortality from stem-snapping is dominant, due no doubt to the prevalence of decay fungi as the determining disturbance agent in old-growth forests. Excluding the one study conducted on southern hemisphere *Nothofagus*, the amounts of standing dead are quite similar among all forest types, ranging from 14% to 17%. Mortality from uprooting ranges from 20% to 30% among all forest types.

Variation in the mortality of gap-makers is determined by a multitude of factors. In their extensive review of treefalls, Everham and Brokaw (1996), divided the factors that predetermine the type of tree mortality into two classes: biotic and abiotic. Biotic factors include stem size, stand conditions, species differences and tree pathogens. Abiotic factors
Table 2-1. Mode of mortality of gap-makers in gap-disturbed forests.

<table>
<thead>
<tr>
<th>Location</th>
<th>Forest type</th>
<th>Mortality of gap maker (%)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Standing dead</td>
<td>Snapped off</td>
<td>Uprooted</td>
</tr>
<tr>
<td>Boreal and subalpine forests</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine <em>Tsuga–Abies–Picea–Betula</em></td>
<td>10.7</td>
<td>46.7</td>
</tr>
<tr>
<td>Sweden</td>
<td>Primeval <em>Picea abies</em></td>
<td>13</td>
<td>57</td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine <em>Picea–Abies</em></td>
<td>41.9</td>
<td>48.8</td>
</tr>
<tr>
<td>Japan</td>
<td>Sub-boreal <em>Picea–Abies</em></td>
<td><em>Picea</em>: 8</td>
<td><em>Picea</em>: 61</td>
</tr>
<tr>
<td></td>
<td><em>Abies</em>: 17</td>
<td><em>Abies</em>: 45</td>
<td><em>Abies</em>: 38</td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine <em>Picea–Abies</em></td>
<td>43.7</td>
<td>41.7</td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine <em>Abies–Picea–Tsuga</em></td>
<td>42.6</td>
<td>43.7</td>
</tr>
<tr>
<td>Location</td>
<td>Forest type</td>
<td>Mortality of gap maker (%)</td>
<td>Reference</td>
</tr>
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<td>---------------</td>
<td>----------------------------------</td>
<td>----------------------------</td>
<td>-----------------</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Standing dead</td>
<td>Snapped off</td>
</tr>
<tr>
<td>Tennessee</td>
<td>Mature hardwood</td>
<td>3</td>
<td>87</td>
</tr>
<tr>
<td>United States</td>
<td>Old-growth mesic hardwoods</td>
<td>10</td>
<td>58</td>
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<tr>
<td>Japan</td>
<td>Primary evergreen broad-leaved</td>
<td>17.3</td>
<td>51.4</td>
</tr>
<tr>
<td>Japan</td>
<td>Cool-temperate Fagus–Quercus–Acer</td>
<td>45.2</td>
<td>27.9</td>
</tr>
<tr>
<td>Japan</td>
<td>Warm-temperate Castanopsis–Persea–Quercus</td>
<td>17.3</td>
<td>51.5</td>
</tr>
<tr>
<td>Japan</td>
<td>Fagus: seral stages</td>
<td>39.2&lt;sup&gt;c&lt;/sup&gt;</td>
<td>13.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>47.0&lt;sup&gt;c&lt;/sup&gt;</td>
<td>35.3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>44.5&lt;sup&gt;c&lt;/sup&gt;</td>
<td>22.2</td>
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<tr>
<td></td>
<td></td>
<td>42.9&lt;sup&gt;c&lt;/sup&gt;</td>
<td>50.0</td>
</tr>
<tr>
<td></td>
<td></td>
<td>20.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>40.0</td>
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<td></td>
<td></td>
<td>5.0&lt;sup&gt;a&lt;/sup&gt;</td>
<td>75.0</td>
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<tr>
<td>Oregon–</td>
<td>Old-growth Pseudotsuga–Tsuga</td>
<td>55.4&lt;sup&gt;a&lt;/sup&gt;</td>
<td>17.9</td>
</tr>
<tr>
<td>Washington</td>
<td></td>
<td>73.8&lt;sup&gt;b&lt;/sup&gt;</td>
<td>13.8</td>
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<td>Columbia</td>
<td>Temperate rainforest</td>
<td>27.2</td>
<td>37.7</td>
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<tr>
<td>Alaska</td>
<td>Old-growth Tsuga</td>
<td>0</td>
<td>95</td>
</tr>
<tr>
<td></td>
<td></td>
<td>15</td>
<td>64</td>
</tr>
<tr>
<td></td>
<td></td>
<td>4</td>
<td>69</td>
</tr>
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<td></td>
<td></td>
<td>6</td>
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</table>
Table 2-1. (Continued)

<table>
<thead>
<tr>
<th>Location</th>
<th>Forest type</th>
<th>Mortality of gap maker (%)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Standing dead</td>
<td>Snapped off</td>
</tr>
<tr>
<td>Tropical forests</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Panama</td>
<td>Tropical moist</td>
<td>14</td>
<td>60</td>
</tr>
<tr>
<td>Mexico</td>
<td>Tropical cloud</td>
<td>13.9</td>
<td>29.1</td>
</tr>
<tr>
<td>Mexico</td>
<td>Pinus–Quercus</td>
<td>26.4</td>
<td>39.5</td>
</tr>
<tr>
<td>Costa Rica</td>
<td>Cloud forest</td>
<td>2</td>
<td>39</td>
</tr>
<tr>
<td>Southern hemisphere forests</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>New Zealand</td>
<td>Old-growth Nothofagus</td>
<td>31</td>
<td>41</td>
</tr>
</tbody>
</table>

Summary statistics (range values; median values in parentheses)

<table>
<thead>
<tr>
<th></th>
<th>Standing dead</th>
<th>Snapped off</th>
<th>Uprooted</th>
<th>Other</th>
</tr>
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<td>Boreal and alpine</td>
<td>8–44 (17)</td>
<td>42–61 (47)</td>
<td>7–42 (29)</td>
<td>0–2 (1)</td>
</tr>
<tr>
<td>Temperate hardwoods</td>
<td>3–45 (17)</td>
<td>28–87 (52)</td>
<td>10–37 (20)</td>
<td>0–13 (9)</td>
</tr>
<tr>
<td>Temperate coniferous</td>
<td>0–55 (15)</td>
<td>13–95 (64)</td>
<td>5–27 (19)</td>
<td>0–57 (2)</td>
</tr>
<tr>
<td>Tropical</td>
<td>2–26 (14)</td>
<td>29–60 (40)</td>
<td>17–53 (31)</td>
<td>4–18 (12)</td>
</tr>
<tr>
<td>Southern hemisphere</td>
<td>31</td>
<td>41</td>
<td>24</td>
<td>4</td>
</tr>
</tbody>
</table>

a Old-growth stands.
b Mature stands.
c Developing stands.
include storm intensity, timing and associated precipitation, topographic features, edaphic conditions and disturbance history. The complex interaction of a multitude of factors certainly accounts for the variability in gap-maker mortality in global forests. Putz et al. (1983) attempted to understand why trees uproot or snap in terms of their mechanical and architectural properties. Uprooted tropical trees tend to be stronger, larger, and shorter for a given stem diameter than trees that snap off.

An understanding of how trees have died is important in any study of gap dynamics. Gaps are created by individual tree mortality, the complexity of which has only recently been appreciated (Maser et al. 1988; Lugo and Scatena 1996). Pathogens may or may not play a role in tree death. Cause of mortality is important in assessing the degree to which site resources may be changed when a tree dies. A tree that dies and remains standing for a long time or that slowly breaks up over time will affect resource release and allocation differently than one that is suddenly snapped off or windthrown (Krasny and Whitmore 1992).

Of particular importance, but little studied, is the role of pathogens as a disturbance factor in forests. In Canadian boreal forests, extensive research has provided detailed understanding of the pathological vectors responsible for trunk and root rots in spruce and fir (Basham et al. 1953; Davidson 1957; Redmond 1957; Basham and Morawski 1964; Basham 1973a, 1973b; Whitney et al. 1974; Whitney 1976; Whitney and Myren 1978; Lavallée 1986, 1987; Whitney 1995). Much of this work, however, has focused on estimating the level of cull in commercial forests and on understanding the types of pathogenic decay fungi responsible for the loss of merchantable wood fibre. Therefore, little consideration was given to viewing tree stem and root decay as a mechanism of biotic
disturbance in boreal forests. Results from studies on fir and spruce pathology repeatedly underline the importance of root and associated butt rots in determining growth increment patterns and timing and etiology of tree death (Whitney and MacDonald 1985; Whitney 1989, 1995). As root and butt decay progresses, trees are susceptible to windthrow and stem breakage, both of which determine the rate and type of gap disturbance in old boreal forests.

Worrall and Harrington (1988) examined the disease vectors responsible for canopy gaps in old-growth subalpine spruce-fir forests in New Hampshire. Biotic diseases (root and butt rots, stem decays, cankers, and dwarf mistletoe) accounted for up to 66% of the gap area at the lowest elevation. At higher elevations, chronic wind stress accounted for up to 72% of the gap area. Butt and root rots predisposed trees, particularly balsam fir, to stem breakage at ground level. The authors attributed the relative rarity of balsam fir at lower elevations to its high susceptibility to root pathogens. In a central British Columbia spruce (Picea glauca x engelmannii)–subalpine fir system, butt rots were deemed essential in determining the differential mortality of the shorter-lived subalpine fir and as agents of gap dynamics in these wet sub-boreal spruce forests (Lewis and Lindgren 1999). Heart rot fungi were responsible for the high degree of stem snap and associated gap dynamics in wind-sheltered old-growth western hemlock (Tsuga heterophylla (Raf.) Sarg.) forests of southeast Alaska (Nowacki and Kramer 1998). An early work pointed to the significant role of butt and root rots in the promotion of windthrow and stem breakage (Hubert 1918). The role of pathogens as gap makers, and therefore determinants of forest structure and dynamics, needs greater attention in gap studies (van der Kamp 1991; Castello et al. 1995; Hennon 1995). In boreal forests or high-altitude coniferous forests at lower latitudes, snow
loading and ice damage may open up gaps in the forest canopy through top and stem breakage (Gill 1974). In subalpine coniferous forests in Japan, typhoon-mediated gaps are a common occurrence (Naka 1982; Kanzaki 1984; Kanzaki and Yoda 1986). Spruce budworm-mediated small gap processes have also been documented for southern boreal forests in Quebec (Kneeshaw and Bergeron 1998).

2.5 RESEARCH METHODOLOGY

2.5.1 Gap Measurement

How one defines a forest canopy gap is of the utmost importance. This is true especially if one wishes to quantify forest disturbance in terms of “turnover rates” which are defined as the mean time between gap creation events at any point in the forest (Brokaw 1982; Green 1996). Both gap size and turnover rate are significantly influenced by the particular gap definition chosen (van der Meer et al. 1994). Comparisons among small-scale disturbance events in different forest types are valid only if researchers employ a standard methodology (Runkle 1992).

A number of gap definitions have been suggested. Working in old-growth mesic hardwood forests in the eastern United States, Runkle (1981, 1982) defined two types of gaps. The simplest to consider is the surface of the forest floor directly under the canopy opening. Additional areas of forest floor may be included in what has been termed the “expanded gap” that Runkle (1982) defined as the canopy gap plus the adjacent area extending to the bases of canopy trees surrounding the canopy gap. Trees growing in gaps
were considered as part of the surrounding canopy when they had reached heights of 10 to 20 m.

In tropical ecosystems, one of the earliest definitions of a canopy gap was provided by Brokaw (1982) who defined a gap as “a ‘hole’ in the forest extending through all levels down through an average height of 2 m above ground. The sides of forest openings are irregular in profile, but, for a workable definition, the sides of that space defined as a gap are vertical. The side at a particular place on the perimeter is located at the innermost point reached by foliage, at any level, at that place on the perimeter.”

It is often difficult to distinguish gaps in the field. Gaps, once formed, do not remain static but exist in various states of “filling in” that can range from a fresh, newly opened, relatively well-defined gap, to one that for all intents and purposes is no longer a gap, having filled in from the growth of advanced regeneration or lateral branch growth of surrounding trees. A basic assumption is that gaps can be effectively and accurately distinguished from the surrounding background trees. Various researchers, depending on the type and height of the forest in question, have determined a critical regeneration height beyond which the gap is considered as closed. This critical height will depend, of course, on the height of the dominant canopy and the practical difficulties of readily observing the canopy opening.

Most gap research involves ocular recognition of canopy gaps and use of either Brokaw’s or Runkle’s gap definition or some similar variant. Most forest stands of interest are subsampled for gaps using line intersect sampling or strip transects (Runkle 1985b, 1992). Gaps are often considered to approximate an ellipse and are measured accordingly. It has been noted, however, than such assumptions regarding the shape of gaps are often
unfounded and appropriate adjustments must be taken if gap geometry and gap fraction are to be accurately determined (Battles et al. 1996).

2.5.2 Retrospective Gap Analysis

History of forest disturbance, including small-scale gap dynamics, may be inferred from retrospective studies (Lorimer 1985; Foster et al. 1996). The method of choice is determined by the questions posed by each study, particularly the temporal and spatial scale for which information is required. Methods may include the analysis of age and size structure of stands (Whipple and Dix 1979; Ågren and Zackrisson 1990; Hiura et al. 1996), radial and height growth increment patterns (Lorimer 1985), stand reconstruction (Oliver and Stephens 1977; Suzuki et al. 1987; Deal et al. 1991), soil microtopography and coarse woody debris (Henry and Swan 1974), repeat measurements of permanent sample plots (Hofgaard 1993a) and even fine-resolution, stand-level pollen analysis (Mitchell 1988; Bradshaw and Zackrisson 1990; Foster and Zebryk 1993; Ritchie 1995). Each technique employed in the study of disturbance dynamics has its particular limitation. For example, good age data are often difficult and time consuming to gather, dendroecological techniques are restricted to surviving and decay-free trees, and pollen analysis may often be too coarse-filtered for a study of stand-level dynamics. Therefore, an integrated approach that uses a combination of techniques and data will often provide the best insight into stand dynamics (Lorimer 1980; Foster 1988).

Spatial analysis of mapped tree stem data is assuming increasing importance in the analysis of small-scale canopy disturbance. Aside from the significant benefit achieved from the analysis of ecological systems using spatial data (Legendre and Fortin 1989; Rossi
et al. 1992), the use of spatial analysis in studies of gap dynamics is important from a methodological point of view. Traditional studies of gap dynamics have been carried out in temperate and tropical forests characterized by closed canopies in which gap openings are generally easily verified and measured. However, despite the relative ease with which gaps are identified in these high forest canopies, methodological assumptions and sampling protocols are items of concern, especially in the determination of gap area. Furthermore, what a particular investigator measures in terms of gap structure may not be that to which individual trees are actually responding. As gap studies consider patchier and open-canopied situations, such as may be found in slow-growing boreal forests, the use of traditional gap methodology ceases to be useful. In these forests, stands may not achieve anywhere near full crown closure, making the delineation of gap openings extremely problematic. A need, therefore, exists for some form of gap quantification that does not depend on the ocular measurement of holes in the canopy.

Characterization of gap structure and dynamics in old-growth stands has been achieved by the use of spatial analysis of stem-mapped point data (Leemans 1991; Moeur 1993, 1997; Chokkalingam 1998; Chen and Bradshaw 1999; Parish et al. 1999; Chokkalingam and White 2001). The acquisition of stem map data may be time consuming, especially in multi-stage stands, but is facilitated by recent developments in hand-held laser technology (Peet et al. 1997). The stem map data may be analyzed by Ripley's univariate K function (Ripley 1977, 1981; Upton and Fingleton 1985; Cressie 1993; Diggle 2003) which compares the distances between all possible point pairs and tests whether an observed spatial pattern is random, aggregated or regularly spaced. The null hypothesis is that the spatial pattern of measured points is not significantly different from
that observed in a random population. Bivariate spatial interactions between two groups of
trees may also be performed. The null hypothesis assumes complete spatial independence
between the two populations in question. Both univariate and bivariate analysis are very
useful in detecting spatial patterns associated with gap structure and dynamics across a
continuum of spatial scales.

Interest has grown in the use of retrospective dendroecological techniques to
describe and quantify small-scale forest disturbance history, particularly of old-growth
forest systems (Fritts and Swetnam 1989; Schweingruber 1996). Tree ring patterns,
particularly patterns in relative ring width, are able to provide information on the pattern of
establishment, suppression and release of individual trees. These patterns furnish essential
clues to the disturbance history of forest stands (Lorimer 1985; Lorimer and Frelich 1989).
Both annual growth increment and ring-width patterns of shade-tolerant species have been
used as proxy evidence of past canopy disturbance caused by gap dynamics (Lorimer 1980;
Canham 1985; Lorimer and Frelich 1989; Canham 1990; Payette et al. 1990; Frelich and
Lorimer 1991a; Fajvan and Seymour 1993; Frelich and Graumlich 1994; Orwig and
Abrams 1994; Abrams et al. 1995; Cho and Boerner 1995; Orwig and Abrams 1995;
Parshall 1995; Cherubini et al. 1996; Daniels and Klinka 1996; Abrams and Orwig 1996a,
1996b; Nowacki and Abrams 1997; Abrams et al. 1998; Ishikawa et al. 1999; Ziegler
2002). In response to the creation or infilling of canopy gaps, trees experience periods of
release or suppression, evidence of which is preserved in the growth rings. The frequency,
duration and spatial pattern of the release and suppression events provide a helpful picture
of historic canopy disturbance and recruitment dynamics.
Most dendroecological studies have been aspatial in nature, randomly sampling a select number of canopy and understory trees for radial growth analysis. The insights gained from such studies may be enhanced by including dendroecological data and spatial statistics on completely mapped tree point data (Payette et al. 1990; Chokkalingam 1998). This form of analysis provides additional insight into the spatio-temporal dynamic of gaps across a continuum of spatial scales, allowing a fine-scale delineation of gaps through time and across the physical space of the plot.

Though employed more rarely, other methods in gap studies include repeated measurements in permanent sample plots (Nakashizuka et al. 1992), measurement of actual canopy height in a mapped stand (Parker et al. 1985), hemispherical photographs (Whitmore et al. 1993), repeat aerial photography (Tanaka and Nakashizuka 1997) and other remote sensing techniques (Bradshaw and Spies 1992; Blackburn and Milton 1996).

2.6 GAP SIZE AND TURNOVER RATE

As noted above in the discussion on methodology, the measurement of gap size and the calculation of gap turnover rates are heavily influenced by the gap definition employed. Combined with the inherent subjectivity in field assessment of gaps, this creates a difficulty in making comparisons among studies. However, a comparison among gap studies made in different forest ecosystems may be instructive (Table 2-2). Certain trends are evident and provide useful information on comparative forest gap dynamics, as described below.

Gap size is often used as an indicator of environmental heterogeneity and resource sequestration in gaps. The degree to which light, moisture and nutrient resources are available to vegetation occupying a newly formed gap is often dependent on gap size.
Table 2-2. Gap characteristics of gap-disturbed forests.

<table>
<thead>
<tr>
<th>Location</th>
<th>Forest type</th>
<th>Gap fraction (％)</th>
<th>Average gap size (m²)</th>
<th>Gap range (m²)</th>
<th>Annual gap formation rate (%)</th>
<th>Turnover rate (years)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Boreal and subalpine forests</strong></td>
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<td></td>
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<tr>
<td>New Hampshire</td>
<td>Subalpine <em>Abies-Picea</em></td>
<td>24¹</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Foster and Reiners 1983</td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine <em>Tsuga-Abies-Picea-Betula</em></td>
<td>10.8-17.2</td>
<td>83.8-133.7</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Kanzaki 1984</td>
</tr>
<tr>
<td>North Carolina–Tennessee</td>
<td>Old-growth subalpine <em>Picea-Abies</em></td>
<td>36</td>
<td>66</td>
<td>15-150</td>
<td>0.6-0.9</td>
<td>111-178</td>
<td>White et al. 1985a</td>
</tr>
<tr>
<td>New Hampshire</td>
<td>Subalpine <em>Picea-Abies</em></td>
<td>33</td>
<td>-</td>
<td>18 m²</td>
<td>12.2 ha</td>
<td>303</td>
<td>Foster and Reiners 1986</td>
</tr>
<tr>
<td>New Hampshire</td>
<td>Subalpine <em>Picea-Abies</em></td>
<td>6-33</td>
<td>45-145ᵇ</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Worrall and Harrington 1988</td>
</tr>
<tr>
<td>Japan</td>
<td>Mixed <em>Abies</em>-hardwoods</td>
<td>21.5</td>
<td>141</td>
<td>22-318</td>
<td>-</td>
<td>-</td>
<td>Ishikawa and Ito 1989</td>
</tr>
<tr>
<td>Sweden</td>
<td>Old-growth <em>Picea abies</em></td>
<td>28</td>
<td>100</td>
<td>71-139</td>
<td>-</td>
<td>-</td>
<td>Leemans 1990</td>
</tr>
<tr>
<td>Sweden</td>
<td>Old-growth <em>Picea abies</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>200</td>
<td>Hofgaard 1993b</td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine coniferous</td>
<td>7.3-8.5</td>
<td>40.8-42.5</td>
<td>1.2-285</td>
<td>-</td>
<td>-</td>
<td>Yamamoto 1993</td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine <em>Picea-Abies</em></td>
<td>19.3</td>
<td>-</td>
<td>5-1245</td>
<td>-</td>
<td>-</td>
<td>Kubota et al. 1994</td>
</tr>
<tr>
<td>Location</td>
<td>Forest type</td>
<td>Gap fraction (%)</td>
<td>Average gap size ($m^2$)</td>
<td>Gap range ($m^3$)</td>
<td>Annual gap formation rate (%)</td>
<td>Turnover rate (years)</td>
<td>Reference</td>
</tr>
<tr>
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<td>----------------------</td>
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<td>--------------------------</td>
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<td>-------------------------------</td>
<td>-----------------------</td>
<td>--------------------------------</td>
</tr>
<tr>
<td>New York</td>
<td>Subalpine <em>Abies—Picea</em></td>
<td>15</td>
<td>72&lt;sup&gt;c&lt;/sup&gt;</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Battles et al. 1995</td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine <em>Abies—Tsuga</em></td>
<td>7.3</td>
<td>43.3</td>
<td>3.6–369.6</td>
<td>–</td>
<td>–</td>
<td>Yamamoto 1995; Yamamoto 1996</td>
</tr>
<tr>
<td>New York–New Hampshire</td>
<td>Subalpine <em>Picea—Abies</em></td>
<td>15–42&lt;sup&gt;b&lt;/sup&gt;</td>
<td>25–93&lt;sup&gt;bc&lt;/sup&gt;</td>
<td>12–1135&lt;sup&gt;b&lt;/sup&gt;</td>
<td>–</td>
<td>–</td>
<td>Battles and Fahey 1996</td>
</tr>
<tr>
<td>Japan</td>
<td>Subalpine <em>Abies—Picea—Betula</em></td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>1.2–2.4</td>
<td>87–99</td>
<td>Hiura et al. 1996</td>
</tr>
<tr>
<td>Russia</td>
<td><em>Picea abies</em></td>
<td>35</td>
<td>&lt;200 (95% of all gaps)</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Drobyshov 1999</td>
</tr>
<tr>
<td><strong>Temperate hardwood forests</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>Tennessee</td>
<td>Mature hardwoods</td>
<td>–</td>
<td>90&lt;sup&gt;cd&lt;/sup&gt;</td>
<td>8–404&lt;sup&gt;d&lt;/sup&gt;</td>
<td>–</td>
<td>–</td>
<td>Barden 1981</td>
</tr>
<tr>
<td>Japan</td>
<td>Evergreen broadleaf</td>
<td>20</td>
<td>92</td>
<td>19.5–390</td>
<td>0.56</td>
<td>180</td>
<td>Naka 1982</td>
</tr>
<tr>
<td>United States</td>
<td>Old-growth mesic hardwoods</td>
<td>9.5</td>
<td>28–69</td>
<td>25–1500</td>
<td>1</td>
<td>100</td>
<td>Runkle 1982</td>
</tr>
<tr>
<td>Japan</td>
<td>Climax <em>Fagus</em></td>
<td>20</td>
<td>137</td>
<td>10–470</td>
<td>0.45–1.03</td>
<td>100–200</td>
<td>Nakashizuoka 1984a</td>
</tr>
<tr>
<td>Japan</td>
<td>Primary <em>Fagus</em></td>
<td>–</td>
<td>–</td>
<td>54–144</td>
<td>–</td>
<td>–</td>
<td>Ohkubo et al. 1988</td>
</tr>
<tr>
<td>Indiana</td>
<td>Old-growth hardwoods</td>
<td>9</td>
<td>52.4</td>
<td>25–375</td>
<td>–</td>
<td>–</td>
<td>Ward and Parker 1989</td>
</tr>
<tr>
<td>Japan</td>
<td>Climax <em>Fagus</em></td>
<td>12</td>
<td>92</td>
<td>≤728</td>
<td>–</td>
<td>134</td>
<td>Yamamoto 1989</td>
</tr>
<tr>
<td>Location</td>
<td>Forest type</td>
<td>Gap fraction (%)</td>
<td>Average gap size (m²)</td>
<td>Gap range (m²)</td>
<td>Annual gap formation rate (%)</td>
<td>Turnover rate (years)</td>
<td>Reference</td>
</tr>
<tr>
<td>------------</td>
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<td>------------------------------</td>
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<td>-----------------------------------</td>
</tr>
<tr>
<td>Ohio</td>
<td>Old-growth Acer–Fagus</td>
<td>7</td>
<td>≤ 200</td>
<td>–</td>
<td>0.8–0.9</td>
<td>110–125</td>
<td>Runkle 1990</td>
</tr>
<tr>
<td>Michigan</td>
<td>Old-growth Acer–Tsuga</td>
<td>14.1b</td>
<td>100–400b</td>
<td>–</td>
<td>0.57–0.69</td>
<td>145–175</td>
<td>Frelich and Lorimer 1991a</td>
</tr>
<tr>
<td>New York</td>
<td>Mature northern hardwoods</td>
<td>8.4</td>
<td>42.8</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Krasny and Whitmore 1992</td>
</tr>
<tr>
<td>Japan</td>
<td>Old-growth temperate deciduous</td>
<td>6.2</td>
<td>–</td>
<td>–</td>
<td>0.42</td>
<td>58–240</td>
<td>Nakashizuka et al. 1992</td>
</tr>
<tr>
<td>Japan</td>
<td>Primary evergreen broadleaved</td>
<td>15.7</td>
<td>80.3</td>
<td>–</td>
<td>–</td>
<td>–</td>
<td>Yamamoto 1992b</td>
</tr>
<tr>
<td>North Carolina</td>
<td>Mixed Quercus</td>
<td>2</td>
<td>239</td>
<td>40–850</td>
<td>0.8</td>
<td>–</td>
<td>Clinton et al. 1993</td>
</tr>
<tr>
<td>North Carolina</td>
<td>Mixed Quercus</td>
<td>–</td>
<td>227</td>
<td>60–630</td>
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<td>0.72–1.3</td>
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<td>–</td>
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<td>158</td>
<td>Arriaga 1988a</td>
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Table 2-2. (Continued)

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<th>Location</th>
<th>Forest type</th>
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<th>Average gap size (m$^2$)</th>
<th>Gap range (m$^3$)</th>
<th>Annual gap formation rate (%)</th>
<th>Turnover rate (years)</th>
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<td>26–342$^i$</td>
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<td>Lowland rainforest</td>
<td>1.1</td>
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<td>0.96</td>
<td>-</td>
<td>van der Meer and Bongers 1996a</td>
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<td>French Guiana</td>
<td>Lowland rainforest</td>
<td>-</td>
<td>-</td>
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**Southern hemisphere forests**

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<tr>
<th>Location</th>
<th>Forest type</th>
<th>Gap fraction (%)</th>
<th>Average gap size (m$^2$)</th>
<th>Gap range (m$^3$)</th>
<th>Annual gap formation rate (%)</th>
<th>Turnover rate (years)</th>
<th>Reference</th>
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<td>Chile</td>
<td>Temperate rain forest</td>
<td>8.6$^k$</td>
<td>432$^{bck}$</td>
<td>120–1532$^{bk}$</td>
<td>-</td>
<td>392$^k$</td>
<td>Veblen 1985a</td>
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<td>Old-growth</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
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<td>Veblen 1989a</td>
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<tr>
<td></td>
<td><em>Nothofagus</em></td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>New Zealand</td>
<td>Old-growth</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>Steward and Rose 1990</td>
</tr>
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<td><em>Nothofagus</em></td>
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<td>-</td>
<td>-</td>
<td>-</td>
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<tr>
<td>New Zealand</td>
<td>Subalpine montane</td>
<td>2.8$^m$</td>
<td>39.5$^m$</td>
<td>-</td>
<td>0.28$^m$</td>
<td>360$^m$</td>
<td>Ogden et al. 1991</td>
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### Table 2-2. (Continued)

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<th>Location</th>
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<th>Average gap size (m²)</th>
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<th>Annual gap formation rate (%)</th>
<th>Turnover rate (years)</th>
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<td>143c</td>
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<td>320–448</td>
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<td>9.1</td>
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<td>26–898</td>
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<td>331–415</td>
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**Summary statistics for Table 2-2** *(Range values; median values in parentheses)*

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<th>Boreal and subalpine</th>
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<td>Gap fraction (%)</td>
<td>6–36 (21)</td>
<td>2–20 (10)</td>
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<td>0.8–8 (4)</td>
<td>3–35 (8)</td>
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<td>Average gap size (m²)</td>
<td>41–141 (78)</td>
<td>28–239 (79)</td>
<td>77–131 (85)</td>
<td>10–120 (50)</td>
<td>40–143 (93)</td>
</tr>
<tr>
<td>Gap range (m²)</td>
<td>15–1245</td>
<td>8–2009</td>
<td>5–734</td>
<td>4–700</td>
<td>24–1476</td>
</tr>
<tr>
<td>Annual gap formation rate (%)</td>
<td>0.6–2.4 (1.0)</td>
<td>0.4–1.3 (0.8)</td>
<td>0.2</td>
<td>0.5–6.5 (1.0)</td>
<td>0.25–0.28 (0.3)</td>
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<tr>
<td>Turnover rate (years)</td>
<td>87–303 (174)</td>
<td>45–240 (134)</td>
<td>280–1000 (650)</td>
<td>80–244 (137)</td>
<td>320–794 (408)</td>
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</table>

* Unless otherwise noted, all gap measures refer to actual canopy gaps which are defined as the projection of the canopy edge on the forest floor (Runkle 1992).
* b Expanded canopy gap is defined as the area circumscribed by the boles of the canopy trees whose foliage borders the actual gap.
* c Median values.
* d Single-tree gaps.
* e Multi-tree gaps.
* f Stands dominated by *Acer saccharum*.
* g Stands dominated by *Tsuga heterophylla*. 
\textsuperscript{h} Developing stands.
\textsuperscript{i} Old-growth stands.
\textsuperscript{j} Mature stands.
\textsuperscript{k} Montane stands.
\textsuperscript{l} Lowland stands.
\textsuperscript{m} Subalpine stands.
\textsuperscript{n} Figures for South Africa were excluded.
Furthermore, among other factors, gap dimensions often determine whether the available growing space will be occupied by early or late successional species (Pickett 1983; Denslow 1987).

Gap size will obviously differ depending on tree size and crown dimensions, whether gaps are formed from single- or multiple-tree falls, the age of the gap, as well as the methodology employed by the respective researcher. For the most part, gap-size distributions are negatively exponential in form, with the largest percentage of gaps in the lowest size range, indicating that small, single-treefall gaps form more frequently than large multi-treefall gaps. Gap size for single treefalls normally ranges from 50 to 200 m² (Table 2-2). In old-growth Swedish boreal forests, Liu and Hytteborn (1991) found that 98% of the sampled gaps were smaller than 250 m². For subalpine coniferous forests, Yamamoto (1993) suggested an upper limit of 200 m² below which exists the vast majority of gaps. This would seem reasonable, given similar findings in work conducted in other boreal and subalpine coniferous forests (White et al. 1985a; Foster and Reiners 1986; Hytteborn et al. 1991; Yamamoto 1995; Battles and Fahey 1996). Median values of average gap size are lowest for tropical forests and highest for the temperate coniferous forests and southern hemisphere forests dominated by large-sized canopy trees.

Single-treefall gaps often enlarge as a result of subsequent fall of gap border trees. Thus, many gaps measured in the field are the result of a series of treefall events covering a substantial period of time (Lertzman and Krebs 1991). Evidence for such multiple events includes the wide range in degree of necrotization in the gap-maker trees now forming part of the coarse woody debris. Liu and Hytteborn (1991) found that up to 65% of the sampled gaps contained more than one age-class of logs, indicating successive periods of gap
enlargement. Working in tropical systems, Young and Hubbell (1991) found that gap-edge trees were much more likely to fall into pre-existing gaps than in other directions. The preponderance of asymmetrical crowns of gap-edge trees proved to be the main factor influencing direction of tree fall.

Gap turnover time will depend on the rate of gap-infilling, the recruitment and growth of seedlings in the gaps, and the rate of gap expansion (Valverde and Silvertown 1997). In turn, the growth of seedlings, whether established before the gap event as advance regeneration, or subsequently recruited after gap establishment, is determined by the rate and quantity of resource allocation in the newly acquired growing space. Closure of small gaps will depend to a large degree on lateral branch infilling by surrounding canopy trees, whereas closure of large gaps occurs more through the growth of released or newly recruited trees (Runkle 1990). Annual lateral growth rates of hardwoods have been calculated at 4 to 26 cm (Runkle 1985a), 18 cm (Runkle 1990) and 12 cm (Runkle 1998). Gaps were considered closed when hardwood saplings had reached a height of 10 to 20 m (Runkle 1981). This height growth, combined with the estimated rates of lateral infilling, resulted in a range of maximum possible gap ages of 10 to 40 years (Runkle 1982). In montane and lowland Chilean rain forests, gaps were determined to be no older than 32 and 50 years, respectively (Veblen 1985a). Gaps in old-growth Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) were estimated to have begun at least 50 years ago, with gaps in the mature 140 year-old forest being much younger (Spies et al. 1990). The oldest gaps in a Swedish boreal forest were at most 70 years old (Liu and Hytteborn 1991). Median values for the annual gap formation rate are quite similar for boreal, temperate hardwood and tropical forests, ranging from 0.8% to 1.0% (Table 2-2). Both temperate coniferous and
Southern hemisphere forests have lower gap formation rates of 0.2%. This translates into almost equal turnover rates for temperate and tropical forests (135 years) with a slightly higher figure of 174 years for northern boreal forests. Temperate coniferous forests and southern hemisphere *Nothofagus* forests exhibit the slowest turnover rates of 400 to 650 years (Table 2-2). Gaps are shorter lived in temperate and tropical forests, tending to fill in at a quicker rate. Slow turnover rates for the northern and southern hemisphere temperate rain forests are in part attributable to the relatively long life span of the respective tree species. It is interesting to note the generally large area in gaps documented for the Appalachian and Swedish boreal forests relative to other studies. Furthermore, these gaps tend to be much older than gaps in tropical and temperate forests. Gap recruitment and gap filling in cold, slow-growing northern forests are probably very slow compared with that occurring in most temperate and tropical forests. As expected, gap fraction is lowest in tropical forests.

2.7 GAPS AND TREE RECRUITMENT

2.7.1 Availability of Light

Most studies on tree regeneration and gap structure have focused on the relationship among gap size, associated light levels and regeneration success. Of particular interest has been the effect of gap size and gap position on the flux of solar radiation and its effect on the germination, survival and growth of tree species. The spatial and diurnal flux of photosynthetically active radiation in forest gaps has been shown to be a pre-eminent factor in seedling survival and growth, particularly in tropical forests (Denslow 1987; Denslow
and Hartshorn 1994; Nicotra et al. 1999). At any particular location, the amount of light entering the gap depends on the size and topographic position of the gap, the position within the gap, the height of the surrounding canopy, the sun angle and sky conditions (Messier 1996).

Chazdon and Fetcher (1984), in their study of light fluxes in tropical forests, estimated total incident photosynthetically active radiation at 1% to 2% of full sunlight in the understory, 9% in the centre of a 200 m² gap and 20% to 35% in a 400 m² gap. In similar forests, Denslow et al. (1990) determined the total incident radiation to be the highest in gap centres (9% to 23% of full sunlight). At the gap–forest edges, radiation was 3% to 11% of the full sunlight with the understory showing a low 0.4% to 2% of full sunlight.

Differential response of tree species to light flux under closed forest canopies and in gaps has long been known to foresters who have provisionally segregated tree species in terms of their ability to germinate, survive and grow under varying degrees of shade (Baker 1949). Such defined differences in shade tolerance, though often expressed in relative, descriptive terms, have long provided a useful and functional foundation to silvicultural systems in many forest types around the world.

According to Marks (1974), forests respond to canopy openings from disturbance in two major ways: (1) by responding through reorganization of vegetation established prior to disturbance or, (2) by responding as vegetation that becomes established following disturbance. The coupling of the long-held notions of shade tolerance with the recent interest in gap dynamics has emerged as workers attempt to relate gap physiognomy with differential recruitment of tree species. The size of gaps in closed forests has been shown
to determine the type of trees recruited in the gaps. Small gaps coupled with advance regeneration of shade-tolerant species would favour the "reorganization" response as defined by Marks (1974). Seed colonization of large gaps by shade-intolerant species would define the other extreme.

Using extensive work in tropical forests as a basis, Whitmore (1978, 1989) and Brokaw (1985b) divided trees that colonize gaps into two contrasting ecologic groups: those termed climax or primary species (non-pioneer) and pioneer species. Despite the recognition that a continuum of regeneration strategies exist, the classification of trees into two regeneration types has proven quite useful. Climax or shade-tolerant species are able to establish themselves under shade as advance regeneration and will respond to small gaps. Light-demanding or pioneer species are often recruited only in larger gaps and are usually established after gap formation. Gap formation, therefore, not only drives the forest growth cycle but also determine forest floristics (Whitmore 1982). Gap regeneration behaviors have also been delineated for tree species in undisturbed primary forests in Japan (Yamamoto 1989, 1992b).

Gap research has focused heavily on the preference of different tree species for larger or smaller gaps in determining forest regeneration dynamics. It has been well established that gap size is a major factor determining post-disturbance tree species composition. Shade-intolerant and shade-tolerant species exhibit differential recruitment depending on the size of canopy gaps (Hartshorn 1978; Whitmore 1978; Barden 1979, 1980; Hibbs 1982; Runkle 1982; Pickett 1983; Nakashizuka 1985; Brokaw 1985a, 1985b, 1987; Denslow 1987; Bongers et al. 1988; Brokaw and Scheiner 1989; Raich and Khoon 1990; Nakashizuka et al. 1992; Veblen 1992; Orwig and Abrams 1994; Abe et al. 1995;
Tanouchi and Yamamoto 1995; Abe et al. 1998). Species considered intolerant are relatively more abundant in large gaps, while tolerant species often grow more abundantly in smaller gaps. Large gaps in old-growth stands are generally considered essential for the establishment of shade-intolerant species such as tulip tree (*Liriodendron tulipifera* L.) (Buckner and McCracken 1978; Runkle 1984; Clebsch and Busing 1989; Busing 1995). Pin cherry (*Prunus pensylvanica* L. f.) and paper birch both require conditions associated with larger gaps relative to beech (*Fagus grandifolia* Ehrh.) and sugar maple which are usually considered as adapted to conditions characteristic of small gaps (McClure and Lee 1993). Busing (1994), in a study of old-growth Appalachian cove forests, determined that a gap size of 0.04 ha was a threshold size below which intolerant species were not able to establish. Although able to germinate in a shaded understory, seedlings of the Brazil nut (*Bertholletia excelsa* Humb. and Bonpl.) need gaps greater than 95 m$^2$ to survive and grow into saplings (Myers et al. 2000).

In general, shade-tolerant species, usually existing as advance regeneration, have a greater chance of responding to small gap openings or even to small increases in ambient light levels from diffuse radiation. The physiological and morphological plasticity of shade-tolerant species allows rapid response to increased light environments. Less tolerant species, on the other hand, may still persist in canopies of shade-tolerant forests because of their opportunistic exploitation of larger gaps. A diversity of gap sizes may therefore be significant in the maintenance of canopy diversity in old-growth forests (Barden 1979, 1980, 1981; Runkle 1982; Canham 1989; Clebsch and Busing 1989; Ward and Parker 1989; McClure and Lee 1993; Tanouchi and Yamamoto 1995; Busing and White 1997; Busing 1998a, 1998b).
Much study has been made of the compositional stability of beech–sugar maple forests (Poulson and Platt 1996) and the hemlock (*Tsuga canadensis* (L.) Carr)–beech–maple forests in the Great Lakes region (Frelich and Lorimer 1991a; Frelich et al. 1993; Tyrrell and Crow 1994a). Allogenic coexistence of shade-tolerant species is explained by a long-term disturbance regime characterized by small light gaps. Beech, maple and hemlock, being able to persist as advance regeneration in the shaded conditions of the dominant canopy, may fluctuate in relative dominance, but will maintain control of the canopy. This self-replacement of beech, sugar maple and eastern hemlock via small-scale gap dynamics has been noted by a number of workers (Brewer and Merritt 1978; Woods 1979; Runkle 1981; Woods and Whittaker 1981; Runkle 1984, 1990, 1998). Under present climatic conditions, gap phase dynamics is sufficient to maintain canopy species composition. Small gap maintenance of canopy compositional stability has also been reported for several forest types in Japan (Shimizu 1984; Hara 1985). Catastrophic canopy disturbances would be required to significantly change canopy species composition.

Along with gap size, heterogeneity of light flux and regeneration response are also dependent on gap position and orientation. In the northern hemisphere, the north end of an open gap is subject to higher light fluxes than the more shaded southern edge. Coates (1998, 2000), in a study of tree response to gaps in partially cut western red cedar (*Thuja plicata* Donn)–hemlock forests, demonstrated an increase in light gradients throughout the growing season from the southern to the northern edge of gaps. Emergence and early survival of all species were greatest in the shade of the south gap edge, a fact attributed to the negative effects of direct sunlight in the northern gap edges. For planted seedlings, however, the best growth was found in the sunnier middle to northern ends of the gaps.
Such discordance between regeneration niche and growth niche is common among forest tree species of western North America (Coates 1998). Differential patterns of tree growth in different gap positions have also been determined for *Nothofagus* species in New Zealand (Runkle et al. 1995), old-growth eastern hardwoods of Michigan (Poulson and Platt 1989) and for Norway spruce in Sweden (Dai 1996).

Other than the study by Dai (1996), no detailed work seems to have been done on the relationship among gap geometry, light availability and tree recruitment in boreal forests. For the most part, work to date has focused on confirming the importance of canopy gap size for seedling recruitment and growth in old-growth boreal forests (Leemans 1990; Liu and Hytteborn 1991; Drobyshev 1999; Drobyshev and Nihlgård 2000).

2.7.2 Light, Canopy Architecture and Latitude

Light regimes under gaps and forest canopy are significantly affected by both canopy architecture and latitude (Poulson and Platt 1989; Canham et al. 1994; Lieffers et al. 1999). One would expect that single tree gaps formed in tall, closed-canopy tropical forests would produce different light regimes than gaps formed in more open, boreal conifer forests growing at high latitudes. Canham et al. (1990), in their comparative study of light regimes in gap-disturbed temperate and tropical forests, were able to demonstrate the significant effect of latitude and canopy architecture on gap light regimes. The high ratio of tree height to crown width in old-growth Douglas fir forests, for example, minimized any change in gap light regimes. Gaps of up to 500 m² had little effect on light levels on the forest floor. Similar effects of the height and architecture of the gap periphery trees on gap light regimes were noted in montane rain forests of Costa Rica (Lawton 1990).
In northern latitude boreal forests, where canopies may be more open due to slow growth rates and nutrient limitations, the interaction of the gap aperture and the low angle of solar radiation produces a different gap light regime than that found in temperate or tropical forests. Canham et al. (1990) demonstrated the significant penetration of light into the understory adjacent to a gap (extended gap), particularly at high latitudes. In a study of gap dynamics in high latitude *Larix gmelini* old-growth in northeastern China, Ban et al. (1998) found that obliquely projected gaps were more important than vertically projected gaps in explaining regeneration patterns. Direct beam radiation is less intense and able to spread though the stand much beyond the actual vertical gap. It has been suggested that the transition to narrow crowned, strongly epinastic boreal forests in the high latitudes is partly a function of the greater ability of vertically extended crowns to utilize photosynthetically active radiation compared to the broad, horizontally stratified crowns of the lower latitudes (Kuuluvainen 1992). In high latitudes, vertical crown growth is seen as the prime mechanism enabling trees to capture a greater amount of the low angle radiation.

Developers of recent gap light models have recognized the critical importance of latitude in determining gap light regimes (Canham 1988a; Dai 1996; Weishampel and Urban 1996). Gaps in boreal forests are therefore not the same environments as gaps in lower latitudes in terms of changed gap light regimes. Overall, high light levels should occur under much more restricted conditions in boreal forests. This lower light flux, however, is offset by the generally broader transmission of light through conifer canopies, the photosynthetic significance of sunflecks and specific adaptive mechanisms of northern conifers to low light availability.
2.7.3 Below-Ground Competition

The majority of gap studies have focused on changes in light availability with gap formation. Concurrent with the changes in the above-ground plant competitive environment may be changes in the below-ground competitive environment (Caspar and Jackson 1997). The flux and heterogeneity of solar radiation across the gap–non-gap interface is important in determining regeneration dynamics in many forest types. Little work, however, has been conducted on the role of gap formation on below-ground competition. An emphasis on the relationship between gap dynamics and below-ground competition may be particularly fruitful, especially in sub-boreal or boreal forests. The generally open nature of many old-growth boreal forests (Liu and Hytteborn 1991; Kneeshaw and Burton 1997) and the well-established acceptance of boreal forests as nitrogen limited (Krause et al. 1978) both support the hypothesis that reduction in root competition with tree death and fall is a major determinant of regeneration dynamics in these forests.

In open-grown, nutrient-poor, boreal forests where the canopy never closes, the overstory trees may be expected to suppress any advance regeneration through extensive root competition (Ågren and Zackrisson 1990; Tilman 1997). In such open forests at high latitudes, one would not expect light to be the dominant limiting factor. Even in light openings, seedlings and saplings may remain in a suppressed state for long periods of time, waiting for sufficient reduction in root competition before being released. Evidence is accumulating that below-ground competition for nutrients is a major factor affecting growth on nutrient-poor Scots pine (Kuuluvainen et al. 1993; Kuuluvainen 1994) and black spruce sites (Newton and Jolliffe 1993). Trenching studies in temperate forests have
confirmed the importance of significant below-ground competitive effects (Toumey and Kienholz 1931; Korstian and Coile 1938; Christy 1986; Coomes and Grubb 2000).

Actual measurements of temporal and spatial dynamics of nutrient fluxes under distinct gaps in boreal forests are not available. Work to date has focused on tropical and temperate forests, but conclusions are not entirely consistent. Early work in tropical forests by Vitousek and Denslow (1986) and Uhl et al. (1988) failed to detect consistent, significant differences in nutrient levels in gaps relative to closed canopy. Recent work by Denslow et al. (1998) found that increases in nitrate-N and extractable phosphate-P in artificially created gaps may enhance growth rates of pioneer tree species. Zhang and Liang (1995) and Zhang and Zak (1995), working in Chinese subtropical forests, observed that a gap threshold of about 15 m in diameter was critical in determining the rate of nutrient release from plant decomposition. Below this gap size, decomposition processes were not affected. Above this gap size, however, nutrient release from litter decomposition was strongly inhibited. In single-treefall gaps in hemlock and sugar maple stands, differences in nitrogen dynamics were significant (Mladenoff 1997), with the doubling of nitrate levels in the hemlock gaps of greatest import. Palik et al. (1997) also found increased nitrogen levels in the centres of large openings in generally open-canopied longleaf pine (Pinus palustris Mill.) stands in Georgia. Seedling growth was related to both light and below-ground nitrogen levels. Similarly, in lodgepole pine (Pinus contorta Dougl.) forests, root gaps were detected in artificially created light gaps of at least 30 trees (Parsons et al. 1994a) with increases in mineralized nitrogen evident in gaps created by the removal of at least 15 to 30 trees (Parsons et al. 1994b). In German beech forests, root gaps were present up to three years after the creation of artificial gaps 30 m in diameter (Bauhus and Bartsch 1996).
Below-ground root gaps were also found under experimentally created canopy gaps in deciduous forests (Wilczynski and Pickett 1993) and in naturally uneven-aged longleaf pine forests in Florida (Brockway and Outcalt 1998). In tropical forests, conflicting results have emerged with tree falls either creating root gaps (Sanford 1989; Ostertag 1998) or having no effect on below-ground root distribution (Sanford 1990). In a single study in the boreal forest, no evidence was found for reduction in fine root production in small (< 100 m$^2$) above-ground gaps (Campbell et al. 1998).

Despite the somewhat ambiguous results, partly explained, no doubt, by high soil variability, diverse methodological procedures, and inherent problems encountered in studying below-ground structure and processes, it is clear that changes in forest stand structure and density can significantly affect below-ground nutrient processes and plant competitive relationships. On nutrient-limited sites in generally open-grown boreal forests, competition for nitrogen rather than light may play a more significant role in determining regeneration recruitment and growth. Loss of mature trees from the canopy may reduce competition for nitrogen and promote release of previously suppressed seedlings. Reduction of intense below-ground competition in combination with increased light levels in canopy gaps may promote seedling establishment and release of suppressed trees.

2.7.4 Resource Heterogeneity

The preceding discussion has emphasized the relationship between gap size and geometry and light resources in the determination of the species composition of forest gaps. However, many other factors determine which individuals or species are able to successfully establish themselves in forest gaps. Hartshorn (1978) recognized the
importance of variables other than gap size that influence the successful regeneration of
tree species in gaps. These included: (1) time of gap occurrence, (2) proximity of seed
source to gaps and mechanism of seed dispersal, (3) substrate conditions, and (4) plant-
herbivore relations. Furthermore, Bazzaz (1996) described a number of plant traits that
even further complicate gap dynamic processes: (1) many shade tolerant species require
gaps in the canopy to reach maturity, (2) understory seedlings may experience damage or
mortality in response to sudden increases in light flux, (3) some pioneer species may be
able to take advantage of diffuse radiation, whereas many shade tolerant species are
dependent on some brief period of direct radiation, and (4) even when resources such as
light and nutrients are limiting, tree seedlings may not always respond to increased resource
levels.

Bazzaz and Wayne (1994) stressed the complicated nature of resource heterogeneity
across the gap–non-gap continuum. Because spatiotemporal heterogeneity is scale
dependent, it may not be obvious which scale is appropriate to detect meaningful variation
that is causing differences in species composition and density. Furthermore, Bazzaz and
Wayne (1994) distinguished between what they termed “measured” and “functional”
heterogeneity. Measured heterogeneity is what ecologists record with their instruments in
the field. Functional heterogeneity, on the other hand, is what plants actually respond to.
Therefore, the gradients of one or several variables measured across the gap–closed canopy
continuum may not correspond to the actual gradients experienced by different species,
genotypes or phenotypes. For example, changes in gap size may not result in concomitant
changes in gap microclimate (Brown 1993) or resource allocation (Kuuluvainen et al.
Therefore, it is with caution that one accepts the simple gap–non-gap or "Swiss cheese" description of forest ecosystems (Lieberman et al. 1989).

While cognizant of this fact, however, the vast majority of gap researchers have focused on the resource gradient and species response across the gap–understory continuum. Bazzaz and Wayne (1994) described it succinctly: "The primary questions we focus on (in gap dynamic research) are: What are the ecologically relevant quantitative and/or qualitative differences in the microenvironmental conditions at different points across the gap–understory continuum, and what are the physiological and demographic characteristics of species' seedlings that occupy different portions of the continuum?"

However, it is evident that an understanding of the gap–non-gap interface as a continuum is somewhat limited. Resources do not necessarily display a gradual continuum in flux and concentration, but are inherently heterogeneous from the gap centre into the closed forest. A prime determinant of such heterogeneity is the microsite.

2.7.5 Microsite

Of particular importance in determining seed germination and early tree establishment in gaps is the nature and abundance of forest floor substrates or microsites found in subcanopy and open gap positions (Zasada et al. 1992; Duchesneau and Morin 1999; Greene et al. 1999). Tree recruitment is often more dependent on microsite quality, which may override the effect of standing tree basal area, gap size and resource gradients in gaps (Houle 1992; Lundqvist and Fridman 1996; Gray and Spies 1997), especially for shade-tolerant fir and spruce. Microsite variability may be a factor of forest floor
disturbance and the presence of exposed mineral soil, amount and type of coarse woody debris, and degree of competing vegetation.

Recent studies have emphasized the role of coarse woody debris as an important structural component of balsam fir forests (Lang 1985; Sturtevant et al. 1997), northwest coniferous forests (Sollins 1982; Spies et al. 1988), old-growth Scandinavian boreal forests (Linder et al. 1997; Jonsson 2000; Siitonen et al. 2000), European mixedwood forests (Falinski 1978) and old-growth hemlock–hardwood forests (Tyrrell and Crow 1994b). The amount, type and degree of decomposition of coarse woody debris on the forest floor significantly determine seed germination and survival and growth of tree seedlings in many forest ecosystems (Harmon et al. 1986). Fallen logs, upon suitable decay, act as nurse logs or preferred sites of germination. Fallen wood, although making up only a small percentage of the microsites, accounts for a disproportionate percentage of established seedlings. This phenomenon is well documented for a variety of forest types including the temperate rainforests of western North America (Christy and Mack 1984; Harmon and Franklin 1989; Deal et al. 1991) and Chile (Lusk 1995), Rocky Mountain spruce–fir forests (Knapp and Smith 1982), balsam fir forests (McLaren and Janke 1996), Japanese spruce–fir forests (Takahashi 1994) and Scandinavian Norway spruce-dominated forests (Sirén 1955; Jonsson 1990; Hofgaard 1993b; Hörnberg et al. 1997). Similarly, Szewczyk and Szwagrzyk (1996) observed that spruce and fir seedlings were much more pronounced on rotten wood compared to mineral soil. Such differentiation in density and species composition on rotten wood has been attributed to the reduced competition from herbs and mosses on the raised surfaces of the coarse woody debris (Harmon and Franklin 1989) and retention of favourable moisture supplies (Place 1955). Well documented is the
observation that spruce seedlings, when compared to fir seedlings, show a preference for coarse woody debris as a site of germination and early growth (Bedell 1948; Rowe 1955; Horton 1959; Day 1964; Wagg 1964; DeLong et al. 1997; Hörnberg et al. 1997). Fir seedlings, while possessing the ability to germinate on decayed wood, are also able to germinate on a variety of other microsites, including thick litter layers and sites dominated by mosses (Nakamura 1992; Simard et al. 1998). This is generally attributed to the more robust nature of the fir seedling, which possesses greater root growth and deeper penetration than spruce seedlings (Place 1955).

Uprooting of trees normally exposes the mineral soil and disrupts the soil profile (Brown 1977; Bormann et al. 1995). Treefalls that expose mineral soil and produce pit and mound topography create a diversity of microsites conducive to the establishment and growth of particular tree, moss and herbaceous species (Beatty and Stone 1986; Schaetzl et al. 1989a; 1989b; Jonsson and Esseen 1990; Jonsson and Dynesius 1993; den Ouden and Alaback 1996; Rydgren et al. 1998; Ulanova 2000). The etiology of any particular gap-maker (Putz et al. 1983) should significantly affect resource heterogeneity and flux in the gap. Whether a tree dies and remains standing for a significant period of time, breaks off above the ground, or uproots to create forest floor and soil disturbance will determine the type of microsite available for subsequent colonization.

The pit and mound topography characteristic of uprooting may persist for centuries (Lyford and MacLean 1966; Schaetzl and Follmer 1990). The pit and the mound act as unique microsites that can determine tree species composition, growth and density (Peterson et al. 1990; Peterson and Pickett 1990). Trees classified as pioneers are often found regenerating preferentially on disturbed soil in treefall gaps (Henry and Swan 1974;
Putz 1983; Nakashizuka 1989). Hence, so-called "early successional species" are able to persist in the canopy dominated by late successional species due to periodic tree-uprooting. This is quite evident in the boreal forests of Newfoundland where shade-intolerant white birch persists in the mature canopy of old-growth balsam fir–spruce forests. This is due, probably, to the prolific seedling and robust dissemination of white birch and its ability to germinate well on the exposed mineral soil of root mounds (Marquis et al. 1964; Safford et al. 1990).

Non-tree vegetation may often respond to the increased resource fluxes in gaps and act as an important factor mitigating against the successful response of tree species. Trees may not respond, therefore, in a predictable fashion to gap openings due to above- and below-ground competition effected by a flourishing ground vegetation. Response of competing vegetation may depend on gap size. Single elm (*Ulmus americana* L.) tree gaps resulted in the regeneration of canopy dominants whereas multiple-tree gaps enhanced successful shrub regeneration, effectively suppressing regeneration of the tree dominants (Huenneke 1983). On productive sites in the boreal and hardwood forests, red raspberry (*Rubus idaeus* L.) may germinate profusely from the abundant forest floor seed bank in response to canopy disturbance and quickly occupy the growing space (Ruel 1992; Osawa 1994; Ricard and Messier 1996), effectively competing with conifer regeneration (Lautenschlager 1999). Bamboo may act as an effective competitor of fir in Chinese, Japanese and Himalayan forests (Taylor and Zisheng 1988a; Kojima 1995; Gratzer et al. 1999). In boreal forests, competition from members of the *Ericaceae* (e.g. *Vaccinium, Kalmia, Empetrum*) is common, particularly on the generally poorer, late successional sites. These shrubs possess strong ability to negatively affect the successful establishment of
conifer seedlings (Damman 1967; Meades 1983b; Jäderlund et al. 1997; Zackrisson et al. 1997). Most of these studies showing intense competitive effects of the Ericaceae, however, have been conducted on open sites, often after significant site disturbance such as clear-cutting. In small gap disturbance, however, advance tree regeneration may respond more vigorously than any shrubs that are present, effectively minimizing any potential competitive interactions (Alaback and Tappeiner 1991).

Herb patches have also been shown to exercise significant effects on the density and distribution of seedlings of canopy dominants (Maguire and Forman 1983). In hardwood forests, herb density, leaf cover and species richness have increased in response to forest gaps (Moore and Vankat 1986; Goldblum 1997). Studies that included the creation of artificial gaps have shown both positive response (Reader and Bricker 1992) or no real response (Collins and Pickett 1987, 1988a, 1988b) of herbs to canopy openings. The short time span of various studies, a lack of soil disturbance in artificially created gaps, and a host of other constraints on herb response in gaps may account for the ambiguous results (Collins et al. 1985).

2.7.6 Gap Partitioning

The gap partitioning hypothesis was initially proposed as a mechanism to help explain the well known difference in species diversity between tropical and temperate forests (Ricklefs 1977; Denslow 1980). It was proposed that the gradients of environmental heterogeneity between closed forest canopy and gaps within the canopy were much steeper or broader in tropical forests compared to temperate forests. It was thought that the greater micro-heterogeneity found in tropical gaps would promote increased niche
specialization (Grubb 1977), resulting in greater species diversity in tropical forests. The hypothesis assumes that generalist species are not common, but that species have evolved to take advantage of the range of resource fluxes found in the gap-closed forest continuum. Species are not generally able to take full advantage of the wide gradient of resources available across the gap. Instead, species differ in habitat preference and therefore perform differentially in different positions in the gap. In other words, species have the potential to partition the gap understory environment (Bazzaz 1996).

Despite the theoretical recognition of the possibility of gap partition, results in field situations have proved inconsistent, with no clear picture of gap partitioning emerging. Concerns surround methodology, particularly control over field experiments. Sipe and Bazzaz (1995) noted that an adequate experimental test of gap partitioning would have to include simultaneous measurements of field microclimates, species ecophysiology, and growth responses over time in a fully controlled field experiment. Studies supporting the theory of gap partitioning in tropical systems have based their conclusions on floristic analysis of recognized zones in gaps (Brandani et al. 1988; Núñez-Farfán and Dirzo 1988). Other studies characterized by a stronger, more controlled experimental methodology failed to find adequate evidence that different tree species consistently favoured distinct gap positions (Whitmore and Brown 1996). Acknowledging a photosynthetic potential for gap partitioning among species of New England Acer (Sipe and Bazzaz 1994), limited evidence of gap partitioning was identified (Sipe and Bazzaz 1995). Both Barton (1984) and Gray and Spies (1996) provided limited evidence of gap partitioning, while Wright et al. (1998) noted little evidence of gap partitioning in interior cedar–hemlock forests of northwest
British Columbia. As far as is known, no study of gap partitioning has been conducted in boreal forests.

2.7.7 Short-Term Climatic Change

Gap disturbance occurs within the context of changing climatic parameters. In northern boreal forests, climate–vegetation interactions are significant (Bonan and Shugart 1989). Recent research has treated the advance and retreat of tree-line forests as proxy indicators of long-term millennial climatic change (Payette and Lavoie 1994). It has been noted, however, that boreal forests, at both the tree line and in denser forests to the south, are able to undergo important decadal-level changes in regeneration, mortality and canopy structure in response to climatic variability (Hofgaard 1997). Of note is the documented phenotypic plasticity of spruce canopies (Hofgaard et al. 1991) and tree forms (Lavoie and Payette 1992, 1994) in response to climatic variability, a phenomenon of importance for the long-term understanding of gap dynamics in northern boreal forests. Annual variations in snow loads, mean summer temperatures and winter frost injury, for example, have been implicated in significant structural and mortality changes in boreal forests. Recent studies in high elevation spruce–birch and pine forests in the Swedish Scandes demonstrated the relatively rapid change in forest structure induced by short-term climatic disturbance (Kullman 1989; Kullman and Högberg 1989; Kullman 1991, 1996).

Other studies in the Scandinavian boreal forest have emphasized the importance of relatively short-term climatic influences in determining forest development and regeneration. Steijlen and Zackrisson (1987), in their investigation of virgin pine–spruce–birch forests in northern Sweden, concluded that the regeneration dynamics and age
structure were influenced by low-frequency climatic fluctuations. Snow-rich winters promoted spruce establishment with the recruitment of Scots pine favoured by warm summer temperatures. Climatically-induced regeneration and mortality events seem to determine the gap phase replacement of these northern forests. Multi-modal age structures of Scots pine stands on poor sites in northern Sweden provide further evidence of climatically-induced regeneration pulses in boreal forests (Zackrisson et al. 1995). Distinct pulses of pine regeneration occurred during the mid-1970s, mid-1800s and during the 1930s-1940s, known periods of general warming throughout Scandinavia. Between these temporal pulses, the absence of pine regeneration was noticeable. Seed crops in boreal Sweden are significantly affected by climatic periodicity (Hofgaard 1993c), a fact which probably explains the synchronous regeneration patterns found in the pine stands. The age class structure did not exhibit the classical reverse-J distribution characteristic of continuously recruiting gap-driven forests. In any study of gap dynamics in boreal forests, due recognition must be given to the possible complicating influence of short-term climatic changes on gap dynamics and stand recruitment.

2.8 TREE RECRUITMENT: GAP SPECIALISTS

Different tree species have been identified as either small gap or large gap specialists. In tropical forests, large gap specialists have been defined as species that “require the high light intensities and temperatures of large gaps for germination and seedling establishment. Early growth is rapid, and saplings are able to reach the upper forest strata during the lifetime of a single gap” (Denslow 1987). On the other hand, small gap specialists “germinate in the understory or in small clearings. Saplings are able to
survive understory light conditions owing to low respiration rates and low light requirements at saturation, but they are dependent on some canopy opening for substantive growth and reproduction.” (Denslow 1987). Typical small gap specialists found in temperate forests include eastern hemlock (Busing 1994), sugar maple (Runkle 1984; Canham 1985; Runkle 1990) and beech (Canham 1988b, 1990). Shade-tolerant species are able to respond to minimum levels of increased light and often experience several periods of suppression and release before reaching the canopy (Canham 1985, 1989, 1990).

Small and large gap specialists may also be differentiated in terms of their respective growth patterns. Early successional or large gap specialists exhibit what is termed a “height-growth type” which is characterized by greater photosynthetic allocation to plant height growth than to construction of lateral branches and foliage. Late successional or small gap specialists, on the other hand, are termed “crown growth type” in which photosynthate is allocated preferentially to the construction of lateral branches and foliage rather than to plant height growth. This distinction in plant assimilate partitioning is paralleled by differences in successional status, shade tolerance and gap reproductive success (Marks 1975; Boojh and Ramakrishnan 1982a, 1982b).

Relative to tropical and temperate forest systems, less work has been conducted on the relationship between forest composition and gap dynamics in boreal and sub-boreal forests. Evidence, however, points toward the recognition of both small and large gap specialists in forests dominated by fir, spruce and birch species. Both fir and spruce are generally able to perpetuate themselves in forests dominated by single tree gaps, with the less shade-tolerant birch maintaining itself only in larger-sized gaps. This is no doubt attributable to the contrasting growth patterns and life history traits of fir and birch (Hara et
al. 1991). In Swedish forests, Leemans (1991) found that smaller gaps caused by the death of one or two trees promoted directional succession towards a forest dominated by shade-tolerant Norway spruce. Large patches (up to 1 ha) resulting from large-scale disturbance allowed the recruitment of both late successional and early successional birch species. Coexistence of fir and birch (Taylor et al. 1996) and pine and birch (Kuuluvainen and Juntunen 1998) was mediated by the tendency for birch to regenerate in large-sized gaps. Furthermore, tip-up mounds associated with the gap disturbance generally provide excellent microsites for birch germination and early development (Carlton and Bazzaz 1998). In spruce-dominated systems in Sweden (Liu and Hytteborn 1991) and British Columbia (Kneeshaw and Burton 1997), micro-scale gap disturbance effectively maintained spruce dominance in the canopy. Although gap dynamics were not explicitly studied, Bergeron and Dubuc (1989) and Bergeron (2000) also noted the successional convergence of southern boreal forests in Quebec toward shade-tolerant conifer-dominated forests. Work in the same area of Quebec confirmed that spruce budworm-mediated patch dynamics promoted a gradual transition to fir-dominated forests (Kneeshaw and Bergeron 1998).

Most true fir species, especially balsam fir, are classified as shade tolerant (Baker 1949; Frank 1990). Their ability to germinate under a closed canopy, to persist as a seedling bank (advance regeneration) for decades, often in a suppressed state, and then to respond to increases in light levels, allow them to self-perpetuate in forests characterized by small gap disturbance (Messier et al. 1999). Balsam fir possesses the three characteristics deemed essential for a seedling bank species: (1) a narrow range of heights in the shade, (2) persistence in the shade, and (3) the retention of the capacity to grow
rapidly in height once light levels have increased after some degree of canopy disturbance (Morin and Laprise 1997; Marks and Gardescu 1998). True firs exhibit a high degree of morphological and physiological plasticity in response to light gradients (Klinka et al. 1992; Mitchell and Arnott 1995; Parent and Messier 1995; Sprugel et al. 1996; King 1997). Under low understory light levels, the growth of lateral branches is favoured at the expense of height growth, a growth strategy ostensibly favouring light sequestration under shaded conditions and minimizing respiration losses from non-photosynthetic tissues. As well, needles generally assume a more horizontal display, maximizing reception of incoming radiation. Highly suppressed fir seedlings, therefore, generally exhibit a characteristic umbrella-shaped form (Kohyama 1980; Küppers 1989; Takahashi 1996). Similar suppression-induced phenotypic plasticity also occurs in Norway spruce (Greis and Kellomäki 1981). Suppression of balsam fir may occur for decades, even up to 100 years (Morris 1948). Characteristic of this period of intense suppression are reductions in photosynthate production and allocation resulting in many missing and partial rings. Missing rings are characteristic of understory suppressed trees (Turberville and Hough 1939; Bormann 1965; Lorimer et al. 1999). When released after years of suppression, such seedlings respond vigorously and often grow at rates equal to that of seedlings which did not experience suppression (Hatcher 1960, 1964; Logan 1969; Crossley 1976; Herring 1977; Seidel 1977; Ferguson and Adams 1980; Seidel 1980; Alexander 1987; Tucker et al. 1987; Kneeshaw et al. 1998; Antos et al. 2000). True fir species may thus be considered as small gap specialists, but not in an obligate sense, for fir will grow rapidly and vigorously in large patches created after removal of the parent canopy as a result of clearcutting (Vincent 1956; Hughes 1964), insect outbreaks (Vincent 1962; Fye and Thomas 1963;
Bakuzis and Hansen 1965), windthrow (Kimura et al. 1986), stand attrition and breakup (Baskerville 1965a) and wind-induced wave forests in high-altitude fir forests (Iwaki and Totsuka 1959; Sprugel 1976).

Black spruce, often growing in association with balsam fir, is also adapted to forests characterized by gap disturbance. Though generally considered to be less shade tolerant than balsam fir, black spruce may form abundant advance growth which can develop in as little as 10% of full sunlight (Viereck and Johnston 1990). Furthermore, black spruce’s well known ability to reproduce vegetatively through layering (Kenety 1917; Stanek 1961) in the moist feathermoss and *Sphagnum* moss carpets commonly associated with black spruce sites, produces mature stands with abundant advance growth. The majority of young trees respond well to release, both after cutting (Doucet 1990; Paquin and Doucet 1992a, 1992b) and in response to small-scale canopy disturbance in multi-cohort stands (Groot and Horton 1994). Furthermore, black spruce’s competitive ability to persist under cold, wet, nutrient-poor edaphic conditions (Newton and Jolliffe 1998b) and its phenotypic plasticity under changing climatic conditions (Lavoie and Payette 1992, 1994) makes it particularly suitable for self-perpetuation in gap-driven forests. Under marginal climatic conditions commonly found in the northern fringes of the boreal forest, the climatically-controlled accumulation of peat under both balsam fir and black spruce promotes reproduction principally by layering (Sirois 1997). Under such conditions, self-perpetuating, old-growth forests driven by gap dynamics may dominate the forested landscape.

It is instructive to note some of the studies that have examined the recruitment of fir and spruce species in forests dominated by small gap disturbance processes (Table 2-3).
Table 2-3. *Abies* and *Picea* forests dominated by gap disturbance.

<table>
<thead>
<tr>
<th>Location</th>
<th><em>Abies</em> species</th>
<th><em>Picea</em> species</th>
<th>Associated species</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spain</td>
<td><em>Abies pinsapo</em></td>
<td>-</td>
<td>-</td>
<td>Arista 1995</td>
</tr>
<tr>
<td>China</td>
<td><em>Abies faxoniana</em></td>
<td>-</td>
<td>Betula utilis, Betula albosinensis</td>
<td>Taylor and Zisheng 1988a, 1988b</td>
</tr>
<tr>
<td>China</td>
<td><em>Abies faxoniana</em></td>
<td><em>Picea purpurea</em></td>
<td>Betula albosinensis, Betula utilis, Larix potaninii, Sabina saltuaria</td>
<td>Taylor et al. 1996</td>
</tr>
<tr>
<td>Japan</td>
<td><em>Abies sachalinensis</em></td>
<td>-</td>
<td>Acer mono, Quercus mongolica, Tilia japonica, Betula ermani</td>
<td>Ishikawa and Ito 1989</td>
</tr>
<tr>
<td>Japan</td>
<td><em>Abies mariesii</em></td>
<td><em>Picea jezoensis</em></td>
<td>Tsuga diversifolia, Betula corylifolia, Betula ermani, Betula lutea</td>
<td>Kubota et al. 1994, Hiura et al. 1996</td>
</tr>
<tr>
<td>Japan</td>
<td><em>Abies veitchii</em></td>
<td><em>Picea jezoensis</em></td>
<td>-</td>
<td>Kanzaki 1984, Yamamoto 1993, 1995, Yamamoto 1996</td>
</tr>
<tr>
<td>Northern Appalachians, USA</td>
<td><em>Abies balsamea</em></td>
<td><em>Picea rubens</em></td>
<td>Betula papyrifera var. cordifolia, Betula lutea</td>
<td>Foster and Reiners 1983, 1986; Worrall and Harrington 1988; Perkins et al. 1992; Battles et al. 1995; Battles and Fahey 1996, 2000</td>
</tr>
<tr>
<td>Southern Appalachians, USA</td>
<td><em>Abies fraseri</em></td>
<td><em>Picea rubens</em></td>
<td>Betula lutea, Betula alleghaniensis</td>
<td>White et al. 1985a, 1985b; Busing 1996; Wu et al. 1999</td>
</tr>
<tr>
<td>Location</td>
<td>Abies species</td>
<td>Picea species</td>
<td>Associated species</td>
<td>Reference</td>
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<tr>
<td>------------------</td>
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<td>---------------------</td>
<td>----------------------------------------------</td>
<td>------------------------------------------</td>
</tr>
<tr>
<td>Quebec</td>
<td>Abies balsamea</td>
<td>Picea mariana</td>
<td>Betula papyrifera</td>
<td>Kneeshaw and Bergeron 1998</td>
</tr>
<tr>
<td></td>
<td>Abies</td>
<td>Picea glauca</td>
<td>Populus tremuloides</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Pinus banksiana</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Thuja occidentalis</td>
<td></td>
</tr>
<tr>
<td>British Columbia</td>
<td>Abies amabalis</td>
<td>—</td>
<td>Tsuga heterophylla</td>
<td>Lertzman 1992</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Tsuga mertensiana</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Chaemecyparis nootkatensis</td>
<td></td>
</tr>
<tr>
<td>British Columbia</td>
<td>Abies lasiocarpa</td>
<td>Picea engelmannii x</td>
<td>Pinus contorta</td>
<td>Kneeshaw and Burton 1997</td>
</tr>
<tr>
<td></td>
<td></td>
<td>glauca</td>
<td>Populus tremuloides</td>
<td></td>
</tr>
<tr>
<td>Western Canada</td>
<td>Abies lasiocarpa</td>
<td>Picea engelmannii</td>
<td>—</td>
<td>Oosting and Reed 1952; Day 1972</td>
</tr>
<tr>
<td>(Alberta–)</td>
<td></td>
<td></td>
<td></td>
<td>Whipple and Dix 1979</td>
</tr>
<tr>
<td>United States</td>
<td></td>
<td></td>
<td></td>
<td>Veblen 1986a, 1986b</td>
</tr>
<tr>
<td>(Wyoming,</td>
<td></td>
<td></td>
<td></td>
<td>Aplet et al. 1988</td>
</tr>
<tr>
<td>Colorado)</td>
<td></td>
<td></td>
<td></td>
<td>Roovers and Rebertus 1993</td>
</tr>
<tr>
<td>Finland</td>
<td>–</td>
<td>Picea abies</td>
<td>Pinus sylvestris</td>
<td>Kuuluvainen 1994</td>
</tr>
<tr>
<td>Sweden</td>
<td>–</td>
<td>Picea abies</td>
<td>Pinus sylvestris Betula pendula</td>
<td>Sernander 1936; Hytteborn and Packham</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>Leemans 1990, 1991; Liu and Hytteborn</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1991; Hofgaard 1993d</td>
</tr>
<tr>
<td>Russia</td>
<td>Abies siberica</td>
<td>Picea abies</td>
<td>Pinus sylvestris</td>
<td>Syrjänen et al. 1994</td>
</tr>
</tbody>
</table>
Table 2-3. (Continued)

<table>
<thead>
<tr>
<th>Location</th>
<th>Abies species</th>
<th>Picea species</th>
<th>Associated species</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Russia</td>
<td>–</td>
<td>Picea abies</td>
<td>Betula pubescens</td>
<td>Kuuluvainen et al. 1998; Drobyshev 1999; Drobyshev and Nihlgård 2000</td>
</tr>
</tbody>
</table>

Due to their shade tolerance, both fir and spruce are able to self-perpetuate in forest systems dominated by small gap disturbance regimes. Note that Englemann spruce—subalpine fir forests are included in Table 2-3. Much research has been devoted to the successional relationship between fir and spruce in these generally cold, high altitude forests. While little actual work has been conducted on the role of gap dynamics in these forests, pathological, autecological and successional studies would seem to indicate that, between long fire return intervals of 500 to 1000 years, fungal-induced gap dynamics may play a significant role in the perpetuation of the spruce–fir complex. Despite it greater shade tolerance and predominance in the regenerating layer, subalpine fir is usually not able to achieve canopy dominance due to the greater longevity of spruce and the shorter pathological rotation of fir (Hanley et al. 1975; Alexander 1985; Veblen 1986a, 1986b; Aplet et al. 1988; Lewis and Lindgren 1999).

2.9 FEASIBILITY OF GAP-BASED SILVICULTURE

The goals and methods of contemporary forestry practice are undergoing a paradigmatic shift. Notwithstanding the early recognition of the need to develop a “nature-based” silviculture (Smith 1962; Schütz 1999), contemporary forestry is experiencing a
radical shift in perspective. The change is characterized by a shift in emphasis on single commodity goods from forests to a recognition of management foci that address the ecological integrity of the natural ecosystem being managed. The traditional emphasis on wood production, for example, required a silviculture which focused on the techniques required to maximize a forest owner’s rate of return through a series of interventions in the development of a stand. Whether silviculture worked with nature, improved on nature or deviated from nature, was often of little concern. Emphasis was placed, instead, on the maximization of wood of a certain quality within the economic, political and social constraints operative at the time.

Under the current umbrella of forest ecosystem management, silviculture is being defined more broadly. Forest ecosystem management is predicated on the assumption that present patterns of productivity, resilience and biodiversity developed within the context of recurrent, historical disturbance patterns. Such patterns are to be respected, therefore, if both flow of desired goods from the forest and ecological integrity of the forests are to be maintained. If such values are to be preserved into the future and intergenerational needs assured, then silvicultural practices must somehow “mimic” the intensity, frequency and scale of natural disturbance patterns (Kohm and Franklin 1997).

Such forms of “naturalistic silviculture” are of critical importance in uneven-aged, old-growth forests maintained by disturbance patterns characterized by gap dynamics. Complex structural heterogeneity such as standing dead snags, coarse woody debris, multi-storied canopies and presence of canopy gaps plays a significant role in both long-term ecosystem functioning and the maintenance of biological diversity (Peterken 1996; Voller and Harrison 1998). Contemporary approaches to forest landscape management focus on
the desire to “mimic” or emulate the spatial and temporal characteristics of the natural disturbance regimes of the particular landscape in question (Angelstam 1998a, 1998b; Niemelä 1999). While this is no easy task, indicator species, structure, and processes are being identified for the range of disturbances such that forest management options are being clarified. In the case of old-growth stands slated for harvesting, a particular challenge consists in being able to maintain an acceptable flow of wood, while at the same time maintaining old-growth characteristics considered essential for the preservation of biodiversity and the conservation of significant structural features or biological legacies.

Under current systems of clear-felling and even-aged management, such structural heterogeneity and maintenance of the potential for biodiversity is minimized. In boreal forests, many of which are even-aged from extensive, catastrophic insect outbreaks and fires, the dominant silvicultural system of clearcutting may be considered ecologically viable and sustainable (Weetman 1996). It would be unrealistic, however, to think that large, extensive clearcuts with removal of most of the biomass essentially mimics natural processes such as fire and extensive insect herbivory. In other forest ecosystems, including areas of the boreal, where mixed-aged and old-growth, uneven-aged, structurally diverse forests predominate, alternative silvicultural methods are being considered. Silvicultural options needed to meet these goals, while specific to different forest types, may include long rotations, various types of patch cutting, and degrees of variable retention and promotion of all-aged stand structures (Alexander 1987; Runkle 1991; Coates and Steventon 1995; Kimball et al. 1995; Franklin et al. 1997; Bergeron et al. 1999; Burton et al. 1999; Lähde et al. 1999). There exists a legacy of diameter-limit cutting in sub-boreal
and subalpine forests that may serve as a reference for the effects of partial cutting on stand structure (Weetman et al. 1990).

Research in gap dynamics has increased our understanding of small-scale disturbance in many forest ecosystems. Given the growing desire to emulate natural disturbance patterns in forest activities, new attention is being given to gap-based silvicultural systems. Such systems attempt to mimic the natural gap size and frequency in gap-disturbed forests through judicious use of well-planned partial cutting. In their study of undisturbed interior cedar–hemlock forests of northwestern British Columbia, Coates and Burton (1997) found that a gap-based partial cutting silvicultural system is particularly effective, allowing for timber extraction while at the same time maintaining mature or old-growth structure and process. Similarly, in uneven-aged Norway spruce sites in Sweden, Fries et al. (1997) recognized that traditional clear-cutting and shelterwood regeneration methods were not able to maintain significant historic structures and processes that promoted biodiversity. Proposed management options included a shift to selection systems or even no cutting in gap-driven forests. The feasibility of gap-based silviculture as an effective management option in Indonesian dipterocarp forests (Tuomela et al. 1996), Peruvian tropical forests (Hartshorn 1989) and Southern Cape forests in South Africa (Geldenhuys and Maliepaard 1983) has also been examined. Uneven-aged management and appropriately devised selection systems are receiving increasing interest in North America as well (Nyland 1996, 1998; Emmingham 1997, 1998; Guldin and Baker 1998; Long 1998; O'Hara 1998; Seymour and Kenefic 1998).

The natural filling-in of gaps with regeneration of trees would appear to suggest that silviculture prescriptions should logically follow this natural precedent. Such reasoning,
along with the increasingly accepted notion that forest management should produce “natural-looking” forests, has invigorated the long tradition of uneven-aged silviculture (Emmingham 1997) that has been traditionally practiced in mountainous forests of central Europe under the rubric of selection systems and irregular shelterwoods. The classic selection silvicultural system as originally devised in Europe (Knuchel 1953; Kostler 1956) was based on a gap-replacement scenario. The shade-tolerant species mix of silver fir (Abies alba Mill.), European beech and Norway spruce, along with economic, ecological and cultural incentives provided the *raison d'être* for the successful, though geographical limited, implementation of uneven-aged silviculture in central European forests (Kenk 1995). Early attempts to transfer European silvicultural ideas (i.e. uneven-aged selection systems) into North America were made by Meyer (1952) and Meyer et al. (1961).

Under uneven-aged management using variations of the selection system, there exists a traditional reliance on advance regeneration that will release into the gaps created by canopy removal. The selection silvicultural system is characterized by continuous forest cover, continuous or episodic advance regeneration, little or no relationship between individual tree size and tree age because of long periods of suppression, and continuous harvest removals. Such stands are traditionally characterized by reverse-J (Meyer 1952; Leak 1996) or reverse sigmoidal (Goff and West 1975; Goodburn and Lorimer 1999) diameter class distributions. Under $BDq$ regulation (basal area level ($B$), maximum diameter ($D$) and a $q$ factor that defines the regular change of numbers across consecutive diameter classes), periodic harvests are carried out in such a manner that an uneven-aged, reverse-J residual stand is created and maintained, theoretically providing for a sustained yield of wood volume (Nyland 1996).
Although boreal forest stands are usually even-aged in structure, with normal diameter distributions due to catastrophic stand-initiating events such as fire, insect outbreaks and blowdown, multi-cohort stands do persist where these events are rare. This situation is most common at high elevations and where climatic and edaphic conditions prevent the spread of fire or the development of insect outbreaks. In boreal spruce–fir and northern conifer cover types, attempts have been made to use classic \( BDq \) regulation with gap regeneration as a silvicultural system (Frank and Bjorkbom 1973; Frank and Blum 1978; Seymour and Kenefic 1998) or more rudimentary variations of the selection system (Groot 1995). On harsh sites where regeneration is slow to occur and where survival may depend on overstory protection, uneven-aged management with selection cuts may be the only successful way to maintain forest cover protective functions.

Despite the biological feasibility of some form of gap-based silvicultural systems in the boreal forest, classical selection forestry has not been generally accepted or even perceived to be of relevance. This is understandable given the fact that the boreal forest is generally even-aged, having originated from massive fires and insect outbreaks. Furthermore, the common occurrence in Canada of extensive areas of old, unmanaged forests subject to high risk from fire and insects has mitigated against the use of selection silvicultural systems which have generally assumed detailed inventories, individual tree selection, extensive road access, and a detailed understanding of individual stand structure and dynamics. Wedeles et al. (1995), in their assessment of various silvicultural systems in the boreal mixedwoods of Ontario, pointed to the uncertainty over patterns and composition of regeneration and stand dynamics as well as operational and economic constraints as important factors preventing acceptance of the selection system. In the Canadian boreal
forest, commercial volumes and assessed values of timber are often low, providing little financing or incentive for the development of alternative silvicultural systems. The contemporary focus is on the protection of advanced regeneration under conditions of mechanized harvesting. This reliance on advance regeneration, often gap-related, has initiated debate concerning the degree to which residual advance growth is abundant enough, vigorous enough, and spatially distributed such that future stands of desirable volume and species composition are realized under even-aged management.

Despite the institutional disincentives for gap-based silvicultural systems in the Canadian boreal forest, there is growing public pressure to employ selection and shelterwood systems that are based on gap dynamics. Currently, forestry, including boreal forestry, is marked by a struggle between biologists and foresters. The former are concerned with maintenance of biodiversity and the development of naturally-based silvicultural systems that try to emulate natural disturbance regimes, albeit within a socially acceptable range. The forester, particularly when it comes to the boreal forest, is saddled with the task of rationalizing harvesting and silviculture for a large, publicly owned forest characterized by high risk factors, old age and usually unbalanced age class distributions (Weetman 1995). The public desire for forest ecosystem management is calling them together.

2.10 RESEARCH DIRECTIONS

Multi-cohort stands and associated gap dynamics are much more common in boreal forests than previously assumed. Most of our understanding of gap structure and dynamics in boreal forests has originated from work carried out in Scandinavia and Russia and in the
subalpine boreal "outliers" found in Japan and American Appalachia. To date, the vast amount of disturbance dynamics research in the Canadian boreal forest has focused on fire and insect disturbance. The reasons for such a focus are obvious given the frequency, scale, and economic importance of such disturbance events.

This review suggests a number of possible research priorities. Of first importance is the definition of what constitutes old-growth boreal forest. Our contemporary understanding of what constitutes old-growth has, for the most part, emerged from research in the temperate coniferous forest of western North America and from remnant old-growth hardwood forests throughout the United States. Structural parameters and gap-related processes need to be determined for old-growth boreal forests. Secondly, once identifying parameters have been established, landscape-level identification and mapping of old-growth areas may be initiated. Many government and industrial forest inventories would have to be updated, given the prevailing even-aged assumptions common to many inventory systems.

The increased focus on ecosystem management, maintenance of species, and landscape-level biodiversity, identification of representative protected areas, and natural disturbance-based forest management has initiated a renewed interest in understanding the full range of disturbance processes at play in the boreal forests of Canada. As already noted, disturbance in the boreal forest is assumed to be characterized by catastrophic, stand-replacing events such as fire and insect outbreaks. This assumption may be too simplistic for slow-growing, maritime and more northern regions of the boreal forest. A greater appreciation for the dynamics of these regions of the boreal forest is important, especially if we wish to conduct forest harvesting and develop a protection strategy that maintains the
natural productive dynamics and biodiversity of these primary forests. Contemporary forest management in many parts of the boreal forest is predicated on a scenario of even-aged forest dynamics. Such a fundamental assumption of forest dynamics has in turn produced relatively simple even-aged silviculture and growth and yield modeling. In many cases, this form of management results in a simplification of forest structure and diminution of species and landscape-level biodiversity.

The dynamic relation among different disturbance regimes needs attention. Attention is often focused on one or the other disturbance regime without consideration of the temporal and spatial links to other disturbance events. While this focus is methodologically obvious and often necessary, it is essential to relate the frequency and extent of disturbance from fire, insects, wind, fungi, not to mention harvesting and management activities such as fire suppression and silviculture. Furthermore, we are increasingly aware of the overarching and complicating impact of rapid climate change on forest disturbance history.

The etiology of gap dynamics is poorly understood. Much of the work in forest pathology has focused on the identification of fungal decay agents responsible for the loss of merchantable wood. It will be important to build on this wealth of knowledge by examining the role played by these biotic factors in the development and maintenance of what may be termed “fungal-driven” forests. We need to view fungi as disturbance vectors much as we do fire, wind and insects.

An understanding of the temporal persistence of gap-driven forests is needed. Stand-level pollen records may prove helpful in the retrospective reconstruction of gap forests, giving insight into the long-term continuity of old-growth forests. Related to this
temporal continuity are the floristic and faunal complexity and assemblages. Gap-driven forests, given their structural complexity and temporal stability, may provide regeneration niches not found in forests that experience regular large-scale disturbance.

2.11 GLOSSARY

**Advance regeneration:** Seedlings or saplings that germinate and grow in the understory of a closed canopy. They gradually grow into the canopy as canopy disturbance provides sufficient growing space. Usually associated with shade-tolerant trees such as the true firs, sugar maple, western red cedar, eastern cedar, hemlocks and American beech (Barnes et al. 1998).

**Disturbance:** Any relatively discrete event in time that disrupts ecosystems, community or population structure and changes resources, substrate availability, or the physical environment (White and Pickett 1985).

**Gap:** The physical or growing space occurring in forest stands due to individual or small group mortality, blowdown, or stem breakage. Canopy opening usually $\leq 200 \text{ m}^2$ (adapted from Helms 1998).

**Gap phase:** A term first coined by Watt (1947) who accepted “phase” and “patch” as synonyms. Gap phase is a stage of forest stand development to which tree regeneration is confined, it being excluded from other phases.

**Gap dynamics:** The change in space and time in the pattern, frequency, size, and successional processes of forest canopy gaps caused by the fall or death of one or more canopy trees. Small- or micro-scale disturbance of the forest canopy in which the gaps formed by single tree or small group mortality release sufficient growing space that is
subsequently occupied by tree regeneration, usually a result of released advance regeneration or seedling recruitment from buried or dispersed seed propagules. Tree mortality initiated by decay (root and butt rots) or individual tree blowdown (adapted from Helms 1998).

**Patch:** The physical or growing space occurring in forest stands due to the mortality of a stand or forest or part thereof. A relatively discrete spatial pattern with no constraint on upper limit of patch size, internal homogeneity, or discreteness. Patch implies a relationship of one patch to another in space and to surrounding, unaffected or less affected matrix. Canopy opening usually > 200 m² (adapted from White and Pickett 1985).

**Patch dynamics:** Forest disturbance on the forest or stand level or portion thereof in which new tree cohorts are initiated producing a mosaic of cohort patches of different sizes and discreteness across the forest landscape. Usually associated with large-scale disturbances such as fire, insect outbreaks and windstorms.
CHAPTER 3

BOREAL FORESTS, DISTURBANCE, HETEROGENEITY, AND BIODIVERSITY

3.1 STRUCTURAL HETEROGENEITY, DISTURBANCE AND STAND DEVELOPMENT

Forest composition, and size and age structure are a function of forest disturbance and subsequent successional and stand development processes (Kuuluvainen 2002). Within a specific biogeoclimatic context, the size structure and species composition of any particular stand are determined primarily by both the local disturbance regime(s) and the particular stage of both succession and stand development.

Structure may be considered on the individual tree, stand and landscape level. Included in the term “structure” are all live trees, snags and coarse woody debris, their age and physical condition, as well as their horizontal and vertical arrangement on the stand level (Franklin et al. 1981; Stone and Porter 1998; Franklin et al. 2002). On the landscape level, structural heterogeneity may be viewed in terms of the relative temporal and spatial arrangement of stands. Obviously, all three levels of organization interact one with the other across varying spatial and temporal scales to produce a structural complexity simplistically designated as a “forest.”
3.2 WHY STUDY STRUCTURE?

Ecological processes, especially forest disturbance dynamics, are inherently difficult to study first hand, especially in the case of long-lived forest ecosystems. Permanent plot data that cover the necessary spatial and temporal scales of disturbances are either rare or non-existent and the stochasticity of disturbance events, \textit{a fortiri}, relegate the investigator to examining the effects of the disturbance event, rather than the disturbance event itself. Therefore, recourse is often made to the examination of both static stand- and landscape-level structures that act as proxy indicators of specific processes and disturbance dynamics.

Forest structure becomes the readily measurable signature of particular disturbance events and functional processes such as biogeochemical and hydrologic cycling. The range of structural diversity becomes a reflection of the capacity of the forest to maintain viable populations of particular floral and faunal biodiversity (Franklin et al. 2002; Lindenmayer and Franklin 2002). Furthermore, the capacity of trees to act as "ecosystem engineers" (Kuuluvainen 2002), as regulators of microclimatic and resource availability, is itself a function of structure. The discerned pattern of forest structure becomes, in effect, the basis for the understanding of forest process and function (Lepš 1990).

Of critical importance is the fact that the manipulation of stand structure is the basis of both silvicultural interventions and forest harvesting (Nyland 1996; Smith et al. 1996). Silviculture and forest harvesting exert considerable influence on forest structure. Therefore, knowledge of the relationship between forest structures created by natural disturbances and those created by human activity assumes critical importance.
3.3 BOREAL FOREST DISTURBANCE AND STRUCTURE

Disturbance is ubiquitous in forest ecosystems. Forested landscapes are best viewed as an integration of climatic, biotic, edaphic, and geomorphic processes that determine the character of disturbance events occurring over a wide range of temporal and spatial scales (White 1979; Pickett 1980; Oliver 1981; Pickett and White 1985; Attiwill 1994; Peterken 1996; Rogers 1996; Parminter 1998; White et al. 1999; White and Jentsch 2001; Frelich 2002; Jentsch et al. 2002). Disturbed by the extremes of either catastrophic, stand-replacing events that may include fire, insect outbreak, and extensive windthrow, or periodic, small-scale gap processes mediated by fungal pathogens, forests are in constant flux when viewed from a landscape and long-term perspective. Such a wide range in both the periodicity, intensity and scale of disturbance events, and the diversity of bio-edaphic interactions (Bell 1999; Kruckeberg 2002) creates a complex, fluid, heterogeneous landscape.

In particular, natural disturbance regimes of boreal forests have attracted considerable attention. Disturbance dynamics in boreal forests have been the exclusive focus of four international conferences (Engelmark et al. 1993; Bergeron et al. 1998; Korpilahti and Kuuluvainen 2002; Macdonald and Bergeron 2004). Of particular significance to boreal forests has been the recognition how different disturbances across a wide range of temporal and spatial boundaries play significant roles in determining the structure and function of boreal forests (Engelmark 1999; Agee 2000; Conard 2000; Chen and Popadiouk 2002; Gromtsev 2002).

Boreal forest disturbances that have attracted particular research attention include fire (Wein and MacLean 1983; Payette 1992; Johnson 1995; Goldhammer and Furyaev
1996), windstorms (Robertson 1993a; Ulanova 2000), ungulate herbivory (McInnes et al. 1992; Thompson and Curran 1993; Edenius et al. 2002), and insect herbivory (Brown 1970; Hardy et al. 1986; Simpson and Coy 1999). Increasing attention is now being paid to the role of pathogenic fungi as a significant factor promoting gap dynamics in boreal forests (Kuuluvainen 1994; McCarthy 2001).

The type, frequency, severity and spatial characteristics of any particular disturbance may produce a wide range of live and dead tree biological legacies (MacLean 1980; White and Jentsch 2001; Franklin et al. 2002; Ryan 2002). Disturbances are often classified according to the amount of forest canopy removed: major or stand-replacing disturbances, and minor disturbances that remove a percentage of the canopy (Oliver 1981). The amount and spatial arrangement of dead wood produced in the form of snags or coarse woody debris and the degree of forest floor disturbance and advance regeneration protection complexify even further, the range and diversity of disturbance-induced structural legacies.

3.4 POST-DISTURBANCE STAND DEVELOPMENT, SUCCESSION AND STRUCTURE

As discussed in the preceding section, the primary source of forest structural heterogeneity is the actual disturbance itself. The second source of structural heterogeneity are the processes associated with post-disturbance stand developmental and successional processes. A distinction between succession and stand development is essential. Disturbance will always initiate a new cycle of stand development in the regenerating, post-disturbance forest. However, disturbance may or may not initiate successional change in tree species composition. In boreal forests, for example, a stand-replacing crown fire in a
mature black spruce stand with abundant viable cones will not initiate a species change or a new successional sequence. Black spruce will perpetuate itself and form the new stand. The same scenario occurs for mature balsam fir forests disturbed by stand-replacing insect herbivory. A well-established seedling bank of balsam fir assures that the successional status of the stand is not changed with canopy mortality (Baskerville 1975). On the other hand, a stand-replacing crown fire in a mature balsam fir–white birch stand (in the absence of a black spruce seed source) will revert the stand back to the early successional pure white birch stage, that, in the presence of a balsam fir seed source, will eventually succeed to a balsam fir–white birch stand (Damman 1964).

In this study, successional processes per se will not be considered. Under the hypothesized disturbance regimes of insect-mediated patch dynamics and fungal-mediated gap dynamics, the balsam fir–spruce–birch forest will be maintained after disturbance (parallel successional model, (Frelich 2002)). Of greater relevance, therefore, will be the stages of stand development after disturbance, particularly for the Little Grand Lake forests.

Models of stand development following major exogenous, stand-replacing disturbances have been developed for a range of forest types. Four major developmental stages are typically identified: (1) stand initiation stage (post-disturbance establishment), (2) stem exclusion stage (self-thinning), (3) understory reinitiation stage (transition), and (4) old-growth stage (steady state, shifting mosaic) (Oliver 1981; Oliver and Larson 1996). After disturbance and stand mortality, growing space is available and new individuals occupy the site from advance reproduction or seed propagules. Crown closure initiates a period of intense intraspecific competition or self-thinning in which trees experience high mortality and size differentiation. With continued stand development, the stand begins to
“lose its grip” on the site and advance regeneration, along with increased floral diversity, makes an appearance. The final old-growth stage is characterized by an eventual loss of the initial post-disturbance cohort, and the development of new cohorts through a process of small-scale gap dynamics mediated by pathogens, wind, or insects. Increased structural complexity and a quasi-equilibrium or “steady state” condition persists indefinitely until the next period of major disturbance. Researchers working in different forest ecosystems have produced similar models of stand development (Table 3-1).

The stages of stand development are themselves a source of structural heterogeneity. Of particular importance for dead wood structural heterogeneity are the post-disturbance structural legacies, and the production of new dead wood from both density-dependent, self-thinning-induced tree mortality and density-independent autogenic morality in the transition and old-growth phases of stand development. Live tree structural heterogeneity is a function of biomass accumulation and associated decrease in stem density with self-thinning, and increasing vertical and horizontal heterogeneity associated with gap formation and differential recruitment and growth associated with the structurally heterogeneous old-growth phases of stand development (Oliver and Larson 1996).

Within any forest landscape, the relative proportion of the various stages of stand structural and (or) stand successional development depends to a large extent on the periodicity, magnitude and spatial and temporal stochasticity of any particular disturbance event. Forests dominated by relatively major disturbances (fire, insects, wind) are often viewed as a mosaic of relatively discrete seral or development patches of varying age and size structure. Non-equilibrium patch dynamics have become the dominant ecological
Table 3.1. Comparison of stand developmental stages as given by various classification schemes (adapted from Franklin et al. 2002).

<table>
<thead>
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</thead>
<tbody>
<tr>
<td>Reorganization phase</td>
<td>Stand initiation</td>
<td>Establishment phase</td>
<td>Young forest</td>
<td>Establishment phase</td>
<td>Ecosystem initiative</td>
<td>Disturbance and legacy creation</td>
<td>Initiation</td>
</tr>
<tr>
<td>Aggradation phase</td>
<td>Stem exclusion</td>
<td>Thinning phase</td>
<td>Aggradation stage forest</td>
<td>Thinning phase</td>
<td>Competitive exclusion</td>
<td>Cohort establishment</td>
<td>Stem exclusion</td>
</tr>
<tr>
<td>Transition phase</td>
<td>Understory re-initiation</td>
<td>Transition phase</td>
<td>Mature forest</td>
<td>Mature phase</td>
<td>Understory re-initiation</td>
<td>Canopy closure</td>
<td>Mature (late stem exclusion)</td>
</tr>
<tr>
<td>Shifting mosaic steady-state</td>
<td>Transition phase (early)</td>
<td>Old-growth</td>
<td>Transition phase (late)</td>
<td>Botanically diverse</td>
<td>Biomass accumulation/competitive exclusion</td>
<td>Multi-aged break-up (demographic transition)</td>
<td></td>
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<td>Old-growth</td>
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<td>Multi-aged pole</td>
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<td>Multi-age mature</td>
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<td>Old multi-aged</td>
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<td></td>
<td>Pioneer cohort loss</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td>Steady-state</td>
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</tbody>
</table>


paradigm by which to understand the relationship between forest- and stand-level structure and disturbance (Watt 1947; Whittaker and Levin 1977; Pickett and White 1985; Wu and Loucks 1995; van der Maarel 1996; Pickett et al. 1997). Depending on the scale of inquiry, forests are often best considered as a mosaic of stands in various stages of both stand development and seral succession.

For forests dominated by small-scale gap dynamics, however, the patch model is less applicable. Rather than a patchy mosaic, the forest may be viewed as a relatively homogeneous, old-growth forest, considered more as a fine-grain matrix, the complex vertical and horizontal structure of which is maintained by gap disturbance at the single tree or small group level (McCarthy 2001). Various nominations have been given to this stage of forest development, with the term “old-growth” being the most commonly employed (Hayward 1991; Franklin and Spies 1991a; Kaufmann et al. 1992; Duchesne 1994; Davis 1996; Oliver and Larson 1996; Tyrrell et al. 1998). Other designations include the traditional term “climax” (Whittaker 1953), “shifting mosaic steady state” (Bormann and Likens 1979, 1981), “steady state phase” (Peet and Christensen 1980), and “shifting gap phase” (Spies and Franklin 1996).

Forest structures considered characteristic of old-growth will vary depending on species autecology, stand stature and environmental conditions. In general, old-growth structural features include reverse-J or rotated sigmoidal tree size distributions, standing dead snags in various stages of breakup, accumulations of coarse woody debris covering a wide range of decomposition classes, complex canopy heterogeneity with relatively continuous vertical distribution of foliage, small canopy gaps created by fungal-mediated individual tree mortality, and uneven-aged structure with trees approaching maximal
known ages (Old-growth definition task group 1986; Spies and Franklin 1988; Franklin and Spies 1991a; Oliver and Larson 1996; Kneeshaw and Burton 1998; Wells et al. 1998). An attempt to empirically define old-growth thresholds have led to the development of “indices of old-growth” (Spies and Franklin 1988). A recognition of the structural diversity of old-growth forests is important. Eighteen hundred year-old stunted black spruce clones (Laberge et al. 2000) and 1,890 year-old cliffside cedar (*Thuja occidentalis* L.) forests (Kelly and Larson 1997) do not attain the same size dimensions as old-growth Douglas fir forests, yet all three forest types are classified as old-growth using both conceptual and structural definitions of the term.

3.5 SUSTAINABLE FOREST MANAGEMENT, BIODIVERSITY AND FOREST STRUCTURE

In the study of forest disturbance regimes, particular attention has been given to the relationship between structural heterogeneity and the associated floral and faunal diversity (Hunter 1990, 1999; Haila 1994; Samuelsson et al. 1994; Pickett et al. 1997; Bunnell and Johnson 1998; Voller and Harrison 1998; McComb and Lindenmayer 1999; North et al. 1999; Jonsson and Kruys 2001; Kuuluvainen 2002; Lindenmayer and Franklin 2002). Forest structures are considered the best proxy measures of habitat and forest function and is the forest attribute most readily manipulated by human activity (Franklin et al. 2002). One focuses on the stand and forest structural diversity (biological legacies) as a product of various disturbance regimes, and the associated dynamics of plant and animal populations in response to disturbance-induced structural changes.
Of concern is the tendency of forest management to simplify or homogenize the structural diversity of forests, particularly at the stand level. At the landscape level, the patterns of cutblock may actually increase the structural diversity. These changes in landscape-level diversity may be construed as having positive or negative effects based on the values assumed for the particular landscape. The perceived reduction in stand structural heterogeneity has spawned a host of studies comparing the relationship between structural diversity and species biodiversity in both managed and unmanaged forests (Andersson and Hytteborn 1991; Hansen et al. 1991; Angelstam and Mikusinski 1994; Haila et al. 1994; Angelstam 1996; Essen et al. 1997; Goodburn and Lorimer 1998; Sippola et al. 1998; Martikainen et al. 2000; Imbeau et al. 2001; Siitonen 2001; Desponts et al. 2002; Grove 2002; Koivula and Niemelä 2002; Lindenmayer and Franklin 2002). Of particular concern in Newfoundland has been the effect of forestry-induced structural changes on the demographics of the endangered Newfoundland martin (Thompson and Curran 1995; Sturtevant et al. 1996; Payer and Harrison 2000) and on avian biodiversity (Thompson et al. 1999; Setterington et al. 2000).

Recognition of this essential link between forest and stand structural heterogeneity and organism biodiversity has generated the conceptual and empirical development of a natural disturbance-based forest management, particularly for the boreal forest (Haila et al. 1994; Province of British Columbia 1995; Angelstam 1996; Bergeron and Harvey 1997; Fries et al. 1997; Angelstam 1998b; Bergeron et al. 1999, 2001, 2002; Lähde et al. 1999; Landres et al. 1999; Niemelä 1999; Buse and Perera 2002; Delong 2002; Harvey et al. 2002, 2003; Kuuluvainen 2002; Mitchell et al. 2002; Schneider 2002; Seymour et al. 2002; von Gadow et al. 2002). Forest management based on the “emulation” of the historic
variability in different forest ecosystems has captured the imagination of both researchers and practitioners alike. A commonly accepted assumption is that native flora and fauna have evolved within the boundaries of specific disturbance regimes and that human intervention that conforms "more or less" to the disturbance parameters will merit the best success in conservation of biodiversity. Forest management changes from a focus on wood removals to a focus on retention of various structural characteristics to meet specific biodiversity and ecosystem objectives (Kohm and Franklin 1997; Aber et al. 2000).
CHAPTER 4

STUDY AREAS

4.1 GENERAL

Two study areas were examined: (1) the Little Grand Lake watershed southeast of the western Newfoundland city of Corner Brook, and (2) the Main River watershed east of Gros Morne National Park, in the southern reaches of the Great Northern Peninsula (Figure 4-1).

These two study sites represent some of the most extensive areas of primary forest left on the Island of Newfoundland. The large area of primary forest in both study sites provided an excellent opportunity for the study of natural forest dynamics on both the stand and landscape level. In the mid-1980s, commercial forestry ceased in the Little Grand Lake area. The study area is currently within the boundaries of the proposed Little Grand Lake ecological reserve. Motorized ground access is possible by all-terrain vehicle along a severely washed-out forest access road.

Much of the commercial forest of the Main River watershed is under license to Corner Brook Pulp and Paper Company Ltd., a subsidiary of Montreal-based Kruger Inc. Commercial logging in the lower reaches of the Main River watershed began in 1987, with the construction of approximately 20 km of forest access road and a bridge spanning the lower Main River. Logging operations were suspended as the company attended to salvage
Figure 4-1. Map of Newfoundland showing the location of the Main River and Little Grand Lake study areas.
logging in response to insect outbreaks in the neighbouring Upper Humber watershed to the south. In 1997, logging operations resumed in the Main River watershed and concentrated on road building and clearcut logging in the upper watershed. In March 2001, in response to public concern over the impact of extensive clearcut logging on the wilderness values, pine marten habitat and Heritage River status of the Main River, Corner Brook Pulp and Paper declared a “no clearcut” policy for the watershed. In June 2001, the Main River was declared a Canadian Heritage River because of its significant natural and recreational qualities (Government of Newfoundland and Labrador 2001).

4.2 MAIN RIVER

4.2.1 Topography and Geology

The 225 km\(^2\) study area lies within the 1,048 km\(^2\) Main River watershed located at the southern end of Newfoundland’s Great Northern Peninsula (Figure 4-2). The Main River flows in a general southeasterly direction, from the Long Range Mountains at elevations of 670 m to its mouth emptying into White Bay (Figure 4-3). Within the study area, elevations range from 280 m along the banks of the Main River’s Big Steady to elevations between 550 and 600 m towards the headwaters of the watershed. Stands were sampled between elevations 350 and 490 m in the upper part of the watershed.
Figure 4-2. Map of Main River study area, western Newfoundland.
Figure 4-3. Scenes of the Main River from near its headwaters down to the sea. (A) Characteristic uplands (Long Range Mountains) close to the headwaters. (B) Upper Main River flowing through landscape characterized by extensive peatlands. (C) Big Steady with islands dominated by white spruce. (D) Lower Main River drops quickly to the sea.

The Main River study area occurs in the Humber tectonic zone of western Newfoundland (Rogerson 1981, 1983). Regional geology is dominated by the 9000 km$^2$ Long Range Inlier, a massive of Proterozoic (1550 Ma) crystalline rocks forming the core of the northern Long Range Mountains (Owen 1990, 1991) (Figure 4-4).

Bounded by latitudes 49° 20’ N and 50° 50’ N, the Long Range Inlier is composed of three lithostratigraphic groupings:

(1) a gneiss complex that underlies 60% of the Inlier and that is composed mostly of quartzofeldspathic rocks of granitic or granodioritic composition;
(2) Grenvillian granitic-charnockitic plutons that occupy approximately 35% of the Long Range inlier. Of significance is the Potato pluton, a composite intrusion dominated by hornblende and pyroxene-rich charnockites and granites occupying 65 km² of the southern sector of the study area; and

(3) late Proterozoic mafic dykes, absent from the study area, occurring in only the northern section of the inlier.

4.2.2 Climate

"The Labrador Current is a relentless flood of molten ice, the bloodstream of our near sub-Arctic climate." (quoted in Macpherson and Macpherson (1981)). Thus did Newfoundland's celebrated artist, Christopher Pratt, describe what is probably the prime
determinant of the climate of the island of Newfoundland (Banfield 1981, 1983). Hugging the coast of Labrador and eastern Newfoundland, the cold, ex-Arctic waters of the Labrador Current are the bearers of icebergs and an extensive pack ice (Farmer 1981) (Figure 4-5).

Figure 4-5. True colour Moderate Resolution Imaging Spectroradiometer (MODIS) image of Newfoundland and the eastern Canadian coast taken on March 20, 2003 by the National Aeronautics and Space Administration’s (NASA) satellite Terra. Accumulations of sea ice are evident along the Labrador coast, and throughout the Gulf of St. Lawrence and the eastern seaboard of the Island of Newfoundland. Low-level water clouds cover most of the North Atlantic. Snow covers all land masses, producing shades of grey. Note the ice-free southern coast of Newfoundland. Credit: Jeff Schmaltz, MODIS Rapid Response Team, NASA/GSFC (Goddard Space Flight Center).

The persistence of coastal pack ice well into the months of April to May effectively suppresses the onset of spring along much of Newfoundland’s northeastern and eastern coasts. Cold ocean waters, extensive vernal sea ice accumulations, and persistent and often
high-velocity onshore winds determine the island's vegetative season that may range from 100 to 160 days per year.

The location of the study site at moderately high elevations (300-600 m) on the eastern flank of the Long Range Mountains exposes it to the cold ocean environment of the northeast Atlantic Ocean, and therefore determines a meso-climate distinctive from that of the western or Gulf of St. Lawrence side of the Long Range Mountains (C. Banfield, retired professor of Geography, Memorial University of Newfoundland, pers. comm.).

Two climatic zones exist in the watershed: (1) the "east coast and hinterlands" climatic zone located throughout the lower elevations of the watershed; and (2) the "western hills and mountains" zone covering the higher elevations of the watershed (Banfield 1981, 1983). The lower reaches of the watershed are less wet (900 to 1000 mm per year), with warmer and sunnier summers than the higher elevations of the watershed, where annual precipitation levels may range from 1300 to 1500 mm. Winters are cold throughout the watershed, with higher elevation snow accumulations exceeding 350 to 400 cm per year. Cool, late springs with sea ice persisting until mid-May are characteristic of the coastal regions.

No climatic station exists in the Main River study area. A recommended proxy site is the Upper Humber River Data Collection Platform (DCP) operated by the Newfoundland and Labrador Department of the Environment (K. Rollings, Water Resources Management Division, Government of Newfoundland and Labrador, pers. comm.). Located at an altitude of 300 m in the Upper Humber river watershed, the neighbouring watershed to the south, the DCP provided seven years (1991–1997) of precipitation and temperature data (Figure 4-6).
Figure 4-6. Climatographs for two climatic stations at the base of the Great Northern Peninsula, western Newfoundland. The upper Humber climatograph is based on seven years data (1991-1997) collected by the Water Resources Management Division, Government of Newfoundland and Labrador. The Sop's Arm climatograph is based on the Canadian Climate Normals, 1971-2000, Environment Canada, National Climate Data and Information Archive.

Of note is the relatively high level of precipitation throughout the year (average = 1350 mm) and the low average air temperature (1.7 °C). Snow fell from October to May, with small accumulations (~2 cm) in both June and September. A comparison with long-term climatic data (1971-2000 normals) obtained from the Sop’s Arm climate station (precipitation = 959 mm, temperature = 3.5 °C) at the mouth of the Main River clearly shows the orographic enhancement of precipitation during moist east-northeast airflows (C. Banfield, pers. comm.) and diminution of air temperature, especially winter temperatures, in the upper elevations of the watershed (Figure 4-6, Table 4-1).
Table 4-1. Climatic data for six climatic stations in western Newfoundland. The Burgeo road and Upper Humber stations act as respective proxies for the Little Grand Lake and Main River study areas.

<table>
<thead>
<tr>
<th>Location</th>
<th>Elevation (m)</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Temperature (° C)</th>
<th>Rainfall (mm)</th>
<th>Snowfall (cm)</th>
<th>Total precipitation (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Burgeo road*</td>
<td>420</td>
<td>48° 23'N</td>
<td>57° 34'W</td>
<td>2.4</td>
<td>1002.7</td>
<td>393.0</td>
<td>1376.7</td>
</tr>
<tr>
<td>Deer Lake</td>
<td>11</td>
<td>49° 10'N</td>
<td>57° 25'W</td>
<td>4.0</td>
<td>812.1</td>
<td>315.2</td>
<td>1127.3</td>
</tr>
<tr>
<td>Stephenville</td>
<td>26</td>
<td>48° 31'N</td>
<td>58° 33'W</td>
<td>4.6</td>
<td>984.9</td>
<td>406.9</td>
<td>1352.1</td>
</tr>
<tr>
<td>Cornerbrook</td>
<td>5</td>
<td>48° 57'N</td>
<td>57° 57'W</td>
<td>5.1</td>
<td>848.9</td>
<td>421.9</td>
<td>1270.8</td>
</tr>
<tr>
<td>Upper Humber*</td>
<td>300</td>
<td>49° 37'N</td>
<td>57° 18'W</td>
<td>1.7</td>
<td>986.8</td>
<td>435.0</td>
<td>1350.1</td>
</tr>
<tr>
<td>Sop’s Arm</td>
<td>17</td>
<td>49° 46'N</td>
<td>56° 52'W</td>
<td>3.5</td>
<td>686.0</td>
<td>272.8</td>
<td>958.7</td>
</tr>
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</table>


b Temperature, rainfall and snowfall based on five years of data. Six years used for total precipitation.

c Temperature, rainfall and snowfall based on two years of data. Four years used for total precipitation.
For the Long Range Mountains in general, Solomon et al. (1968) estimated that total precipitation increased at an average rate of 207 mm for each 100 m gain in elevation. Estimated precipitation levels for the high elevations between the source of the Upper Humber river and the northeast corner of Gros Morne National Park (elevation 550 to 600 m, neighbouring on the upper reaches of the Main River watershed) were between 2400 and 2800 mm (Gros Morne National Park 1990). As for air temperature, climatological work carried out by Banfield (pers. comm.) indicated an average lapse rate of 0.64 °C for every elevation increase of 100 m. While the upper Main River watershed may be relatively more sheltered than the west-facing slopes of the Long Range Mountains from moist westerly-southwesterly flows off the Gulf of St. Lawrence (giving it relatively warmer summer weather at a given altitude), the reverse role of moist onshore east-northeasterly flows is also at work. Therefore, assuming orographic enhancement of precipitation and similar lapse rates on the east side of the Long Range, the Upper Main watershed is characterized by generally wet, damp and cool conditions. Average July and August temperatures are around 14 °C. Continuous and complete snow cover persists from November until at least April with average snowfalls exceeding four metres. Data from the Upper Humber DCP confirmed average snow accumulations of 9 and 10 cm for the months of May and October, respectively. Persistent snow into the month of June is not uncommon in these forests. Winters are cold with average January and February temperatures of −9 °C and −7 °C degrees, respectively.
4.2.3 Vegetation and Soils

Forests of the Main River watershed form part of the Northern Peninsula boreal forest region B.29 (Rowe 1977) and the Eastern Long Range subregion of the Northern Peninsula Ecoregion (Damman 1983). The generally open, deep-crowned, slow-growing, old-growth forests dominated by balsam fir with significant occurrence of black spruce flank the eastern slopes of the Long Range Mountains to an elevation of 450 to 500 m (Figure 4-7).

With increasing altitude one approaches the Long Range Barrens ecoregion dominated by extensive areas of mainly black spruce krummholz and alpine heath comprised of open soil and bedrock alternating with cushion vegetation dominated by Empetrum eamesii Fern. & Wieg. (Damman 1983; Meades 1983a) (Figure 4-8).

Both white birch and white spruce occur throughout the area, tending for the most part to occur on the better sites. Eastern larch (Larix laricina (Du Roi) K. Koch) is uncommon, and is associated predominantly with organic soils. A harsher climate compared to the rest of the island prevents the establishment of other island tree species such as white pine (Pinus strobus L.), yellow birch (Betula alleghaniensis Britton), red maple (Acer rubrum L.) and trembling aspen. Peatlands cover 4.7% of the study area and consist mostly of slope bogs (Wells and Pollett 1983).

Until recently, the forests of this area were inaccessible by road. No systematic ecological classification has been carried out in the region. The following general comments are based on both personal observations and a Damman forest type classification (Damman 1967; Meades and Moores 1994) carried out by the Newfoundland
Figure 4-7. Scenes of Main River old-growth forest. (A) Oblique view of old-growth Main River forests. Scattered white birch are readily evident in their fall foliage. (B) Near vertical view showing the relatively open canopy of the old-growth forests. (C) Black spruce is common on organic soils and thin soils over granitic bedrock. (D) Interior forest view.
Figure 4-8. High altitude forests, western Newfoundland. (A) High altitude Main River forests. (B) Krummholz black spruce, Long Range Mountains. Coastal plain and the Gulf of St. Lawrence in the background.

Forest Inventory as part of their ongoing fieldwork (Roberts et al. 1996). The following comments refer to mesic, generally mid-slope forest sites.

Most of the forest sites may be described as balsam fir–black spruce moss-rich forest types that include Pleurozium–balsam fir, Hylocomium–balsam fir, Gaultheria–balsam fir and Sphagnum–balsam fir. In general, these mid-slope forests are mossy, moderately productive to productive balsam fir–black spruce forests with scattered white birch and white spruce. The ground vegetation is dominated by Pleurozium schreberi (Brid.) Mitt. with varying frequency of Hylocomium splendens (Hedw.) B.S.G. and Hylocomium umbratum (Hedw.) B.S.G.. Complete moss coverage of granitic boulders and coarse woody debris is common. The mosses Dicranum spp. and Ptilium crista-castrensis (Hedw.) DeNot. are almost always present. Very sparse herbs include Coptis groenlandica (Oeder) Fern., Clintonia borealis (Ait.) Raf., Cornus canadensis L., Moneses uniflora (L.) Gray, Listera cordata (L.) R. Br., Maianthemum canadense Desf., and Linnaea borealis L. Dwarf shrubs include Vaccinium angustifolium Ait., Gaultheria hispidula (L.) Bigel., and
especially *Vaccinium ovalifolium* Smith. On the better sites, *Solidago macrophyllum* Pursh and two species of twisted stalk (*Streptopus amplexifolius* (L.) DC and *S. roseus* Michx.) are commonly scattered. The wood fern, *Dryopteris spinulosa* (O.F. Mull.) Watt is ubiquitous in low frequency with *Osmunda cinnamomea* L. indicative of wetter, poorer sites. Lush mats of *Sphagnum girgensohnnii* Russ. are common on the lower toe of seepage slopes. The common occurrence of the liverwort *Bazzania trilobata* (L.) Gray indicates constant humid site conditions.

Soils are typically imperfectly to moderately well drained, Gleyed Humo-Ferric, Ferro-Humic Podzols (Silver Mountain Association, dominant association > 50%) developing on exceedingly to excessively stony, moderately coarse-textured shallow glacial till derived from granite, granitic gneiss and schist (Kirby et al. 1992). Landforms are characterized by morainal veneer over hummocky and rolling bedrock.

4.3 LITTLE GRAND LAKE

4.3.1 **Topography and Geology**

The Little Grand Lake study area (106 km$^2$) is situated within the provisional Little Grand Lake ecological reserve in western Newfoundland (Figure 4-9). The steep-sided shores of Grand Lake to the north and Little Grand Lake to the south bound the study area (Figure 4-10). From the lakeshore located at approximately at 100 to 150 m above sea level (asl), the land rises rapidly to 350 to 450 m within 1 km to form a high upland ranging in elevation from 400 to 500 m. To the east, the forested study area is bounded by the higher elevation Buchans Plateau–Topsails ecoregion (600 to 700 m) of the Southern Long
Figure 4-9. Location of Little Grand Lake study area in western Newfoundland.
Figure 4-10. View of Grand Lake and Little Grand Lake. (A) Grand Lake to the south. Note steep-walled slopes of study area to the left and Glover Island to the right. (B) Little Grand Lake to the east. Abandoned logging road (left of lake) provides access to the study area.

Range Mountains, an ecoregion dominated by dwarf shrub heaths (generally *Kalmia angustifolia* L.), shallow patterned peatlands and dwarf black spruce krummholz less than 1 m in height (Damman 1983).

Almost the entire study area is underlain by lower Ordovician volcanic bedrock (pillowed and massive basalts, felsic tuffs) with minor shale and conglomerate occurrences (Currie and van Berkel 1992a). Of the five distinctive geological subzones characterizing the southern Long Range Mountains, the Glover Group (Subzone Notre Dame, Zone Dunnage), includes most of the study area, except for a small section in the eastern end of the study area that is classified as the Topsails Igneous Complex composed of young Silurian leucocratic red amphiboles and biotite granites (Williams et al. 1988; Currie and van Berkel 1992b).

The surficial geology is dominated by a bouldery, veneer glacial till (< 2 m thick) that is broken by bare bedrock (2.7% of study area) in the higher elevations and by open bogs and forested fens (5.7% of study area) throughout the study area (Batterson 1995).
Colluvial deposits, often concealed by white birch stands, dominate the steep-sided lake shores. Ponds and rivers make up 3.5% of the study area. Fast-flowing streams dissect the slopes flowing from the peneplain, particularly the northern slopes facing Grand Lake, with drainage less common into Little Grand Lake.

4.3.2 Climate

Other than the mid-latitudinal position of the Island of Newfoundland, the two main influences that greatly determine island climate are the cold, ex-Arctic waters of the Labrador Current (Farmer 1981), and the Gulf of St. Lawrence and Cabot Strait, both of which are extensive enough to influence the temperature and moisture parameters of easterly flowing air masses from the Canadian mainland (Banfield 1981, 1983). Cold ocean waters, extensive sea ice accumulations, particularly along the northern and eastern coasts, and persistent and often high-velocity onshore winds determine the vegetative season that can range from 100 to 160 days. Total precipitation is generally well-distributed throughout the year, ranging from 1000 mm in northern regions to 1500 mm on the south coast and the eastern Avalon Peninsula that is particularly influenced by moist maritime winds. The range of total precipitation adjusted for observed runoff is up to 50% greater with mean annual figures ranging from 1500 to 2000 mm (den Hartog and Ferguson 1975). Affecting the climate of western Newfoundland, including the Little Grand lake study area, are the 400 to 800 m high Long Range Mountains, the most northern extension of the continental Appalachians.

Given that most climatological stations are located along the coast, climatic data for the upland and mountain areas of Newfoundland are sparse. Therefore, conclusions on
upland climates are necessarily weaker than those for coastal and lower elevation climates. Banfield (1983) distinguished the “west coast” climatic zone of western Newfoundland (Bonne Bay and south) from that of the “western hills and mountains” variant of the “central uplands” to the east. In the west coast climatic zone, summers are moderately warm and sunny, and winters cold and snowy with a relatively early spring and absence of fog. Annual precipitation is moderate near sea level (1100 to 1200 mm) with altitudinal increases. To the east, the central uplands climatic zone has from 1250 to at least 1600 mm a year, cold snowy winters and cool summers. The “western hills and mountains” zone is similar to the highest elevations experiencing lower temperatures, greater precipitation and complete snow cover from December until at least April. Given its geographical location and approximate mid-elevational position, the Little Grand Lake study area is probably best described as transitional between the “west coast” climatic zone and the “western hills and mountains” climatic zone.

No climate gauge exists in the Little Grand lake watershed. A comparable site recommended by the Water Resources Management Division of the Newfoundland and Labrador Department of the Environment was the “Burgeo Road” data collecting platform southeast of the study site (57° 34' W longitude 48° 23' N latitude, 420 m asl) (K. Rollings, pers. comm.). The climatograph (based on data from 1991–1997) from this site is given in Figure 4-11.

Also presented in Figure 4-11 are climatographs from three lower elevations, regional climatological stations for which long-term data exist. The Burgeo road site is marked by a lower average temperature (2.3 °C) compared to that recorded for Stephenville
Figure 4-11. Climatographs of four climatic stations in western Newfoundland. The Burgeo road climagograph is based on seven years data (1991-1997) collected by the Water Resources Management Division, Government of Newfoundland and Labrador. All others are based on Canadian Climate Normals, 1971-2000, Environment Canada, National Climate Data and Information Archive.
(4.6 °C), Corner Brook (5.1 °C) and Deer Lake (4.0 °C) (Table 4-1). The mean total annual precipitation is also greatest for the Burgeo road site, especially relative to both Corner Brook and Deer Lake. Stephenville, exposed to the maritime influence of the Gulf of St. Lawrence and backed by high ground, has comparable precipitation levels. In general, the Little Grand study site, given its 400 to 500 m elevation and distance from the coast, experiences lower mean annual temperatures and higher precipitation levels than those generally associated with the west coast of Newfoundland.

4.3.3 Vegetation and Soils

The study site lies within the generally very rugged, productive Corner Brook boreal forest section B28b (Rowe 1977) and on the western edge of the Corner Brook subregion of the western Newfoundland ecoregion (Damman 1983, Meades and Moores 1994) (Figure 4-12).

A humid climate has precluded fire as a significant disturbance regime and balsam fir dominates the productive, generally calcareous sites underlain by limestone bedrock or calcareous basal till. Some of the most productive forest sites for the entire island occur within this ecoregion. The relatively long vegetative season and generally warm summers favour the growth of specifically southern boreal species including red maple, yellow birch and white pine.

The characteristic calcareous geology of the Corner Brook subregion is, however, absent from the study area, with the latter acting as a transition between the nutrient-rich and productive sites of the lower elevations of the Corner Brook subregion and the higher altitude Portage Pond subregion of the Central Newfoundland ecoregion. The Central
Figure 4-12. Oblique view of the Little Grand Lake landscape. Undulating forest landscape dominated by balsam fir. Bogs and fens can be found in the depressions.

Newfoundland ecoregion is more boreal in character, with a greater predominance of black spruce in a landscape that lists fire as a significant disturbance. Despite the abundance of large old-growth white pine on the warm, south-facing slopes of Little Grand Lake, white pine (as well as red maple and yellow birch) were absent from the higher elevation peneplain of the study area. Therefore, despite its geographical location in the Western Newfoundland ecoregion, the Little Grand Lake study area is better described as a transition to the more continental boreal forests of central Newfoundland. However, the fetch of precipitation from westerly weather systems maintains a humid climate, effectively precluding fire from the balsam fir-dominated landscape.
An exploratory 1:250,000 soil survey classified study area soils as the Topsails association (dominant association 50%) (Woodrow 1988). Washed, partially sorted, coarse-textured glacial till derived from pale red granite, quartz, monzonite and granodiorite characterize the parent materials. Soils on the lake-side slopes (31% to 45%) are mainly Gleyed Ferro-Humic Podzols, poorly drained, excessively stony and very rocky. Mineral soils over the remainder of the study area are mostly Gleyed Ortstein Ferro-Humic Podzols on morainal veneer over hummocky bedrock with slopes of 16% to 30%. Imperfect drainage, excessive stoniness and moderate rockiness characterize the soils. The Damman forest types of the study site, their associated soils and relative fertility and moisture status are given in Table 4-2. A short description of each forest type follows (adapted from Damman 1967; Meades and Moores 1994):

**Dryopteris–Lycopodium–balsam fir:** Classified as a secondary forest type in the study area, these stands grow on generally nutrient-rich tills. The moss layer is dominated by *Hylocomium splendens* (Hedw.) B.S.G. and *Pleurozium schreberi* (Brid.) Mitt.. The forest type is differentiated from other *Dryopteris*–balsam fir forests by the presence of *Lycopodium annotinum* L. and *Lycopodium lucidulum* Michx..

**Dryopteris–Hylocomium–balsam fir:** Occupying a small part of the study area, this zonal forest type for western Newfoundland (Meades and Moores 1994) is fern-rich *Dryopteris spinulosa* var. *americana* (Fisch.) Fern. with very few shrubs and a well developed moss layer dominated by *Hylocomium splendens* (Hedw.) B.S.G.. Stands are well-stocked and productive with excellent regeneration, consisting predominantly of balsam fir. The fern coverage by *Dryopteris spinulosa* var. *americana* (Fisch.) Fern. is usually less than 25%.
Table 4-2. Damman forest types mapped in the Little Grand Lake area. Modified from Kitchen et al. (n.d.). See also Damman (1967) and Meades and Moores (1994) for further details on the Damman forest types.

<table>
<thead>
<tr>
<th>Damman forest type</th>
<th>Topographic position</th>
<th>Soils</th>
<th>Moisture</th>
<th>Fertility</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Dryopteris-</em></td>
<td>Hummocky moraines</td>
<td>Orthic Humic Podzol</td>
<td>4-5</td>
<td>Rich-very rich</td>
</tr>
<tr>
<td><em>Lycopodium</em></td>
<td>near bogs</td>
<td>Placic Humic Podzol</td>
<td></td>
<td></td>
</tr>
<tr>
<td>balsam fir (Fdl)*</td>
<td></td>
<td>Gleyed Ferro–Humic Podzol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Dryopteris-</em></td>
<td>Mid to upper slopes</td>
<td>Orthic Ferro–Humic Podzol</td>
<td>2-3</td>
<td>Medium-rich</td>
</tr>
<tr>
<td><em>Hylcomium</em>-</td>
<td></td>
<td>Fragic Ferro–Humic Podzol</td>
<td></td>
<td></td>
</tr>
<tr>
<td>balsam fir (Fdh)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hylcomium</em>-</td>
<td>Mid to upper slopes</td>
<td>Orthic Gleysol</td>
<td>3-4</td>
<td>Medium-rich</td>
</tr>
<tr>
<td>balsam fir (Fh)</td>
<td></td>
<td>Orthic Humic Gleysol</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Rego Gleysol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Hylcomium</em>-</td>
<td>Mid slope transition</td>
<td>Orthic Podzol</td>
<td>2-3</td>
<td>Medium-rich</td>
</tr>
<tr>
<td>balsam fir (podzol) (Fh(p))</td>
<td>between Fh and Fp</td>
<td>Concretionary Podzol</td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pleurozium</em>-</td>
<td>Upper slopes–ridge</td>
<td>Orthic Humic–Ferric Podzol</td>
<td>1-3</td>
<td>Poor-medium</td>
</tr>
<tr>
<td>balsam fir (Fp)</td>
<td>summits</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Kalmia</em>-</td>
<td>Upper slopes–ridge</td>
<td>Orthic Humo–Ferric Podzol</td>
<td>1-2</td>
<td>Poor-medium</td>
</tr>
<tr>
<td>black spruce (Sk)*</td>
<td>tops</td>
<td>Placic Humo–Ferric Podzol</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black spruce–feathermoss/bedrock (SM/R)</td>
<td>Ridge summits</td>
<td>Typic Folisol</td>
<td>0-2</td>
<td>Very poor-poor</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Lithic Orthic Regosol</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Moisture on a scale of 1 (dry) to 6 (wet).
Fertility on a scale of very poor to very rich.
Tertiary forest types. All other Damman types are classified as primary forest types for the study area.
**Hylocomium-balsam fir:** This forest type is well stocked and moderately productive with good to excellent balsam fir regeneration. *Hylocomium splendens* (Hedw.) B.S.G. may cover up to 100% of the forest floor, with the general absence or rare occurrence of *Rhytidiadelphus loreus* (Hedw.) Warnst. and *Hylocomium umbratum* (Hedw.) B.S.G. differentiating it from the *Dryopteris-Hylocomium* type. In both the *Dryopteris-Hylocomium* and *Hylocomium-balsam fir* types, the herb layer is poorly developed and is usually populated by ubiquitous forest herbs such as *Cornus canadensis* L., *Maianthemum canadense* Desf., *Linnaea borealis* L., *Clintonia borealis* (Ait.) Raf. and *Trientalis borealis* Raf., and to a lesser extent, *Listera cordata* (L.) R. Br., *Goodyera repens* (L.) R. Br., and *Moneses uniflora* (L.) Gray.

**Pleurozium-balsam fir:** A moderately productive to poor mossy forest type of balsam fir and black spruce with the moss layer dominated by *Pleurozium schreberi* (Brid.) Mitt. and sometimes *Hylocomium splendens* (Hedw.) B.S.G.. Balsam fir regeneration is poor to adequate and black spruce reproduces principally by layering. Scattered dwarf shrubs are indicative of poor sites (*i.e.*, *Vaccinium angustifolium* Ait. and *Kalmia angustifolia* L.). *Gaultheria hispidula* (L.) Bigel., *Pyrola secunda* L. and a few scattered specimens of *Cornus canadensis* L. and *Maianthemum canadense* Desf. characterize most stands.

**Kalmia-black spruce:** Poor, relatively open black spruce forests with some balsam fir. The well-developed shrub and moss layer is dominated by *Kalmia angustifolia* L. and *Pleurozium schreberi* (Brid.) Mitt., respectively. This forest site will occur across a range of moisture regimes from dry sands to shallow peatlands.
**Black spruce–feathermoss:** Black spruce forests with a well-developed moss layer dominated by *Pleurozium schreberi* (Brid.) Mitt., *Hylcomium splendens* (Hedw.) B.S.G. and *Ptilium crista-castrensis* (Hedw.) De Not.. The herb layer is poorly developed and some ericaceous shrubs are present including *Kalmia angustifolia* L., *Vaccinium angustifolium* Ait., and *Rhododendron canadense* (L.) Torr. In this case, shallow soils over bedrock support black spruce forests of poor quality.
CHAPTER 5
MATERIALS AND METHODS

5.1 INTRODUCTION

In order to understand the structure and dynamics of the two remarkably different types of forests in the Main River and Little Grand Lake study areas, it was necessary to analyze both forests at the landscape and at the stand level. At the stand level, retrospective studies (stand structural information and dendrochronology) were done in both study areas. A chronosequence study was conducted in the Little Grand Lake forest. Comparison of landscape-level forest structure in the two study areas was conducted using 1:12,500 true colour aerial photographs.

5.2 SELECTION OF STUDY SITES: RECONNAISSANCE

The Main River and Little Grand Lake study sites were selected after a lengthy reconnaissance of the forests of western Newfoundland by road, helicopter and snowmobile. Reconnaissance focused on the identification of areas of old, unlogged forests. Conversations with member of the Newfoundland and Labrador Forest Service confirmed the presence of a large, primary forest landscape along the entire eastern edge of the Great Northern Peninsula. It had been felt for some time that these forests were different in structure from the even-aged forests normally considered in provincial even-
aged forest management. No information on these forests was available, except that generated as part of the normal forest inventory. The stands were unusually old (> 140-160 years old) with complex, multi-storied stand structure including abundant snags.

The Main River watershed at the southern edge of the Great Northern Peninsula was chosen as an old-growth study site. Planned logging operations in the watershed were abandoned in the late 1970s by the forest license holder in favour of extensive salvage operations in response to the current spruce budworm outbreak. Only in the late 1990s did logging operations commence in the upper Main River watershed. Other possible candidate areas along the east coast of the Northern Peninsula were rejected because of the logistical and financial problems associated with accessibility.

Primary forests located in the Little Grand Lake area were chosen as a contrast study site. Reconnaissance confirmed a forest landscape characterized by a patch mosaic of seemingly even-aged stands in various stages of stand development. The area has had a long history of recorded outbreaks of both the spruce budworm and the hemlock looper. Approximately 209 ha of mature forest were logged before commercial operations ceased in the late 1980s. A washed-out forest resource road allowed access by all-terrain vehicles to a large area of unlogged, primary forest.

5.3 MAIN RIVER

5.3.1 Plot Selection and Layout

Given the general inaccessibility of the Main River study area, and the desire to sample stands within a specific range of variability, random sampling was neither possible
nor desirable. Sample plots were chosen using a stratified sampling approach termed "subjective sampling without preconceived bias" (Mueller-Dombois and Ellenberg 1974, p. 32–33). The full range of forest stand variability was not sampled. The range in forest types was determined by an analysis of Geographic Information Systems (GIS)-based forest cover types produced by the Newfoundland Forest Service (1978 photography, 1980 fieldwork) for the 1:50,000 Main River topographic sheet (12 H/14) (Energy Mines and Resources Canada 1990). Stand types of poor, medium and good site quality occupied 35%, 64% and 1% of the productive forest covered by the Main River map. Sampling was confined to the three stand types of medium site quality that occupied 84% of all medium stand types; bF542M, bFbS542M and bF552M (11,583 ha or 54% of the total productive forest area (See Table 5-1 for an explanation of forest cover type coding). Using these criteria, only balsam fir-dominated stands of medium site quality growing on mid-slope zonal sites were sampled.

Prospective study sites were located in the field using 1:12,500 colour aerial photographs and Newfoundland and Labrador Forest Service forest cover type maps. After preliminary reconnaissance, 13 stands were selected across the widest possible extent of the accessible watershed. Emphasis was placed on the selection of relatively "uniform" or "homogeneous" sites (sensu Poore 1962). Criteria for plot selection included the following: (1) structurally homogeneous zonal sites with no history of logging or extensive windthrow, (2) structures characteristic of old-growth sensu Oliver and Larson (1996); multi-staged canopies with trees of all sizes, presence of snags and coarse woody debris in all stages of decomposition, (3) absence of stream channels or interior forest fens, and (4)
Table 5-1. Key to standard terms used in the Newfoundland and Labrador Forest Service stand type classification (adapted from Delaney and Osmond 1977; Newfoundland Forest Service 1993).

<table>
<thead>
<tr>
<th>Stand characteristic</th>
<th>Standard Forest Service code</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tree species</td>
<td></td>
</tr>
<tr>
<td>Balsam fir</td>
<td>bF</td>
</tr>
<tr>
<td>Black spruce</td>
<td>bS</td>
</tr>
<tr>
<td>White birch</td>
<td>wB</td>
</tr>
<tr>
<td>White pine</td>
<td>wP</td>
</tr>
<tr>
<td>Eastern larch (Tamarack)</td>
<td>tL</td>
</tr>
<tr>
<td>Stand age</td>
<td></td>
</tr>
<tr>
<td>0-20</td>
<td>1</td>
</tr>
<tr>
<td>21-40</td>
<td>2</td>
</tr>
<tr>
<td>41-60</td>
<td>3</td>
</tr>
<tr>
<td>61-80</td>
<td>4</td>
</tr>
<tr>
<td>81-100</td>
<td>5</td>
</tr>
<tr>
<td>101-120</td>
<td>6</td>
</tr>
<tr>
<td>121+</td>
<td>7</td>
</tr>
<tr>
<td>Stand height (m)</td>
<td></td>
</tr>
<tr>
<td>0-3.5</td>
<td>1</td>
</tr>
<tr>
<td>3.6-6.5</td>
<td>2</td>
</tr>
<tr>
<td>6.6-9.5</td>
<td>3</td>
</tr>
<tr>
<td>9.6-12.5</td>
<td>4</td>
</tr>
<tr>
<td>12.6-15.5</td>
<td>5</td>
</tr>
<tr>
<td>15.6-18.5</td>
<td>6</td>
</tr>
<tr>
<td>18.6-21.5</td>
<td>7</td>
</tr>
<tr>
<td>21.6+</td>
<td>8</td>
</tr>
<tr>
<td>Crown density (%)</td>
<td></td>
</tr>
<tr>
<td>0-20 year old stands</td>
<td>0</td>
</tr>
<tr>
<td>&gt;75%</td>
<td>1</td>
</tr>
<tr>
<td>51%-75%</td>
<td>2</td>
</tr>
<tr>
<td>26%-50%</td>
<td>3</td>
</tr>
<tr>
<td>≤ 25% (not sufficiently restocked)</td>
<td>NSR</td>
</tr>
<tr>
<td>Site quality</td>
<td></td>
</tr>
<tr>
<td>High</td>
<td>H</td>
</tr>
<tr>
<td>Good</td>
<td>G</td>
</tr>
<tr>
<td>Medium</td>
<td>M</td>
</tr>
<tr>
<td>Poor</td>
<td>P</td>
</tr>
</tbody>
</table>

*a* Tree species that individually comprise ≥ 25% of the total basal area are indicated. One species indicated in the Forest Service type code means that 75%-100% of the total stand basal area is comprised of that species. Two species indicates that 50%-75% of the basal area is comprised of the first species, with the remainder made up of the second species. Three species indicate that 40% of the basal area is comprised of the first species, and that 30% of the basal area is comprised of each of the remaining two species.

*b* Tree age at stump height of dominant trees (generally 30 cm stump height).

*c* Based on height of dominant trees.

*d* Usually measured directly from aerial photographs.

*e* Site codes derived from Canada Land Inventory, Forest Capability Classes (Delaney 1974).
adequate distance from road such that no effect of road opening was evident (i.e. windthrow).

Once a suitable stand was located, the first corner of a 50 m x 50 m plot was randomly located. Each plot was laid out using a hand-held compass and a 50 m measuring tape (Newfoundland Forest Service 1993). To facilitate tree measurements, each plot was divided into approximate 5 x 5 m sections. All 13 plots were located at elevations ranging from 350 to 490 m. Plot locations are given in Figure 5-1.

5.3.2 Tree and Seedling Measurements

All live and dead trees > 1.3 m in height were flagged and numbered. The following were measured for each tree: species, mortality status (dead/alive), caliper diameter outside bark at breast height (dbh; 1.3 m above ground; 0.1 cm), and other distinguishing features such as extent of moose browse, presence of layering, stem forking, etc. For heavily browsed and twisted trees, dbh was recorded just below the extensive forking and deformation. In three plots designated for stand reconstruction, all trees > 1.3 m in height were felled at a point as close to the ground as possible. Layered trees were cut as far as possible along the length of the lower bole. Tree length (height; 0.1 m) was measured with a 30 m measuring tape. Basal area (cross-sectional area) at 1.3 m for each tree was calculated using the formula

\[ \text{Basal area (m}^2\text{ ha}^{-1}) = \frac{\pi d^2}{4(10,000)} = 0.00007854d^2, \]  

where \( d = \text{dbh (cm)} \)  

(Husch et al. 2003, p. 95).
Figure 5-1. Map of Main River study area showing location of sample plots. Non-forested areas include peatlands and heathlands, as well as scrub forests not capable of producing 30 m$^3$ gross merchantable volume ha$^{-1}$ at rotation age.
The structure of the seedling/sapling layer (≤ 1.3m) was intensively sampled in three 0.25 ha (50 x 50 m) stand reconstruction plots. After a random start beginning from a plot corner, 100 1m² subplots were systematically arranged every 5 m throughout each of the three plots. Four percent of each plot was thus sampled. Within each subplot, all seedlings and saplings were identified by species, harvested, transported to the lab and placed in cool storage. Seedling height (0.1 cm) was measured from the root collar. Basal diameter was measured by calipers at the point where the seedlings were cut. The species, height (0.1 m) and basal diameter (0.1 mm) of each seedling were recorded. The number and species of all emergents were recorded in the field. Emergents were then discarded.

5.3.3 Tree Age

The three stand reconstruction plots were chosen for detailed age, height and dendrochronological measurements (Figure 5-2). The dendroecology of these stands will be reported in a later study. Increment cores were inadequate in determining the age of these slow-growing trees, many of which had butt rot. Therefore, cross-sectional disks were sampled from felled trees. All tagged trees were felled in one plot. In the other two plots chosen for age analysis, only trees covering one-half of the plot area were felled. All stand reconstruction plots were located in stands slated for logging.

All trees, both live and dead, were felled as close to the ground as possible. For layered trees, the layer was followed along the ground as far as possible and then cut. Disks were cut as close to the ground as possible for all sample trees devoid of butt rot. For trees with butt rot, percent rot was estimated to the nearest 5%. In trees with advanced butt rot, full disks were removed further up the stem beyond the influence of the fungal decay.
Figure 5-2. Aerial view of one of three stand reconstruction plots, Main River. Plot size is 0.25 ha (50 x 50 m). Note old white birch in fall colour. Photo credit: Len Moores.
In cases where the incidence of rot was relatively low, disks were extracted from the lower portion of the bole. In both cases, disks that were judged to contain the longer ring series were sampled. Selected trees with good form and absence of butt rot were sampled at breast height as well. All disks were transported to the lab and stored in cool dry conditions.

To facilitate sample preparation and measurement, tree disks were cut with a band saw into rectangular cross-sections. All disks were sanded with a hand-held belt sander using 80-120 grit sandpaper. The ages of most trees were determined as part of ring-width measurements conducted on a Windendro™ (Régent Instruments Inc) tree-ring analysis system (version 6.3b) of 0.01 mm resolution (Guay et al. 1992). In situations of intense juvenile suppression, ring measurements were facilitated by hand-sanding of the sample using gradations of sand paper up to 1500 grit and the counting of rings using a dissecting microscope (maximum magnification 40X). For the vast majority of disks, age of each of the two radii was determined, except for disks with fungal decay in which case the greater minimum age was recorded. Discontinuous, partial rings and extremely off-centre piths were not uncommon in small, suppressed trees. In these cases, ring count was taken from the radius of maximum width.

All ages must be accepted as minimum ages. Despite effort to fell all trees as close to the ground as possible, the growth of adventitious roots above the root collar, and the “presence” of missing rings under suppressed conditions (c.f. seedling methods) precluded the determination of actual germination ages (DesRochers and Gagnon 1997, Gutsell and Johnson 2002, Peters et al. 2002). While acknowledging that choice of age class widths
may determine interpretation of static age class data (Wong and Lertzman 2001), it was
considered appropriate to fix the age class width at five years.

5.3.4 Seedling Age

Due to ubiquitous adventitious rooting in balsam fir and spruce in cold feathermoss
and Sphagnum forests (Cooper 1911; LeBarron 1945; Bakuzis and Hansen 1965; Jablanczy
and Baskerville 1969), age determination of seedlings at soil level is inappropriate (Parent
et al. 2000). In many cases the actual root collar occurs well below the shoot-root interface
and the proliferation of adventitious roots. All seedlings were therefore carefully uprooted
to include as much of the root as possible. Care was taken to cut each seedling as close to
the root collar as possible. This was accomplished by cutting the seedling above the
generally smooth hypocotyl region devoid of bud scars and primary roots (Parent et al.
2000). This was especially important for creeping or J-shaped balsam fir seedlings that
formed extensive adventitious rooting. For vertical seedlings with a balanced root form
location of the root collar was easier (Kneeshaw and Claveau 2001). All seedlings
identified as layers were cut from the parent stem and considered equivalent to seedlings of
non-layer origin for the purposes of measurement.

Correct aging of highly suppressed seedlings with adventitious rooting can be
difficult due to the common occurrence of missing rings and practical difficulties in
locating the actual root/shoot interface (Turberville and Hough 1939; Sirén 1950; Strauch
1991; Telewski 1993; Bormann 1965; Kohyama 1980; Villalba and Veblen 1997; Lorimer
et al. 1999; Niklasson 2002). In fact, Parent et al. (2002) suggested that correct age
estimation for suppressed balsam fir saplings required complete stem analysis of the entire
bole. The large number of samples prohibited such an intensive, time consuming procedure. Furthermore, examination of seedling recruitment dynamics was not the goal of this study. Rather, minimum seedling age estimates were suitable in examining relative static age structure among old-growth populations.

Ages of suppressed seedlings were therefore estimated by counting above- and below-ground bud scars (Parent et al. 2000, 2001), as well as ring counts (Kneeshaw and Claveau 2001). For younger, faster-growing seedlings, bud scar counts under a dissecting microscope proved successful. For older and larger seedlings the use of bud scars was problematic because of the “roughening” of the bark. Ages were therefore determined from ring counts on appropriately sanded disks under a dissecting microscope (maximum magnification 40X). In several test cases, the ages determined from ring counts were greater by 10 to 15 years than those determined from bud scales. All ages, therefore, are considered to be minimum ages. For both layered balsam fir and black spruce, the “seedlings” were cut as far back as possible. The age of the white birch seedlings was not determined. Current emergents were identified to species in the field (Jablanczy 1964) and subsequently discarded.

5.3.5 Statistical Analysis

5.3.5.1 Tree Species Composition and Density

Differences in tree species frequency and total basal area among the 13 sample plots were tested by analysis of variance followed by the Tukey’s studentized range test at $P = 0.05$. Homogeneity of variance and normality of residuals were examined using standard residual analysis and normal probability plots coupled with Shapiro–Wilk’s test of
normality. Note that the analysis of variance normality assumptions pertain to the residuals, and not to the raw parameter values (Kéry and Hatfield 2003). All general linear models were carried out using PROC GLM (SAS Institute Inc. 1999a).

5.3.5.2 Tree Diameter Distributions

Non-linear modeling of the reverse-J tree diameter distributions was carried out using the negative exponential function.

\[ \hat{y} = ae^{-bx} \]

Ordinary least squares parameters were estimated using the nonlinear PROC NLIN procedure (SAS Institute Inc. 1999a). In all cases, variances were not homogeneous. Under such conditions, the standard errors associated with the parameter estimates are biased and probability values given with \( t \) or \( F \) values are not valid. However, parameter estimates are unbiased and can therefore can be reported (Zar 1996, p. 325; Neter et al. 1996, p. 20; Montgomery et al. 2001, p. 20), even if confidence limits cannot be assigned to the estimated parameters. Furthermore, the goal was not statistical inference, but rather the use of nonlinear regression and residual analysis to show the degree to which a negative exponential modeled the tree diameter distribution.

Because of the non-additivity of the sum of squares in nonlinear regression, the traditional coefficient of determination (\( R^2 \)) defined as sum squares regression/sum squares total is inappropriate as a measure of model fitness. An alternative measure defined as \( 1 - \) sum squares residual/sum squares total (pseudo-\( R^2 \)) was used as a goodness of fit measure for the non-linear models (Kvålseth 1985; Schabenberger and Pierce 2002, p. 211–213). Note that the pseudo-\( R^2 \) should not be interpreted as the proportion of variability explained by the model.
The 3-parameter Weibull shape parameter (Bailey and Dell 1973) and an index of symmetry (Lorimer and Krug 1983) were used as indices of the reverse-J character of the diameter distributions. The distribution function of a 3-parameter Weibull function is given by

\[ f(x) = \left( \frac{c}{b} \right) \left( \frac{x-a}{b} \right)^{c-1} e^{-\left( \frac{x-a}{b} \right)^c} \]

\( \infty > x \geq a, b > 0, c > 0 \)

The shape of the distribution is dependent on the shape parameter \( c \). If \( c < 1 \), the curve is reverse-J. With \( c = 1 \), the Weibull reduces to the negative exponential distribution. For \( 1 < c < 3.6 \), the density function is modal and positively skewed. A Weibull shape parameter within the range 3.25 to 3.61 approximates a normal distribution. For \( c > 3.6 \), the Weibull is increasingly negatively skewed (Bailey and Dell 1973). Shape parameters < 3.25 indicate progressively more positive skewness, whereas shape parameters > 3.6 indicate progressively more negative skewness (Dell et al. 1984). Shape parameter values calculated as maximum likelihood estimates (SAS Institute Inc. 1999a) have been successfully used by Leblanc and Bélanger (2000) to classify tree diameter distributions for balsam fir–white birch forests in Quebec.

Lorimer and Krug (1983) used an index of symmetry to successfully distinguish among descending monotonic, skewed unimodal, and symmetric unimodal tree diameter distributions in northern hardwood–upland oak forests. The symmetry index \( (I_s) \) is given by

\[ I_s = \frac{(M - X_L)}{(X_{0.95} - X_L)} \]
where \( I_s = \) symmetry index, \( M = \) the mode, \( X_L = \) lower threshold diameter, and \( X_{0.95} = 95^{th} \) percentile of the diameter distribution. In this study, the lower diameter class was 0–2 cm; therefore, the index of symmetry was effectively reduced to the ratio of the mode and the 95\(^{th}\) percentile of the observed diameter distribution. Negative exponential distributions have symmetry values close to 0, while normal distributions have values close to 0.5. Positively skewed distributions have values > 0 and < 0.5, with negatively skewed distributions showing values > 0.5 and ≤ 1.0.

5.3.5.3 Modeling of Tree Diameter Distributions

Sigmoidal semi-logarithmic tree density–diameter and semi-logarithmic tree density-height relationships were assessed by ordinary least squares using both linear and polynomial regression. Data consisted of 2 cm diameter class midpoints and the logarithm of the corresponding density values (Goff and West 1975). Residual analysis and fit statistics were carried out for both linear and polynomial regression. Polynomials were fitted with a backward elimination method (Kleinbaum et al. 1998, p. 302) starting with quartic models in all cases and employing an alpha level of 0.05. The R-square selection method guarantees optimum variable selection (Freund and Littell 2000, p. 108) and was used to confirm the variable subset chosen by the backward method. The validity of the chosen variable subset was carried out by an assessment of the coefficient of determination, the residual mean square, and Mallow's C(p) statistic that compares a specific reduced model to the full model with all parameters included. A variable subset where the minimum C(p) approaches the number of parameters including the intercept + 1 was considered an optimum model (Mallows 1973). Note that, because it is impossible to calculate logarithm values for the value 0, equations were only fitted to dbh data for classes
smaller than the first unoccupied class. Given that the first unoccupied diameter class did not occur until near the end of the diameter class range, this truncation did not prevent appropriate modeling of the sigmoidal diameter relationships.

Multicollinearity is endemic to polynomial regression with the quadratic, cubic, quartic and original variables highly correlated. Detailed multicollinearity diagnostics included variance inflation factors and condition indices (Montgomery et al. 2001, pp. 334-345, Freund and Littell 2000, Ch. 4). Since the goal of polynomial regression was simply prediction and comparison of fit statistics among several data sets, multicollinearity was not considered a problem. Furthermore, all statistical tests for each individual variables were significant ($P < 0.0001$) and standard errors were never large. As well, ordinary least squares methods suited to ill-conditioned data and polynomial models (PROC ORTHOREG) produced identical parameter estimates as given by PROC REG (SAS Institute Inc. 1999a). Regression normality was assessed by both Shapiro-Wilk normality test and normal probability plots. Residual plots were used to judge heteroscedasticity.

5.3.5.4 Regeneration Species Composition and Density

Nonnormal residual errors of discrete seedling count data precluded standard analysis of variance. Furthermore, transformation of the data was not successful in producing normally distributed errors. This is common with data sets having a high frequency of zero values as was the case with seedling frequency at the subplot level. Count data has traditionally been modeled using generalized linear models designed for non-Gaussian probability distributions that belong to the broad family of distributions called the exponential family (McCullagh and Nelder 1989). In particular, count data has historically been handled using a framework that assumes a Poisson distribution.
However, the Poisson distribution is often ill-suited for analysis of count data (White and Bennetts 1996). The Poisson distribution assumes equality of population variance and mean. This assumption is rarely held in biological count data where the variance is often very much larger than the mean. This overdispersion of the data gives a poor fit to the model as the variability of the data exceeds the variability expected under a particular probability distribution. Goodness of fit measures commonly include the deviance and Pearson chi-square statistic, both of which indicate a good model fit when division by the degrees of freedom produces values close to unity.

Overdispersion may be corrected by applying a dispersion factor (deviance/df) producing a quasi-likelihood function, or alternatively, choosing a different probability function more suitable to the data under consideration. A commonly used alternative to the Poisson distribution for count data and the one employed in this study is the negative binomial distribution. This probability distribution naturally accounts for overdispersion in count data by allowing for variance larger than the mean and has proven suitable in the analysis of ecological count data (Young and Young 1998).

Analysis of variance of the nonnormal tree seedling count data was performed by PROC GENMOD using a negative binomial model (log link) for the count data (SAS Institute Inc. 1999a). Preliminary analysis confirmed that the count data was more clustered than would be expected for a Poisson distribution. Both the deviance and Pearson Chi-square statistic were used to examine the model’s goodness of fit. Type 3 analysis is similar to Type III sums of squares in SAS’s GLM procedure and was used to examine both main and interaction effects (SAS Institute Inc. 1999a, Ch. 29).
5.3.5.5 Tree Height–Diameter Relationships

Forked trees and those with broken tops were removed from the data set. Possible height–diameter functions were selected after examination of tree height–tree diameter scatterplots. Given the sigmoidal nature of all height–diameter relationships, four 3-parameter sigmoidal growth curves traditionally used to model tree height–size relationships were selected (Table 5-2). The Chapman–Richards, Weibull, Schnute and modified logistic equations have proven well suited to the modeling of height–size relationships for boreal (Huang et al. 1992, Peng 1999, Peng et al. 2001) and temperate conifers (Zhang 1997).

Table 5-2. Nonlinear predicted tree height–diameter models.

<table>
<thead>
<tr>
<th>Function</th>
<th>Integral form</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapman–Richards</td>
<td>( H_t = 1.3 + a \left( e^{-bD_{bh}} \right)^c )</td>
<td>Richards 1959</td>
</tr>
<tr>
<td>Weibull</td>
<td>( H_t = 1.3 + a \left( 1 - e^{-bD_{bh}^c} \right) )</td>
<td>Yang et al. 1978</td>
</tr>
</tbody>
</table>
| Schnute       | \[
|\text{Ht} &= \left( y_1^b + \left( c^b - y_1^b \right) \left[ 1 - e^{-a(D_{bh}-D_{bh_0})} \right] \right)^{\frac{1}{b}} \\
|\text{where} \ y_1 &= 1.3, \ D_{bh_0} = 0.0, D_{bh_2} = 100.0
| Schnute 1981 |                                                                                     |
| Modified logistic | \( H_t = 1.3 + \frac{a}{1 + b^{-1}D_{bh}^c} \)                                  | Ratkowsky and Reedy 1986 |

Heteroscedasticity of error terms is common in height–diameter relationships of forest trees. Increasing variance is often associated with increases in the size or age of trees. Non-homogeneity of variance was checked by visual examination of scatter plots of studentized residuals against fitted or predicted values. Studentized residuals are simply ordinary residuals divided by their respective standard error. When the model is
appropriate, studentized residuals manifest constant variance, unlike ordinary residuals which have non-independence and intrinsically unequal variances (Bates and Watts 1988, p. 27; Neter et al. 1996, p. 372). For appropriate models, a plot of studentized residuals against the predicted height should show a relatively homogeneous band of data points centred around a mean of zero (Huang et al. 2000).

Studentized residual analysis confirmed heteroscedasticity for all relationships. Weighted least squares nonlinear regression corrected the problem of unequal error variances. A suitable weighing factor was determined by examining residuals after weighted least squares employing weight = 1/dbh^k using k exponent values ranging from 0.5 to 3 (Huang et al. 1992, 2000, Kenefic and Nyland 1999). A weighing factor of 1/√Dbh (k = 0.5) gave the most uniform band of studentized residuals for all models.

Parameters were estimated with PROC NLIN (SAS Institute Inc. 1999a) using the Marquardt iteration method recommended when parameter estimates are highly correlated (SAS Institute Inc. 1999a, p. 2402). The pseudo-R^2 was used as a relative measure of goodness of fit for the different nonlinear equations (Schabenberger and Pierce 2002, p. 211–213).

Appropriate height–diameter models were accepted when the following three criteria were fulfilled: (1) significant asymptotic t-statistics for each parameter, (2) small root mean square error (RMSE) for the overall nonlinear regression, and (3) a relatively homogeneous band of studentized residuals centred on zero across the range of predicted height (Huang et al. 1992; Huang et al. 2000).
5.3.5.6 Tree Diameter/Height–Age Relationships

The relationship between live and dead tree dbh–total age, and live and dead tree height–total age were examined by Spearman rank correlation and non-parametric loess smoothing techniques (Cleveland 1994). As a non-parametric measure of association, Spearman rank correlation may be used to test monotonic linear or curvilinear bivariate relationships when the assumptions of linearity and bivariate normality are not met (Sheskin 2000, p. 864; Quinn and Keough 2002, p. 72–76). Spearman correlation is obtained by ranking of the observations and performing Pearson’s correlation on the ranked data (Conover 1999, p. 315). All correlation analysis were performed with PROC CORR (SAS Institute Inc. 1999b, Ch. 12).

Multiple correlation comparisons run the risk of increasing the probability of Type I error (probability of falsely rejecting the null hypothesis). Adjustment of the probability levels downward to correct for this problem of multiple testing was carried out by using more powerful adjustments to the traditional Bonferroni correction \( a' = \frac{\alpha}{k} \) provided by both Holm 1979 and Hochberg (1988) (Legendre and Legendre (1998), p. 18; Quinn and Keough 2002, p. 50). The latter test is more powerful than Holm’s test, rejecting the null hypothesis more often.

The bivariate dbh–total age scatterplots were examined using non-parametric loess smoothing techniques. Loess smoothing does not assume any particular fit to the bivariate data and is particularly helpful in assessing the suitability of particular linear or nonlinear models. Basically a noise-reduction algorithm, the loess smoother fits linear (or quadratic) fits to specific regions or windows of the data. Weighted least squares are used to compute the line or parabola in each defined window. The joining of the computed Y values for
each X gives a smoothed curve. The data window of interest is determined by the span of
the smoother that ranges from 0 to 1. The higher the span proportion, the greater is the
degree of smoothing. Alternatively, the lower the span proportion, the less the amount of
data assessed in each window, and the less smooth the resulting curve. Loess curves
applied to residual plots confirmed that a span value of 0.5 best captured the bivariate
patterns. Loess smoothing was carried out using Sigmaplot 8 (SPSS Inc. 2002).

All dbh–breast height age and height–breast height age relationships were modeled
with the 3-parameter sigmoidal function given by
\[
\frac{\text{dbh/height}}{1+e^{-\frac{(\text{age}-c)}{b}}} = a
\]

For all species, a weight of 1/age or 1/age\(^2\) (chosen through a process of trial and error)
effectively corrected variance heterogeneity and permitted the assignment of confidence
intervals to the estimated parameters, and significance levels to the model. Error normality
was examined using standard probability plots as well as the Shapiro–Wilks normality test.
Estimation of nonlinear parameters was performed with PROC NLIN (SAS Institute Inc.
1999a) using the Marquardt iteration method.

5.3.5.7 Years to Breast Height

Tests of differences among frequency distributions of age to breast height were
carried out using the Kolmogorov–Smirnov (K–S) test (Conover 1999). Bonferroni
adjustments of 0.05/number of comparisons were applied to keep the Type I error rate
within conservative bounds.

The lognormally distributed data was log transformed to meet both normality and
homoscedasticity assumptions of analysis of variance. Unbalanced analysis of variance
was performed with PROC GLM (SAS Institute Inc. 1999a). Post hoc pairwise comparisons among main effects were carried out using the Tukey–Kramer test that has been shown to hold the Type I experimental error rate at or below the nominal level (Day and Quinn 1989). Homogeneity of variance was tested using both standard residual analysis and Levene’s test.

5.3.5.8 Seedling Size and Age Relationships

Emergents, as well as seedlings with broken tops or those heavily browsed by moose, were excluded from the data used for calculation of allometric relationships. Among the three plots all seedlings of the one species were pooled.

The height–basal diameter relationship was defined by the classic allometric power function.

$$\hat{Y} = aX^b$$

This is common for situations where the ratio between increments in structures of different sizes remains roughly constant across the variable range (Sokal and Rohlf 1995).

All seedling height–age relationships were modeled using the 3-parameter sigmoidal Chapman–Richards equation.

$$\hat{H}_t = 1.3 + a(e^{-b\text{Age}})^c$$

Both the power function and the Chapman–Richards function were used to successfully model the seedling basal diameter–age relationships.

To compare the size and age regressions, covariance analysis of log-transformed allometric power models was carried out for all bivariate relationships (Zar 1996, Ch. 17).
The power function is an intrinsically linearizable function. Therefore the nonlinear power function was expressed in its log–log transformation as:

\[ \log Y = \log a + b \log X \]

The log transformation linearized the regression model, stabilized the error variance and normalized the error terms. An overall test for homogeneity of slopes was carried out using the general linear model \( y = a \times x + a \) (SAS Institute Inc. 1999a, p. 1519). This test considered the interaction between the treatment factor \( x \) and the covariate \( a \). If this test failed to reject, the different regression models were assumed to be parallel and differences among intercepts were tested using the analysis of covariance model \( y = a \times x \). If the null hypothesis of parallelism was rejected, differences among the slopes were determined by a series of contrasts. For parallel models, tests of intercepts were carried out using a Tukey–Kramer all pairwise comparison of least-squares means.

5.4 LITTLE GRAND LAKE

5.4.1 Plot Selection and Layout

Helicopter and ground reconnaissance of the study area was made in the fall of 1997 and summer of 1998. Results of this initial reconnaissance indicated a forest landscape composed of a mosaic of stands of varying age and size structure. In 1997, the entire study area was flown and aerially photographed as part of the Newfoundland provincial forest inventory.

Photo interpretation of 1997 colour aerial photos (scale 1:12,500) of the study area by the Newfoundland and Labrador Forest Service confirmed the landscape-level mosaic
structure. A fine-scale mosaic of stands ranging in age from age class 1 (0–20 years) to age class 7 (120 + years) was identified throughout the study area.

A concerted effort was made to sample the full range of stands throughout the accessible study area. Both limited accessibility and the experimental hypothesis precluded any form of random sampling. Plots were chosen using a stratified sampling approach termed “subjective sampling without preconceived bias” (Mueller-Dombois and Ellenberg 1974). Possible candidate stands within each interpreted age class were identified on the aerial photos and located on the ground. The interpreted stand ages served only as a sampling heuristic and were subsequently refined by stand-level tree age analysis. Due to limitations of accessibility, most of the stands were located near the abandoned road system, although some were located up to 1 km from the road.

Prior to plot layout, a thorough reconnaissance was made of each candidate stand and its surrounding area. Only plots that met the following requirements were chosen: (1) structurally homogeneous stands (sensu Poore 1962) with no history of logging, and (2) adequate distance from road such that no effect of road opening was evident (i.e. windthrow). Care was taken to minimize any overlap of structurally homogeneous (i.e. even-aged) patches. Structurally heterogeneous, reverse-J dbh distribution stands were considered “homogeneous” for purposes of site selection. Excluding the reverse-J and bi-staged stands, 34 of the remaining 36 stands (94%) were either equal to or within one age class of the interpreted age class (Table 5-3).

The first corner of each sample plot was randomly located and the quadrat laid out using hand-held compass and measuring tape. Fifty variable-sized plots were established according to the range of tree densities, with plot size ranging from 100 m² to 750 m².
Table 5-3. Sample plot descriptions, Little Grand Lake.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Elevation (m, asl)</th>
<th>Dimensions (m)</th>
<th>Photo-interpretation</th>
<th>Empirical age class</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>370</td>
<td>25 x 25</td>
<td>bFbS743P</td>
<td>Reverse-J, uneven-aged</td>
</tr>
<tr>
<td>2</td>
<td>410</td>
<td>15 x 15</td>
<td>bF331M</td>
<td>4</td>
</tr>
<tr>
<td>3</td>
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<td>370</td>
<td>20 x 20</td>
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<td>bF662G</td>
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Table 5-3. (Continued)

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<thead>
<tr>
<th>Plot</th>
<th>Elevation (m, asl)</th>
<th>Dimensions (m)</th>
<th>Photo-interpretation b</th>
<th>Empirical age class c</th>
</tr>
</thead>
<tbody>
<tr>
<td>44</td>
<td>360</td>
<td>15 x 15</td>
<td>bFbS222M</td>
<td>Bistaged</td>
</tr>
<tr>
<td>45</td>
<td>355</td>
<td>15 x 15</td>
<td>bFbS222M</td>
<td>Bistaged</td>
</tr>
<tr>
<td>46</td>
<td>420</td>
<td>20 x 20</td>
<td>bFwS110M</td>
<td>2</td>
</tr>
<tr>
<td>47</td>
<td>370</td>
<td>20 x 20</td>
<td>bFbS742M</td>
<td>Reverse-J, uneven-aged</td>
</tr>
<tr>
<td>48</td>
<td>380</td>
<td>25 x 25</td>
<td>bF752M</td>
<td>7 (Bimodal)</td>
</tr>
<tr>
<td>49</td>
<td>365</td>
<td>15 x 15</td>
<td>bF222M</td>
<td>Bistaged</td>
</tr>
<tr>
<td>50</td>
<td>400</td>
<td>20 x 20</td>
<td>bF442M</td>
<td>5</td>
</tr>
<tr>
<td>51</td>
<td>380</td>
<td>20 x 15</td>
<td>bFwS110M</td>
<td>2</td>
</tr>
</tbody>
</table>

a No plot 18
b See Table 5-1.
c Based on actual age data. Age samples taken at ground level.

(Table 5-3). Plot boundaries were roped off and each plot was sectioned into variable-sized strips that facilitated tree measurement. All plots were located at elevations ranging from 320 to 440 m. Plot locations are given in Figure 5-3.

5.4.2 Tree Measurements

All live and dead trees ≥ 1.3 m tall were flagged and numbered. Species, caliper diameter (cm) at breast height (dbh) and mortality (dead or alive) were recorded for each tree, as well as any obvious structural characteristics such as tree forking, broken tops, etc. Tree height was obtained by measuring the length of trees felled for stem analysis and dendrochronological analysis. For all felled trees, tree height (length) was recorded to the nearest 0.1 m using a measuring tape. In modal or even-aged stands, only dominant or codominant trees were sampled. In stands characterized by a complex canopy, trees were sampled at random from strata recognized in the field.
Figure 5-3. Location of Little Grand Lake sample plots. Non-forested areas include peatlands and heathlands, as well as scrub forests not capable of producing $30 \text{ m}^3$ gross merchantable volume ha$^{-1}$ at rotation age.
5.4.3 Tree Age

In what were judged to be even-aged stands of regular stand structure, at least 20 live dominant–codominant trees were selected for age determination. In the more complex, irregularly structured stands, care was taken to sample trees across the range of diameter classes. All sample trees of good form were felled at ground level and a disk removed as close to the ground as possible. Trees with butt rot were not sampled. All tree disks were transported to the lab and stored in a cool, dry environment.

To facilitate age determination, cross-sections containing two radii were cut from each disk using a band saw. All disks were sanded with a hand-held belt sander using 80–120 grit sandpaper. In cases where the trees showed a juvenile core of suppressed growth, ring measurements were facilitated by hand-sanding of the sample using gradations of sandpaper up to 1500 grit. For small tree sections, tree rings were counted under a dissecting microscope with maximum magnification of 40X. The ages of most of the larger trees were determined as part of ring-width measurements conducted on a Windendro tree-ring system (Régent Instruments, Inc., version 6.3b) to a resolution of 0.01mm (Guay et al. 1992). Age was determined for each of the two radii. Despite efforts to fell all trees as close to the ground as possible, the “presence” of missing rings under suppressed conditions and the growth of adventitious roots above the root collar, prevented the determination of actual ages. All age estimates, therefore, must be considered as minimum ages (DesRochers and Gagnon 1997; Gutsell and Johnson 2002; Peters et al. 2002). While acknowledging that choice of age class widths may determine interpretation of static age
class data (Wong and Lertzman 2001), it was considered appropriate to fix the age class width at 10 years.

5.4.4 Regeneration Sampling

Regeneration was sampled in 23 stands across the chronosequence of single-cohort and bimodal stands ranging in age from 61 to 140 years. All sampled stands grew on the better mesic sites, were close-canopied and had entered either the stem exclusion or stand re-initiation phase (Oliver and Larson 1996). Mesic sites were neither xeric nor hydric, and were selected after appraisal of stand species composition, growth characteristics and ground cover. After a random start, subplots of 1 m$^2$ were systematically established throughout each plot at intervals of 5 m. The number of subplots ranged from a low of four in the smallest plots of 100 m$^2$, to a maximum of 25 for the largest plots of 650 m$^2$ (Table 5-4).

Within each subplot all seedlings and saplings ≤1.3 m were sampled. Regeneration in the early germinant stage (few cotyledons and no primary needles) (Jablanczy and Baskerville 1969) were counted and discarded. Because spruce and fir often form adventitious roots above the actual root collar in accumulating feather moss and other organic seedbeds (Cooper 1911; LeBarron 1945; Bakuzis and Hansen 1965; Jablanczy and Baskerville 1969), aging at the soil level is inappropriate (Parent et al. 2000). All seedlings were therefore carefully uprooted to include as much of the root as possible. Care was taken to cut each seedling as close to the root collar as possible. This was accomplished by cutting the seedling above the generally smooth hypocotyl region devoid of bud scars and primary roots (Parent et al. 2000). This was especially important for creeping or J-shaped
Table 5-4. Characteristics of plots sampled for tree regeneration, Little Grand Lake.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Plot size (m$^2$)</th>
<th>Age class (years)</th>
<th>Number of regeneration subplots</th>
</tr>
</thead>
<tbody>
<tr>
<td>19</td>
<td>100</td>
<td>61–70</td>
<td>4</td>
</tr>
<tr>
<td>2</td>
<td>225</td>
<td>71–80</td>
<td>9</td>
</tr>
<tr>
<td>4</td>
<td>225</td>
<td>71–80</td>
<td>9</td>
</tr>
<tr>
<td>10</td>
<td>400</td>
<td>71–80</td>
<td>16</td>
</tr>
<tr>
<td>43</td>
<td>400</td>
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<td>16</td>
</tr>
<tr>
<td>13</td>
<td>400</td>
<td>81–90</td>
<td>16</td>
</tr>
<tr>
<td>16</td>
<td>400</td>
<td>81–90</td>
<td>16</td>
</tr>
<tr>
<td>20</td>
<td>225</td>
<td>81–90</td>
<td>9</td>
</tr>
<tr>
<td>25</td>
<td>400</td>
<td>81–90</td>
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<tr>
<td>21</td>
<td>625</td>
<td>91–100</td>
<td>25</td>
</tr>
<tr>
<td>27</td>
<td>400</td>
<td>91–100</td>
<td>16</td>
</tr>
<tr>
<td>31</td>
<td>625</td>
<td>91–100</td>
<td>25</td>
</tr>
<tr>
<td>32</td>
<td>400</td>
<td>91–100</td>
<td>16</td>
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<tr>
<td>40</td>
<td>400</td>
<td>91–100</td>
<td>16</td>
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<td>400</td>
<td>91–100</td>
<td>16</td>
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<tr>
<td>24</td>
<td>400</td>
<td>101–110</td>
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<tr>
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<td>625</td>
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<td>7</td>
<td>625</td>
<td>111–120</td>
<td>25</td>
</tr>
<tr>
<td>11</td>
<td>450</td>
<td>111–120</td>
<td>18</td>
</tr>
<tr>
<td>29</td>
<td>400</td>
<td>Bimodal (109 years)</td>
<td>16</td>
</tr>
<tr>
<td>37</td>
<td>625</td>
<td>Bimodal (122 years)</td>
<td>25</td>
</tr>
<tr>
<td>12</td>
<td>625</td>
<td>Bimodal (123 years)</td>
<td>25</td>
</tr>
<tr>
<td>48</td>
<td>625</td>
<td>Bimodal (136 years)</td>
<td>25</td>
</tr>
</tbody>
</table>
balsam fir seedlings that can form extensive adventitious rooting within the moist moss layer. For vertical seedlings with a balanced root form, location of the root collar was easier (Kneeshaw and Claveau 2001). All seedlings identified as layers were cut from the parent stem and measured like the seedlings of non-layer origin. All seedlings were harvested in August and September (1999) after the end of the growing season.

All seedlings were bagged by species and plot, transported to the lab and stored in cool, dry conditions prior to measurement for seedling height, basal diameter and age. Total length (0.1 cm) of each seedling was measured using a ruler or tape. Basal diameter (0.1 mm) was measured by calipers at the point where the seedlings were cut. The aging technique used depended on the size of the seedling (Kneeshaw and Claveau 2001). For the younger seedlings, above- and below-ground bud scar counts from the apex to the base of the hypocotyl made under a dissecting microscope (40X) proved successful (Parent et al. 2000, 2001). For older and larger seedlings where the roughening of the bark prevented a clear assessment of bud scars, ages were determined from ring counts made on appropriately sanded basal stem sections under a dissecting microscope.

5.4.5 Classification of Tree Diameter Distributions

Stand structural types among 50 sample stands were distinguished and classified using a multi-step approach. Given their ease of production and classic, historic use in describing stand structure, frequency distributions of tree diameters at breast height (2 cm classes) were used as the measure of stand structure for classification purposes. An initial classification into different structural types was based on the visual examination of the
frequency distributions, combined with an assessment of structural differences based on extensive field observations.

Following this initial "subjective" classification, multivariate cluster and principal component analysis of calculated stand structural indices (based on dbh distributions) were used to complement the first assessment of comparative stand structure. Seven diagnostic indices were calculated for the live tree diameter distribution of each stand: (1) Shannon index of diversity, (2) 3-parameter Weibull distribution shape parameter, (3) skewness, (4) kurtosis, (5) index of symmetry, and two indices of size inequality, (6) the Gini coefficient, and (7) the coefficient of variation. For those stands classified as single-cohort–bimodal in structure, a further grouping was effected using 10-year age classes of sampled dominant–codominant trees.

The Shannon index of diversity has found widespread acceptance as a measure of community or population heterogeneity (Magurran 1988).

\[
H' = - \sum_{i=1}^{s} p_i \ln p_i ,
\]

where

- \(H'\) = Index of species or structural diversity
- \(s\) = Number of species or diameter classes
- \(P_i\) = Proportion of total sample belonging to \(i\)th species or proportion of total trees within a particular diameter class

Based on the random drawing of individuals from an infinite population, the index is a measure of diversity or heterogeneity. The greater the diversity of a species or stand structure, for example, the greater the uncertainty about future sampling, and the greater the value of the Shannon index. Normally, Shannon's index is used with species. However, in
this case, dbh classes were used in an equivalent manner as one would use species. Grouping of the continuous variable dbh into arbitrary 2 cm dbh classes produced proportions that were subsequently used to calculate Shannon indices. Maximum values of the Shannon index occur when the proportions are equal over all tree diameters. Shannon indices have been used to successfully describe stand structural diversity (Neumann and Starlinger 2001; Staudhammer and LeMay 2001; Boucher et al. 2003), although improvements to the traditional use of the Shannon index have been suggested (Zenner and Hibbs 2000; Staudhammer and LeMay 2001; LeMay et al. (Working paper)).

The Weibull distribution has found widespread use in the modeling of tree diameter distributions because of its flexibility in the representation of various shapes (Bailey and Dell 1973). The distribution function of a 3-parameter Weibull function is given by

$$f(x) = \left( \frac{c}{b} \right) \left( \frac{x-a}{b} \right)^{c-1} e^{-\left( \frac{x-a}{b} \right)^c}$$

$$\infty > x \geq a, b > 0, c > 0$$

The shape of the distribution is dependent on the shape parameter $c$. If $c < 1$, the curve is reverse-J. With $c = 1$, the Weibull reduces to the negative exponential distribution. For $1 < c < 3.6$, the density function is modal and positively skewed. A Weibull shape parameter within the range 3.25 to 3.61 approximates a normal distribution. For $c > 3.6$, the Weibull is increasingly negatively skewed (Bailey and Dell 1973). Shape parameters $< 3.25$ indicate progressively more positive skewness, whereas shape parameters $> 3.6$ indicate progressively more negative skewness (Dell et al. 1984). Values of $c$ calculated as maximum likelihood estimates (SAS Institute Inc. 1999a) have been successfully used by...
Leblanc and Bélanger (2000) to classify tree diameter distributions in balsam fir–white birch forests of Quebec.

Skewness (asymmetry) is a measure of the “tailedness” of diameter distributions. Distribution tails may be drawn out in either a positive (skew > 0) or a negative (skew < 0) direction. Symmetrically-shaped bell distributions have skew = 0. Skewness is calculated as the third central moment divided by the cube of the standard deviation.

\[ g_1 = \frac{n \sum (X_i - \bar{X})^3}{(n-1)(n-2)} / s^3 \]

Kurtosis may be considered as a measure of the “peakedness” of the diameter distributions. Kurtosis is considered a more complicated measure of non-normality than skewness. Simply expressed, kurtosis measures the degree to which a distribution is more or less “peaked.” It measures the ratio of the proportions found in the centre and in the tails to those found in the shoulders of any distribution. Kurtosis is calculated as 3 less than the fourth central moment divided by the fourth power of the standard deviation.

\[ g_2 = \frac{\sum (X_i - \bar{X})^4 n(n+1)(n-1) - 3 \left[ \sum (X_i - \bar{X})^3 \right]^2}{(n-2)(n-3)} / s^4 \]

In most cases, values of kurtosis not significantly different from 0 indicate a mesokurtic (normal) distribution. Values of kurtosis significantly < 0 indicate a leptokurtic (peaked) distribution, whereas values > 0 indicate a platykurtic (flat-topped) distribution (Zar 1996, p. 68). In particular, the values of kurtosis were used to assess distribution bimodality. Kurtosis values range from −2 to \( \infty \) with values < −1.2 indicating unquestionable bimodality (Wyszomirski 1992).
Lorimer and Krug (1983) used an index of symmetry to successfully distinguish among descending monotonic, skewed unimodal, and symmetric unimodal tree diameter distributions in northern hardwood–upland oak forests. The symmetry index (Iₘ) is given by

\[ Iₘ = \frac{(M - X_L)}{(X_{0.95} - X_L)} \]

where \( Iₘ \) = symmetry index, \( M \) = the mode, \( X_L \) = lower threshold diameter, and \( X_{0.95} \) = 95ᵗʰ percentile of the diameter distribution. In this study, the lower diameter class was 0–2 cm; therefore, the index of symmetry was effectively reduced to the ratio of the mode and the 95ᵗʰ percentile of the observed diameter distribution. Negative exponential distributions have symmetry values close to 0, while normal distributions have values close to 0.5. Positively skewed distributions have values > 0 and < 0.5, with negatively skewed distributions showing values > 0.5 and ≤ 1.0.

Size inequality (or uneven allocation of mass among individuals in a population) was measured by both the Gini coefficient and the coefficient of variation (Hutchings 1997). The Gini coefficient ranges from a minimum value of zero, when all individuals are equal in size, to a theoretical maximum of one where all but one of the plants are infinitely small with a size value of zero (maximum inequality). The Gini is the mean of the difference between every possible pair of individuals, divided by the mean size.

\[ G = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{2n^2 \bar{X}} \]

The coefficient of variation is given by

5.4.6 Statistical Analysis

5.4.6.1 Multivariate Cluster and Principal Component Analysis

The initial classification of tree diameter distributions was based on a visual comparison of diameter frequencies in conjunction with field observations. Multivariate cluster and principal component analysis (Pielou 1984; Jongman et al. 1997; McGarigal et al. 2000) of the structural indices were used to provide an objective assessment of the initial stand structural classification. Cluster analysis was used to provide a first classification of the heterogeneous array of stand structures into defined groups. Principal component analysis was then used as an ordination technique to explore further possible groupings or gradients of stand size structure. The use of principle component ordination complemented cluster analysis. Clustering provided a discrete, discontinuous analysis of variability, whereas principal component ordination provided better insight into continuous ecological variability.
Cluster analysis was performed using Ward's minimum variance method, an agglomerative hierarchical, space-conserving clustering procedure, using Euclidean distance measure. Given that there are no generally accepted best clustering methods (Manly 2000), it was necessary to test a variety of methods and interpret the results in the light of known stand dynamics. Given that variance among the tested variables differed by two orders of magnitude, all data was adjusted to standard deviate (all variables having mean = 0 and variance = 1). No explicit assumptions about the distributional nature of the variable populations were necessary. Cluster analysis results were presented as a tree diagram or dendrogram that was scaled using Wishart's (1969) objective function converted to a percentage of information remaining. The latter, while similar to a coefficient of determination, is better understood as a measure of the compromise between maximizing the number of groups and maximizing the information retained (McCune and Grace 2002, p. 82).

Principal components were derived from the original data matrix of five structural indices (Weibull, Shannon, index of symmetry, Gini, CV) using the sample correlation matrix. Principal components were assessed by examining the correlation relationship between the variables and the principal components and by plotting the relative positions of the principal component scores in ordination space. Ecological interpretation was conducted on the principal component loadings or correlations between the original variables and the principal components. Eigenvectors are directly proportional to component loadings when the correlation matrix is used in the eigenanalysis. Scores are calculated as the sum of the product of eigenvectors and standardized structural indices for each sampled stand. Scatter plots (ordination plots) of scores given by different principal
components were used to delineate possible groupings of stand diameter distributions. The scores, because they are uncorrelated with each other, and because they represent a measure of the simultaneous structural variance among the stands, were particularly useful in delineating plots of similar size structure. Detrended correspondence analysis was also performed on the structural indices as a precautionary corrective to any arch and compression effects encountered in the principal component analysis (Hill and Gauch 1980).

Prior to multivariate analysis, all bivariate relationships were checked for linearity or near-linearity using scatterplots (Tabachnick and Fidell 2001, p. 77). To improve the bivariate linearity assumptions of the principal component analysis, the kurtosis and the skew indices were dropped from the suite of structural indices. This was necessary to minimize the distorting arch and compression effect characteristic of non-linear data. Logarithmic transformations were applied to the Gini coefficient, the CV and the Weibull shape parameter. All data was standardized to unit variance (mean = 0 and variance = 1). The relative importance of the principal components was determined using scree plots, as well as the broken stick and relative percent variance criterion (McGarigal et al. 2000, pp. 41–45). Ordination plots were presented as biplots, in which the objects (stands) were presented as points and the variables (dbh indices) as vectors. Outlier analysis using a cut-off criterion of 2 standard deviations was conducted for all indices data. All multivariate analysis were carried out using the multivariate analysis software PC-ORD (McCune and Mefford 1999).
5.4.6.2 Tree Species Composition

The tree species frequency data were not normally distributed. Attempts at transformation of the data or normalization of ranked data prior to analysis of variance were unsuccessful in producing normally distributed errors. This is common with data sets that have a high frequency of zero values as was the case with black spruce, white spruce and white birch frequency counts in many plots. Count data has traditionally been modeled using generalized linear models designed for non-Gaussian probability distributions that belong to a broad family of distributions called the exponential family (McCullagh and Nelder 1989). In particular, count data has historically been handled using a framework that assumes a Poisson distribution.

Work has shown, however, that the Poisson distribution is ill-suited to analysis of count data (Littell et al. 2002). The Poisson distribution assumes equality of population variance and mean. This assumption is rarely met in biological count data where the variance is often very much larger than the mean. This overdispersion of the data gives a poor fit to the model as the variability of the data exceeds the variability expected under a particular probability distribution. The negative binomial distribution is a commonly used alternative to the Poisson distribution for count data. It accounts for overdispersion in the Poisson model (Zelterman 1999, p. 30) by allowing for variance larger than the mean and has proven suitable in the analysis of ecological count data (Young and Young 1998). Goodness of fit measures commonly include the deviance and Pearson chi-square statistic, both of which indicate a good model fit when division by the degrees of freedom produces values close to unity.
Analysis of parameter estimates and selected contrast comparisons of the tree frequency data were performed in PROC GENMOD using a negative binomial model with a log link and Wald chi-square statistics (SAS Institute Inc. 1999a). Separate analyses were performed for live and dead trees. Preliminary analysis using the Poisson model confirmed that the frequency data was more clustered than would be expected for a Poisson distribution (overdispersion). The negative binomial distribution successfully accounted for overdispersion in the Poisson model. Deviance was reduced from very high values for the Poisson model (954 for dead trees and 2225 for live trees) to values near unity (1.0576 for dead trees and 1.1698 for live trees) for the negative binomial distribution. The deviance values close to unity confirmed an adequate fit using the negative binomial model.

5.4.6.3 Tree Height–Diameter Relationships

Forked trees and those with broken tops were removed from the data set. Possible height–diameter functions were selected after examination of tree height versus tree diameter at breast height (dbh) scatterplots. Given the sigmoidal nature of the balsam fir height–diameter relationship, four 3-parameter sigmoidal growth curves traditionally used to model tree height–size relationships were selected (Table 5-2). The Chapman–Richards, Weibull, Schnute and modified logistic equations have proven well suited to the modeling of height–size relationships for boreal (Huang et al. 1992; Peng 1999; Peng et al. 2001) and temperate conifers (Zhang 1997).

Heteroscedasticity of error terms is common in height–diameter relationships of forest trees. Increasing variance is often associated with increases in the size or age of trees. Non-homogeneity of variance was checked by visual examination of scatter plots of
studentized residuals against fitted or predicted values. Studentized residuals are simply ordinary residuals divided by their respective standard error. When the model is appropriate, studentized residuals manifest constant variance, unlike ordinary residuals which have non-independence and intrinsically unequal variances (Bates and Watts 1988, p. 27; Neter et al. 1996, p. 372). For appropriate models, a plot of studentized residuals against the predicted height should show a relatively homogeneous band of data points centred on a mean of zero (Huang et al. 2000).

Studentized residual analysis confirmed heteroscedasticity for all relationships. Weighted least squares nonlinear regression corrected the problem of unequal error variances. A suitable weighing factor was determined by examining residuals after weighted least squares employing weight = 1/dbh^k using k exponent values ranging from 0.5 to 3 (Huang et al. 1992, 2000; Kenefic and Nyland 1999). A weighing factor of 1/dbh (k = 1.0) gave the most uniform band of studentized residuals for all models. Parameters were estimated with PROC NLIN (SAS Institute Inc. 1999a) using the Marquardt iteration method recommended when parameter estimates are highly correlated (SAS Institute Inc. 1999a, p. 2402). The pseudo-R^2 was used as a relative measure of goodness of fit for the different nonlinear equations (Schabenberger and Pierce 2002, p. 211–213).

Appropriate height–diameter nonlinear models were accepted when the following three criteria were fulfilled: (1) significant asymptotic t-statistics for each parameter, (2) small root mean square error for the overall nonlinear regression, and (3) a relatively homogeneous band of studentized residuals centred on zero across the range of predicted height (Huang et al. 1992, 2000).
Height–dbh relationships for black spruce and white spruce were modeled with ordinary least squares linear regression. As with the nonlinear model, a weight of 1/dbh was applied to all regressions. Standard tests for error variance and normality were carried out.

5.4.6.4 Tree Height/Diameter–Age Relationships

For all species, distinctions were made between the analysis of single-cohort–bimodal stands and reverse-J–bistaged stands. Relationships between tree height–dbh and tree age (total age and breast height age) were modeled with either 3-parameter sigmoidal nonlinear regression or ordinary least squares linear regression. The nonlinear regression was given by

\[
\frac{\text{height/dbh}}{1+e^{\frac{\text{age}-c}{b}}} = a
\]

Error normality was examined using standard probability plots as well as the Shapiro–Wilk normality test. Heteroscedasticity was examined with standard residual plots. Estimation of nonlinear parameters was performed with PROC NLIN (SAS Institute Inc. 1999a) using the Marquardt iteration method.

In cases where the small sample size precluded model designation, bivariate relationships were examined using Pearson product moment correlation analysis. The assumption of bivariate normality was confirmed using the Shapiro–Wilk test for normality. Analysis was performed using the PROC CORR procedure (SAS Institute Inc. 1999b).
5.4.6.5 Years to Breast Height

Tests of differences among frequency distributions of age to breast height were carried out using the Kolmogorov–Smirnov test (Conover 1999). Bonferroni adjustments of 0.05/number of comparisons were applied to keep the Type I error rate within conservative bounds.

The lognormally distributed data was log transformed to meet both normality and homoscedasticity assumptions of analysis of variance. Unbalanced analysis of variance was performed with the GLM procedure (SAS Institute Inc. 1999a). Post hoc pairwise comparisons among main effects were carried out using the Tukey–Kramer test that has been shown to hold the Type I experimental error rate at or below the nominal level (Day and Quinn 1989). Homogeneity of variance was tested using both standard residual analysis and Levene’s test.

5.4.6.6 Age Range of Stand Types

Differences in the range of stand ages for the four identified stand structures were analyzed using analysis of variance for unbalanced data. All pairwise comparisons were conducted using three methods: (1)Tukey–Kramer method, (2) a simulation based method, and (3) defined contrasts based on one degree of freedom. The Tukey–Kramer method is known to be slightly conservative compared with the simulation method that estimate the precise values of the adjusted \( P \) values. The less balanced the data, the more preferable is the simulation based method over the Tukey–Kramer method (Westfall et al. 1999). In the case of the contrasts, a Bonferroni correction (\( a' = \alpha/k \) ) was applied to all calculated \( P \)
values. The general linear models were carried out using PROC GLM (SAS Institute Inc. 1999a).

5.4.6.7 Seedling Size and Age Relationships

For each plot, seedling height–basal diameter, height–age, and basal diameter–age relationships were all examined using Spearman rank correlations. Multiple correlation comparisons run the risk of increasing the probability of Type I error. Adjustment of the probability levels downward to correct for this problem of multiple testing was carried out using more powerful adjustments to the traditional Bonferroni correction \((a' = \alpha/k)\) provided by both Holm (1979) and Hochberg (1988) (Legendre and Legendre 1998, p. 18; Quinn and Keough 2002, p. 50). The latter test is more powerful than Holm’s test, rejecting the null hypothesis more often.

The pooled bivariate relationship for each species was examined using either the power or exponential nonlinear functions:

\[
\hat{Y} = aX^b \\
\hat{Y} = ae^{bX}
\]

Given the difficulty in meeting the homoscedasticity and normality assumptions for nonlinear regression, no statistical inference was carried out. Least squares parameter estimates, however, are unbiased even under conditions of non-normality and unequal variances (Zar 1996, p. 325; Neter et al. 1996, p. 20; Montgomery et al. 2001, p. 20). Because the error sum of squares and the regression sum of squares do not necessarily sum to the total sum of squares in nonlinear regression, the coefficient of multiple determination is not considered a meaningful statistic for nonlinear regression (Neter et al. 1996, p. 547).
Therefore, both pseudo $R^2$ and the root mean square error were used as goodness-of-fit statistics. Because of the non-additivity of the sum of squares in nonlinear models, the pseudo $R^2$ cannot be interpreted as the proportion of variability explained by the respective model (Schabenberger and Pierce 2002, p. 213). All functions were confirmed by the use of loess smoothing.

5.4.6.8 Self-Thinning Regression Analysis

Empirically derived stand density management diagrams provide a framework by which to understand the dynamics of self-thinning and interspecific competition in even-aged stands. The yield, density and mortality at various stages of stand development are defined for any particular stand. Self-thinning benchmarks include the crown closure line, the lower limit of the zone of imminent competition mortality (ZICM) and the maximum size density line or upper boundary of the zone of imminent competition mortality ($-3/2$ self-thinning line). Prior to crown closure, trees are essentially independent of stand density and grow as isolated individuals. Following crown closure, trees begin to compete with each other, with onset of self-pruning and crown class differentiation. Within the zone of imminent competition mortality, stands undergo active and accelerated self-thinning. The upper limit of the ZICM defines a maximum size–density line near which developing stands experience a reduction in density and an increase in stem diameter as they track relatively parallel to the maximum size–density line (Jack and Long 1996).

Empirical analysis and verification of the $-3/2$ self-thinning rule depends in particular on three components of the statistical methodology used (Weller 1987a; Sackville Hamilton et al. 1995): (1) the criteria used in the selection of the self-thinning
database, (2) mathematical formulation of the self-thinning rule, and (3) the regression algorithm used to fit the thinning line. These three components were dealt with in the following manner:

(1) **Selection of self-thinning stands.** Stem exclusion (*sensu* Oliver and Larson 1996) or self-thinning occurs when stands have assumed maximum site occupancy, full crown closure and maximum biomass at any particular density. Continued stand growth will occur only if tree mortality occurs. Stands in the stage of stand initiation may not be self-thinning because of insufficient height development and hence minimum levels of crowding. Stands in the stand re-initiation and old-growth stages have often surpassed self-thinning as stand density, basal area and leaf-area index decline and density-independent mortality increases. Therefore, successful parameter estimation of a linear log density–log mean tree volume relationship (self-thinning line) is possible only when actively self-thinning stands are examined.

To date, no well accepted *a priori* method of stand selection exists (Bi et al. 2000). To minimize the inherent subjectivity of stand selection, the following criteria of active self-thinning were accepted. Using the criteria established by Bégin et al. (2001), only single-cohort stands having a Weibull distribution shape parameter between 1.5 and 3.6 (Bailey and Dell 1973) and a kurtosis value greater than −1.2 (Wyszomirski 1992) were retained. All bistaged, bimodal and reverse-J stands were excluded from the self-thinning database. All acceptable stands had to lie within the zone of imminent competition mortality (ZICM) on the stand density management diagram developed for mixed balsam fir–black spruce stands in western Newfoundland (Sturtevant et al. 1998). The upper and lower limits of the ZICM were defined as 0.5 and 1.0. Within the ZICM, mortality is
density-dependent and normally defines the zone of active self-thinning (Drew and Flewelling 1977).

The size–density relationship of the bimodal stands as well as a group of post-self-thinning modal stands was also of interest. The old modal stands were identified as those stands showing a noticeable decline in total live basal area with evidence of stand breakup with windthrow and stem breakage. This occurred in stands having reached a height of approximately 15 m and a total age of approximately 90 years. The size–density relationship of these older stands was assessed independently of the size–density relationship of the stands judged to be actively self-thinning.

(2) Mathematical formulation of the self-thinning rule. The self-thinning rule may be expressed in terms of either mean plant volume (or biomass) or stand biomass density (total stand volume). The former is expressed as $w = kd^{3/2}$ (where $w =$ mean plant mass, $k =$ a parameter, $d =$ plant density, and $-3/2 =$ a constant independent of plant species), whereas the latter is expressed as $B = kd^{1/2}$ (where $B =$ total plant mass). While both equations are mathematically equivalent, Weller (1987a) argued that both equations are not statistically equivalent. Because $w = B/N$, density occurs on both sides of equation and can therefore produce what are termed spuriously high correlations between log $w$ and log $N$. Weller (1987a) termed high correlations between log $w$ and log $N$ “unsurprising” given that log $d$ is typically used to calculate log $w$. Other authors, however, support the use of mean volume, rather than total volume, in self-thinning regressions (Prairie and Bird 1989; but see Jackson and Somers 1991; Kenney 1991). Furthermore, averages are not considered the same as derived ratios, and therefore do not suffer the same “spurious correlation” problems (Petraitis 1995).
Prairie and Bird (1989) maintained that the $-3/2 \ w.d$ formulation should be used if the rule is believed to relate to plant size; a fact that is patently obvious when considering competition-induced self-thinning in trees where tree height is considered paramount in driving self-thinning. Thus, individual tree size (expressed as mean volume) is a better indicator of the degree of self-thinning in forest stands than is total stand volume. Furthermore, mean tree volume is used as the standard abscissa value in operationally effective stand density management diagrams (Newton and Weetman 1993, 1994; Farnden 1996; Wilson et al. 1999). In this study, I accept the conclusion of Bégin et al. (2001) who accepted the use of mean volume because of its wide use, and its expression of the original self-thinning formulation, thus ensuring effective comparison with extant studies. Balsam fir tree volumes were estimated using the equations provided by Warren and Meades (1986).

(3) Regression algorithm. Central to the debate surrounding the universality of the self-thinning rule has been the precision of the log–log slope estimation. Of critical importance to the debate has been the comparison of the empirically calculated regression slope with the theoretical slope of $-1.5$ first confirmed by Yoda et al. (1963). However, the choice of regression algorithm to define the straight line regression has confounded the debate because different algorithms will produce different slope estimates, depending on the error structure of the data and the correlation between the bivariate data.

It is well known that ordinary least squares are unsuitable for bivariate data in which both $X$ and $Y$ variables are measured with error (as is the case with the log volume–log density relationship) (Laws and Archie 1981; Jensen 1986; LaBarbera 1989; Sokal and Rohlf 1995, p. 541–549; Webster 1997; Draper and Smith 1998, p. 89–96; Montgomery et
Linear regressions in which both variables show random variation are termed Model II regressions. These are opposed to Model I linear regressions in which the independent variable $X$ is measured without error. When both variables have non-zero error variance, neither can be clearly designated as the dependent or independent variable. In this case, a least squares regression of $X$ on $Y$ yields different parameter estimates from the regression of $Y$ on $X$. In the case of random error in $X$, the slope estimate is biased, tending toward zero. The lower the correlation between the bivariate data the more will the slope estimates differ among the various algorithms.

In the development of self-thinning theory, ordinary least squares (OLS) regression was used to fit the log size–log density data (White and Harper 1970; Ford 1975; Sprugel 1984). Mohler et al. (1978) recognized the unsuitability of ordinary least squares and recommended the use of principal component analysis for parameter estimation, a recommendation taken up by a number of researchers (Lonsdale and Watkinson 1983; Weller 1987a; Bégin et al. 2001). Reduced major axis (RMA) has also been used for modeling random bivariate self-thinning data (Zeide 1991, Osawa and Allen 1993; Wilson et al. 1999; Solomon and Zhang 2002). Unlike least squares analysis, both principal components (also called major axis (MA)) and reduced major axis regressions assume an associated error term for both variables.

McArdle (1988) compared the use of OLS, MA, and RMA in bivariate analysis. Reduced major axis was found to be more efficient and less biased than the MA regression. Sackville Hamilton et al. (1995) made similar conclusions in a comparison of the three regression algorithms. Ordinary least squares consistently underestimated the slope of the log size–log density relationship, whereas PCA or MA consistently overestimated the slope.
estimates. Reduced major axis was judged to be approximately correct for the $-3/2$
formulation. Differences among the three algorithms decrease as the variable correlation
increases, assuming equality at $r = 1.0$. The relative superiority of RMA over MA for the
modeling of Model II functional regressions has been suggested by a number of authors
(Ricker 1973, 1984; Rayner 1985; Leduc 1987). Draper and Smith (1998) also
recommended the ad hoc use of RMA (also called geometric mean regression) when $X$ and
$Y$ variables are subject to random variation. An alternate approach to Model II regression
has been provided by Legendre and Legendre (1998) (p. 511–512) who proposed a ranged
major axis regression.

All self-thinning bivariate relationships were analyzed using Model II simple linear
regression using the following methods: standard major axis (SMA), ordinary least squares
(OLS) and ranged major axis (RMA) (Legendre 2001). Note that the designation “standard
major axis” is equivalent to “reduced major axis” commonly found in the literature
permutations were used to test for significance for all regression models except SMA which
cannot be formally tested. In practice, this poses no problem given that the null hypothesis
that the population correlation coefficient equals zero is essentially the same (McArdle
1988; Quinn and Keough 2002, p. 102). For SMA, the confidence interval of slope
followed Jolicoeur and Mosimann (1968) and McArdle (1988).

Each of the log–log linear regressions of mean tree volume, quadratic mean
diameter (qmd) and tree height versus tree density were compared for two groupings: (1) all
single-cohort stands 60 to 90 years old, and (2) all single-cohort stands $> 90$ years plus all
bimodal stands. Stands 60 to 90 years of age were judged to be undergoing active self-
thinning, whereas the older stands (> 90 years) were judged increasingly influenced by
density-independent mortality processes. The log qmd–log density relationships of the two
stand types were also compared.

All linear regressions were fit by ordinary least squares. Normality and variance
assumptions were tested by standard residual and statistical analysis. For each regression
couplet of interest, heterogeneity of slopes was assessed by a covariance analysis of both
the treatment (equation) and the X covariate (tree density) (Littell et al. 2002). A
significant interaction (equation–tree density) confirmed heterogeneity of slopes and a
separation of the stands into two distinct groupings (60 to 90 years and > 90 years including
bimodal).

5.4.6.9 Basal Area Trends

A locally weighted regression (loess) was used to model basal area trends (as well
as balsam fir height–total age relationships) for both live and dead trees in a
chronosequence of single-cohort and bimodal stands. Loess is a non-parametric, extremely
flexible, model-free technique especially suited to smoothing bivariate data for which
neither a trend nor a specific parametric regression model is obvious (Trexler and Travis
1993; Cleveland 1994; Montgomery et al. 2001, p. 239) These curves do not provide an
analytic expression for the functional form of a regression relationship and thus are
particularly suited for trend analysis of bivariate data for which a parametric function is
either not obvious or does not meet parametric OLS regression assumptions.

Loess produces smoothed values for a chosen neighbourhood of values along the X
scale. This neighbourhood is defined as the span or smoothing parameter, the value of
which lies between 0 and 1. The higher the span value, the greater the degree of
smoothing. The best smoothing parameter is considered one that makes the curve as
smooth as possible without distorting the pattern given by the data. Choice of the proper
smoothing parameter was determined by plotting $Y$ residuals against $X$ and applying a loess
smoothing to the residuals. Loess analysis of residuals should produce a near horizontal
line if the variation in the data has been adequately explained by the original model
(Cleveland 1994, p. 173). Based on loess analysis of the residual plots, a span of 0.5 was
chosen as the value that provided a smoothing curve that best reflected the pattern in the
data. Loess smoothing was performed using Sigmaplot 8.0 (SPSS Inc. 2002), which uses a
tri-cube weighting function as the default. In all cases, the influence of any outliers was
minimized and the weighted least-squares procedure used a simple linear regression model.

The trend of the relative proportion of live and dead basal area across the
chronosequence was examined using the Cochran–Armitage test. The Cochran–Armitage
test is appropriate when the contingency table has one variable of two levels (mortality) and
the other variable is ordinal (age classes of modal stands). (Zar 1996, p. 562; SAS Institute
Inc. 1999a, p. 1302, 1349).

5.4.6.10 Seedling–Stand Relationships

Relationships between stand and seedling bank attributes were examined using
Spearman rank correlation coefficients. Multiple correlation comparisons run the risk of
increasing the probability of Type I error. Adjustment of the probability levels downward
to correct for this problem of multiple testing was carried out using more powerful
adjustments to the traditional Bonferroni correction ($a' = \alpha / k$) provided by both Holm
(1979) and Hochberg (1988) (Legendre and Legendre 1998, p. 18; Quinn and Keough 2002, p. 50). The latter test is more powerful than Holm’s test, rejecting the null hypothesis more often.

5.4.7 Stand Density Management Diagram

Mean tree volume–stand density data from all single-cohort, bimodal and bistaged stands were plotted unto the stand density management diagram developed by Sturtevant et al. (1998) for mixed balsam fir–black spruce stands in western Newfoundland.

5.4.8 Stand and Regeneration Chronosequence Development

Five measures of asymmetry and size inequality were used to describe the age, height and diameter development of both stands and the seedling bank regeneration: (1) Shannon index of diversity (stands only), (2) Weibull shape parameter (regeneration only), (3) skewness, (4) Gini coefficient, and (5) coefficient of variation. Each index was described in section 5.4.5. (Classification of tree diameter distributions).

5.4.9 Determination of Site Index

A comparative measure of stand productivity was given by the site index (dominant stand height at breast height age of 50 years). In 44 of the 50 sampled plots, one to ten dominant trees were sampled for stem analysis and provided age at breast height. Six of the youngest stands (6, 8, 15, 38, 39, and 51) were not sampled for age at breast height. Mean tree height and breast height age of each stand were used to estimate site index (Husch et al. 2003, p. 195). The traditional use of breast height age is especially significant
for the determination of site index of shade-tolerant species such as spruce and fir that can experience variable growth patterns associated with suppression.

Site indices were estimated from western Newfoundland site index equations (Page 1968), as well as site index equations provided for central Newfoundland (Newton 1992) and the balsam fir forests of Quebec (Pothier and Savard 1998). Each site index methodology possessed its own unique limitations with respect to the sampled data set. Page’s (1968) site index curves for the combined regions of western and northern Newfoundland do not distinguish among species, but combine balsam fir, black spruce and white spruce. Newton’s (1992) curves are designed specifically for upland pure black spruce and mixed black spruce–balsam fir stands in central Newfoundland and Pothier and Savard’s (1998) curves use a reference age at 1 m above ground (not 1.3 m), and address forests growing under different climatic conditions, of which wind velocities are probably of significance in determining maximum tree heights (Page and van Nostrand 1971).

As site index varies according to species (Husch et al. 2003), an attempt was made to use species-specific curves where feasible. The majority of sampled trees, however, were balsam fir, and furthermore, Page’s (1968) curves do not distinguish among tree species. Despite the fact that the concept of site index is not well suited to uneven-aged stands, site index values were estimated for the reverse-J stands, if only as a relative measure of site quality among all plots.

Differences in site index were analyzed using one-way and two-way unbalanced analysis of variance followed by the Tukey–Kramer multiple comparison method. The main problems associated with analysis of variance of unbalanced data occurs not with one-way analysis of variance, but rather with a two-way or greater classification of data (Littell
et al. 2002, Ch. 5). A main question is the proper weighing of the respective means, given that the means are determined with different precision, thus making interpretation difficult (Quinn and Keough 2002). In all cases, Type III sum of squares was used for the unbalanced, two-factor analysis of variance (Shaw and Mitchell-Olds 1993; Quinn and Keough 2002, p. 242–244), thus attaching equal weight to all respective means. Type III sum of squares for each main effect is the sum of the squared differences of unweighted means, rather than means that depend on sample size. Note, however, that the power of the Type III sum of squares can be very low, especially if sample sizes for some cells are small compared to the sample sizes for other cells (Littell et al. 2002, p. 146).

5.4.10 Little Grand Lake and Main River Landscape Analysis

Production of GIS data layers for both study areas was carried out by the data acquisition and mapping division of the Newfoundland and Labrador Forest Service. The forest inventory mapping process involved four main steps: (1) acquisition of colour aerial photography, (2) photo-interpretation, (3) orthorectification of interpreted photography, and (4) construction of the GIS database layers (Strickland 2002).

Description of the landscape-level forest structure was based on the interpretation of 1:12,500 true-colour aerial photographs of both study areas. The Main River and Little Grand Lake study areas were photographed in 1993–1994 and 1997, respectively, as part of the regular forest inventory activity of the Newfoundland and Labrador Forest Service. Photographic stereo pairs were examined by experienced Forest Service photo-interpreters. Among the usual landscape and cultural features, two main types of forest cover were identified: productive commercial forest (forest lands capable of producing 30 m³ gross
merchantable volume ha\(^{-1}\) at rotation age), and non-commercial forest that usually consists of both hardwood and softwood scrub, and slow-growing forests on sites of low site index. Productive stands were given a complete forest type designation that included species composition, age class, height class, crown density class, and site quality class (Table 5-1). Success of interpretation was checked on an ad hoc basis by field checks of the height and age of interpreted stands.

To facilitate the digitization process, all features and stands were delineated on the stereo pairs using line patterns and pen colours. All aerial photos were orthorectified to remove camera tilt and terrain variability. Aerial camera parameters, ground control points, and a digital elevation model were used in the orthorectification process to produce planimetrically-correct orthophotos where all photo features corresponded to true ground position. All interpreted photographs were manually digitized and the data files used to construct the GIS database layers that were used for subsequent analysis and map production. Quality control checks were maintained throughout the entire map production process.

Study areas were interpreted at a resolution of approximately 0.5 ha. Landscape-level analysis were made of the following parameters: (1) land type, (2) tree species composition, (3) stand age class, (4) stand height class, (5) stand density class, and (6) stand site quality.

Before analysis of the landscape-level data, several refinements to the database were made. Except for landtype calculations, all calculations excluded regenerating cutovers so that percent calculations were based on total area of primary, unlogged forest. These
included 209 ha of age class 1 stands in the Little Grand Lake area, and 91 ha of age class 2 and 3 stands in the Main River study area.

Polygons designated as W (windfall) and NSR (not sufficiently restocked) were converted to age class 1 (0–20 years). These “W” polygons usually consisted of recently insect-killed, windthrown stands (< 25% crown density) in which no regeneration could be discerned by the photo interpreter. Regeneration was often present on these sites but height growth was often retarded by recurrent moose browsing. For the Main River maps, all stands of age class 5 and 6 were converted to age class 7. When forest cover type maps were initially produced for the Main River area, the old-growth nature of the forests was not generally appreciated. Subsequent field checks of a sample of stands of age class 5 and 6 (including actual stand reconstruction plots) confirmed that these stands were indeed age class 7.
CHAPTER 6
MAIN RIVER: STAND STRUCTURE IN QUASI-EQUILIBRIUM OLD-GROWTH STANDS

6.1 TREE SPECIES COMPOSITION AND DENSITY

Balsam fir, black spruce, white spruce and white birch occurred in the sampled stands. Balsam fir dominated all plots (Tukey studentized range test, $P = 0.05$), comprising 73% of the total live tree density of 4,165 stems ha$^{-1}$ (Figure 6-1, Table 6-1). Black spruce, white spruce and white birch made up 15%, 10%, and 2%, respectively, of the total tree density. Average tree densities (standard error of the mean = SEM) for balsam fir, black spruce, white spruce and white birch were 3,054.4 (203.9), 618.2 (140.5), 428 (101.3), and 64 (15.7) stems ha$^{-1}$, respectively.

Among black spruce, white spruce and white birch, density values were variable with black spruce $>$ white birch (Tukey's test, $P = 0.05$). White spruce was not significantly different from either black spruce or white birch, although average values were of the order black spruce $>$ white spruce $>$ white birch. No significant differences in tree density among the thirteen plots were noted ($P = 0.8627$). It should be noted, of course, that the relative frequencies are a function of site variability and simply describe the average trends in the sampled "zonal" plots.
Figure 6-1. Box plots showing live tree density by species for 13 Main River stands. Box limits represent the 25th and 75th percentiles of the data. Error bars represent the 10th and 90th percentiles. Mean and median density are given by the dashed and solid line, respectively.

Table 6-1. Live species composition of 13 Main River stands.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Balsam fir Trees ha⁻¹</th>
<th>Black spruce</th>
<th>White spruce</th>
<th>White birch</th>
<th>Total Trees ha⁻¹</th>
<th>Balsam fir</th>
<th>Black spruce</th>
<th>White spruce</th>
<th>White birch</th>
</tr>
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<td>248</td>
<td>28</td>
<td>3736</td>
<td>76</td>
<td>16.6</td>
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<td>1600</td>
<td>4</td>
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<td>33.1</td>
<td>0.08</td>
<td>1</td>
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<td>6</td>
<td>20.4</td>
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<td>26.5</td>
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<td>232</td>
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<td>73.3</td>
<td>14.8</td>
<td>10.8</td>
<td>1.5</td>
</tr>
<tr>
<td>sᵃ</td>
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<td>506.6</td>
<td>365.1</td>
<td>56.4</td>
<td>763.6</td>
<td>6.9</td>
<td>11.3</td>
<td>9.2</td>
<td>1.5</td>
</tr>
</tbody>
</table>

ᵃ s = Standard deviation.
6.2 TOTAL BASAL AREA

Total live tree basal area ranged from 30.2 to 42.7 m$^2$ ha$^{-1}$ with an average of 35.8 m$^2$ ha$^{-1}$ (SEM = 1.0 m$^2$ ha$^{-1}$) (Table 6-2).

Table 6-2. Basal area composition by species for 13 Main River stands.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Balsam fir</th>
<th>Black spruce</th>
<th>White spruce</th>
<th>White birch</th>
<th>Total</th>
<th>Balsam fir</th>
<th>Black spruce</th>
<th>White spruce</th>
<th>White birch</th>
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<td>8.7</td>
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<td>23.8</td>
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<td>0.1</td>
<td>1.0</td>
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<td>31.2</td>
<td>1.1</td>
<td>2.8</td>
<td>3.0</td>
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<td>3.0</td>
<td>7.3</td>
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<td>0.8</td>
<td>1.5</td>
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<td>4.3</td>
<td>1.5</td>
<td>1.2</td>
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<td>76.9</td>
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<td>76.9</td>
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<tr>
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<td>3.8</td>
<td>1.9</td>
<td>35.8</td>
<td>75.7</td>
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<tr>
<td>$s^a$</td>
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<td>2.9</td>
<td>3.2</td>
<td>1.1</td>
<td>3.7</td>
<td>4.8</td>
<td>8.9</td>
<td>7.9</td>
<td>3.0</td>
</tr>
</tbody>
</table>

$s^a$ = Standard deviation.

Balsam fir dominated the basal area in all plots (Tukey test, $P = 0.05$) (Figure 6-2).

On average, balsam fir made up 76% of the live basal area with black spruce, white spruce and white birch comprising 9%, 10% and 5% of the total basal area, respectively. No significance differences were noted among the total basal area for black spruce, white spruce and white birch (Tukey test, $P = 0.05$). Total basal area values did not differ significantly among plots ($P = 0.9580$).
Figure 6-2. Box plots showing live basal area by species for 13 Main River stands. Box limits represent the 25th and 75th percentiles of the data. Error bars represent the 10th and 90th percentiles. Mean and median values are given by the dashed and solid line, respectively.

All stands exhibited similar frequency distributions of basal area by 2 cm tree diameter classes (Figure 6-3). Generally speaking, higher black spruce basal areas were associated with lower white spruce basal areas, and vice versa. This was no doubt due to the site variability exhibited across the range of sampled stands. In general, black spruce comprised a greater percentage of the spruce basal area on poorer sites, whereas white spruce made up the greater percentage of spruce basal area on the better sites. All three conifers had basal area accumulations across the full range of tree diameters. White birch basal area was noticeably concentrated on trees in the 20 to 30 cm dbh range (Figure 6-4).
Figure 6-3. Stand basal area by 2 cm dbh classes for 13 Main River stands.
A sigmoidal relationship defined the cumulative basal area distribution (Figure 6-5). The greatest increase in basal area accumulation occurred with trees in the diameter range of approximately 15 to 36 cm, after which cumulative increases in basal area began to level off.
Figure 6-5. Cumulative total basal area for the Main River study stands. Data are means ± SEM, $n = 13$ plots.

Almost half of the total stand basal area (48.6%, SEM = 1.7%) was concentrated on trees of approximately mid-diameter range (18 to 32 cm dbh). This was evident in the basal area distributions, many of which exhibited a “step-up” in basal area accumulation around tree diameters of 18 to 20 cm. Trees ≤25 cm dbh (approximate mid-diameter range) accounted for an average of 57.1% (SEM = 3.2%) of the standing basal area in each stand. Of note is the 11.1% (SEM = 0.6%) of the total basal area attributable to the small trees ≤10 cm dbh.
6.3 DIAMETER DISTRIBUTION

Tree diameters of each plot followed a classic reverse-J distribution (Figure 6-6). The exponential character of the diameter distributions was confirmed by a 3-parameter Weibull shape parameter approximately equal to 1 (1.0073, SEM = 0.0073) (Bailey and Dell 1973) and an index of symmetry approximately equal to 0 (0.0404, SEM = 0.0045) (Lorimer and Krug 1983). Diameters ranged from 0.1 to 51.0 cm. The vast majority of trees occurred in the smaller diameter classes (Figure 6-7). For example, 70% to 86% of the total number of trees in all plots were ≤10 cm dbh. By contrast, trees ≤10 cm dbh accounted for only 8% to 15% of the total basal area.

All diameter distributions of the 13 sampled plots were pooled for analysis. Similar reverse-J diameter distributions occurred for balsam fir, black spruce and white spruce (Figure 6-8). The exception was white birch. Except for a spike of small trees in the 0 to 2 cm dbh class (approximately 15 trees ha⁻¹), white birch had a modal dbh distribution centred on the mid-sized and large diameter trees.

The composite dbh distribution curve failed to show a systematic monotonic decline normally associated with negative exponential functions. Of particular interest was a “bulging” or “flattening out” of the composite curve at diameters between 14 and 26 cm (Figure 6-8). The monotonic decrease in diameter frequency was not consistent, but was interrupted in the noted diameter range, after which the diameter distribution continued a monotonic decline. Such a physiognomy was characteristic for all the individual conifer distributions as well, with white birch a notable exception.
Figure 6-6. Live tree diameter distribution by species for 13 Main River stands. $n =$ number of sample trees, $I_s =$ index of symmetry (Lorimer and Krug 1983), $c =$ Weibull shape parameter.
Figure 6-7. Cumulative tree dbh distribution for pooled species, Main River. Values at midpoint of 2 cm dbh classes are means ± SEM, $n = 13$ plots.
Figure 6-8. Live tree dbh distribution for all pooled species and for each individual species, Main River. Note the different ordinate scales. Values are means ± SEM, n = number of trees.
The lack of a regular monotonic decline in diameter distribution was demonstrated by both residual analysis of the fitted negative exponential function \( Y = ae^{-bx} \) (1) and the semi-logarithmic presentation of the diameter distribution. Equation (1) has traditionally been employed to model the diameter distributions of theoretically balanced uneven-aged stands (Meyer 1952; Meyer et al. 1961). The inadequacy of the negative exponential model for the current data was evident, however, both for the fitted model of the mean diameter distribution and for the residual analysis of the modeled diameter distribution for each individual plot (Figure 6-9).

![Figure 6-9. Modeling and residual analysis of pooled live tree dbh frequency, Main River. (A) Dbh frequency fitted with negative exponential function \( Y = ae^{-bx} \), \( n = 13 \) plots, 13,535 trees. (B) Pattern of residuals for negative exponential model of live tree dbh frequency. Values are means ± SEM.](image)

Despite the high pseudo-\( R^2 \) values for each negative exponential modal and a pseudo-\( R^2 \) value of 0.9841 for the combined data set, it was obvious that equation (1) did not adequately fit the data (Table 6-3).
Table 6-3. Parameters and regression statistics for the negative exponential modeling of the diameter (dbh) distribution for 13 Main River stands.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Parameters</th>
<th>Pseudo-R²</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
</tr>
<tr>
<td>1</td>
<td>1485.99</td>
<td>0.2179</td>
</tr>
<tr>
<td>2</td>
<td>2000.03</td>
<td>0.2232</td>
</tr>
<tr>
<td>3</td>
<td>1737.37</td>
<td>0.2496</td>
</tr>
<tr>
<td>4</td>
<td>1707.66</td>
<td>0.2103</td>
</tr>
<tr>
<td>5</td>
<td>880.45</td>
<td>0.1272</td>
</tr>
<tr>
<td>6</td>
<td>2614.37</td>
<td>0.2597</td>
</tr>
<tr>
<td>7</td>
<td>2530.02</td>
<td>0.3206</td>
</tr>
<tr>
<td>8</td>
<td>1161.71</td>
<td>0.2811</td>
</tr>
<tr>
<td>9</td>
<td>2347.06</td>
<td>0.2297</td>
</tr>
<tr>
<td>10</td>
<td>1204.02</td>
<td>0.1974</td>
</tr>
<tr>
<td>11</td>
<td>1802.68</td>
<td>0.2222</td>
</tr>
<tr>
<td>12</td>
<td>2857.40</td>
<td>0.4064</td>
</tr>
<tr>
<td>13</td>
<td>1839.08</td>
<td>0.2698</td>
</tr>
<tr>
<td>All plots</td>
<td>1797.82</td>
<td>0.2386</td>
</tr>
</tbody>
</table>

Obvious was the underestimation of the diameter frequency in the mid-diameter range. A greater proportion of trees occurred in the mid-diameter range than were theoretically described by the negative exponential model. A semi-logarithmic presentation of the diameter data for all species produced a well-defined rotated sigmoidal curve (Figure 6-10).

A monotonic or regular decline in the frequency of trees of the smallest and largest dbh classes contrasted with the flattening out of the curve for trees of mid-sized diameter range. Rotated sigmoid curves indicated that the diameter distributions were not of the classic (balanced) reverse-J type. Semi-logarithmic representation of a regular monotonic decline in dbh frequency normally produces a straight line of negative slope.

All rotated sigmoidal curves were best modeled with either 3rd or 4th degree polynomials (Table 6-4). Linear regression fits have been included by way of comparison.
Figure 6-10. Semi-logarithmic representation of tree diameter (dbh) frequency distribution for 13 Main River stands. Diameter class midpoint values are means ± SEM, $n = 13$ plots, 13,535 trees.
Table 6-4. Model parameters (standard error) and fit statistics for linear and polynomial models of 13 Main River semi-logarithmic tree diameter (dbh) frequencies.

**Linear regression**

<table>
<thead>
<tr>
<th>Plot</th>
<th>Intercept</th>
<th>Slope</th>
<th>$R^2$</th>
<th>RMSE*</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>2.7822 (0.1063)</td>
<td>-0.04515 (0.0046)</td>
<td>0.8424</td>
<td>0.2374</td>
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<tr>
<td>2</td>
<td>3.08035 (0.0965)</td>
<td>-0.06042 (0.0044)</td>
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<td>0.2100</td>
</tr>
<tr>
<td>3</td>
<td>2.78554 (0.1118)</td>
<td>-0.04656 (0.0046)</td>
<td>0.8429</td>
<td>0.2560</td>
</tr>
<tr>
<td>4</td>
<td>2.82061 (0.1005)</td>
<td>-0.04426 (0.0040)</td>
<td>0.8621</td>
<td>0.2356</td>
</tr>
<tr>
<td>5</td>
<td>2.79754 (0.0732)</td>
<td>-0.04171 (0.0037)</td>
<td>0.8927</td>
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</tr>
<tr>
<td>6</td>
<td>3.00138 (0.1118)</td>
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</tr>
<tr>
<td>7</td>
<td>2.88986 (0.0918)</td>
<td>-0.04959 (0.0038)</td>
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<td>0.2373</td>
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<tr>
<td>8</td>
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<td>-0.04474 (0.0050)</td>
<td>0.8621</td>
<td>0.2356</td>
</tr>
<tr>
<td>9</td>
<td>2.83393 (0.1411)</td>
<td>-0.04719 (0.0058)</td>
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<td>0.3230</td>
</tr>
<tr>
<td>10</td>
<td>2.69288 (0.1046)</td>
<td>-0.04248 (0.0039)</td>
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<td>0.2506</td>
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<tr>
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<td>0.2847</td>
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<tr>
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<td>-0.05194 (0.0045)</td>
<td>0.8873</td>
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<td>13</td>
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<td>-0.04106 (0.0038)</td>
<td>0.9026</td>
<td>0.2029</td>
</tr>
<tr>
<td>All plots</td>
<td>3.03984 (0.0953)</td>
<td>-0.05969 (0.0032)</td>
<td>0.9365</td>
<td>0.2427</td>
</tr>
</tbody>
</table>

**Polynomial regression**

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<th>$\text{Dbh}^2$</th>
<th>$\text{Dbh}^3$</th>
<th>$\text{Dbh}^4$</th>
<th>$R^2$</th>
<th>RMSE*</th>
</tr>
</thead>
<tbody>
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<td>3.22440 (0.0934)</td>
<td>-0.12429 (0.0122)</td>
<td>-0.00021922</td>
<td>-0.00000462</td>
<td>0.9615</td>
<td>0.1244</td>
<td></td>
</tr>
<tr>
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<td>3.46992 (0.0999)</td>
<td>-0.19432 (0.0228)</td>
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<td>(0.00000663)</td>
<td>0.9810</td>
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<tr>
<td>3</td>
<td>3.43343 (0.1383)</td>
<td>-0.21145 (0.0286)</td>
<td>0.00912</td>
<td>0.00013746</td>
<td>(0.0000242)</td>
<td>0.9475</td>
<td>0.1565</td>
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<tr>
<td>4</td>
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<td>-0.18434 (0.0262)</td>
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<td>-0.00010191</td>
<td>(0.000207)</td>
<td>0.9470</td>
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<tr>
<td>5</td>
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<td>-0.09316 (0.0139)</td>
<td>-0.0001869</td>
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<td>0.9534</td>
<td>0.1543</td>
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<td>-0.19269 (0.0203)</td>
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<tr>
<td>8</td>
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<td>(0.0000434)</td>
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<td>9</td>
<td>3.63491 (0.1563)</td>
<td>-0.21679 (0.0276)</td>
<td>0.00668</td>
<td>-0.00000188</td>
<td>(0.00000354)</td>
<td>0.9313</td>
<td>0.1890</td>
</tr>
<tr>
<td>10</td>
<td>3.28777 (0.1319)</td>
<td>-0.18584 (0.0249)</td>
<td>0.00742</td>
<td>-0.00010406</td>
<td>(0.0000180)</td>
<td>0.9460</td>
<td>0.1565</td>
</tr>
<tr>
<td>11</td>
<td>3.41655 (0.1324)</td>
<td>-0.15749 (0.0203)</td>
<td>-0.0001462</td>
<td>-0.00001041</td>
<td>(0.0000721)</td>
<td>0.9413</td>
<td>0.1622</td>
</tr>
<tr>
<td>12</td>
<td>3.42046 (0.0983)</td>
<td>-0.21129 (0.0225)</td>
<td>0.01020</td>
<td>-0.00017590</td>
<td>(0.0000238)</td>
<td>0.9759</td>
<td>0.1055</td>
</tr>
<tr>
<td>13</td>
<td>3.22290 (0.1197)</td>
<td>-0.13464 (0.02077)</td>
<td>0.00398</td>
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<td>0.1483</td>
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<tr>
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<td>-0.00034672</td>
<td>(0.00000505)</td>
<td>0.9934</td>
<td>0.0837</td>
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</table>

*RMSE = root mean square error.*
Both the R-square and backward elimination variable selection methods produced the same variable subset for each of the polynomial models. Most relationships were best expressed by a cubic polynomial, with the remaining models including a quartic term. The mean plot relationship was modeled by a significant \( P < 0.0001 \) quartic polynomial having an \( R^2 \) of 0.9934 and a root mean square error of 0.0837. In all cases, residual analysis confirmed the inadequacy of the linear models and the need for higher power polynomial models (Figure 6-11). The curvilinear residual pattern of the linear model was corrected for the most part in the residual pattern of the polynomial model. In contrast to the polynomials, the explanatory power of all linear regressions was reduced by 5% to 16% (mean = 9.1%).

6.4 TREE HEIGHT DISTRIBUTION

As with tree diameter distributions, tree height distributions exhibited a general monotonic decrease in tree frequency followed by a second rounded peak beginning with trees of approximately 10 m in height (Figure 6-12). A semi-logarithmic representation of the tree height frequency produced a rotated sigmoid relationship not unlike that seen for the diameter distributions (Figure 6-13). Between tree heights of 8 to 14 m, the observed distributions showed a plateau with a small positive slope among the taller trees. After tree heights of approximately 15 m, tree frequency declined at a rate similar to that of the shortest trees. All semi-logarithmic rotated sigmoid relationships were modeled by both linear and polynomials equations (Table 6-5).
Figure 6-11. Residual plots for (A) linear and (B) polynomial regression of live tree density–tree dbh class, 13 Main River stands.
Figure 6-12. Trees ha\(^{-1}\) by 1 m height class for three Main River stands.
Figure 6-13. Semi-logarithmic representation of tree height frequency distribution for three Main River stands. Height class midpoints are mean ± SEM, n = 2,147 trees.
Table 6-5. Parameters and fit statistics for linear and polynomial regression of semi-logarithmic tree height frequencies, Main River.

<table>
<thead>
<tr>
<th>Model and fit statistics</th>
<th></th>
<th></th>
<th>R²</th>
<th>RMSE⁹</th>
</tr>
</thead>
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<td><strong>Linear regression</strong></td>
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<td></td>
</tr>
<tr>
<td>Plot</td>
<td>Intercept</td>
<td>Slope</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>2.13920</td>
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<td>7</td>
<td>1.94625</td>
<td>-0.08885</td>
<td>0.6145</td>
<td>0.3872</td>
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<tr>
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<td>-0.09062</td>
<td>0.7314</td>
<td>0.3021</td>
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<tr>
<td><strong>Polynomial regression</strong></td>
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<td></td>
</tr>
<tr>
<td>Plot</td>
<td>Intercept</td>
<td>Height</td>
<td>Height²</td>
<td>Height³</td>
</tr>
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<td>3.24296</td>
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</tr>
<tr>
<td>2</td>
<td>2.94374</td>
<td>-0.35094</td>
<td>–</td>
<td>0.00273</td>
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<tr>
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<td>0.07926</td>
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<tr>
<td>Pooled</td>
<td>3.38913</td>
<td>-0.60656</td>
<td>0.04333</td>
<td>–</td>
</tr>
</tbody>
</table>

⁹ RMSE = root mean square error.

In all cases, polynomial models provided a better description of the height frequency curves than did linear regressions. Increases in the coefficient of determination were in the order of 12% to 33% (mean = 24%). Residual analysis confirmed the better polynomial fit of the height frequency distributions. As with the semi-logarithmic dbh frequency regression, the curvilinear residual patterns of the linear regression analysis was corrected in the case of the polynomial regression. A quartic polynomial with R² = 0.9768 and RMSE = 0.0950 best explained the average height distribution frequency. Maximum tree height was exceptional at 20 m. Among the three plots, between 86% to 92% of all trees were less ≤10 in height. Between 77% and 81% of all trees were <5 m in height.
6.5 HEIGHT–DIAMETER RELATIONSHIP

The weighted height–diameter relationships for balsam fir, black spruce and white spruce were sigmoidal in character with an upper and lower inflection point plus a distinct height asymptote characterizing each species (Figure 6-14). For each species, all four 3-parameter sigmoidal functions modeled the height–dbh relationship equally well (Table 6-6).

Nonlinear regression fits were similar for both balsam and white spruce (balsam fir: \(R^2\) range = 0.9527 to 0.9596; white spruce: \(R^2\) range = 0.9524 to 0.9636), both of which were greater than black spruce that showed a range of \(R^2\) values from 0.8858 to 0.8904. Within each species, the curves deviated from each other for trees generally > 30 cmdbh and 15 m in height. In all cases, the Chapman–Richards and modified logistic curves shared the greatest height asymptote, while the logistic curve showed the lowest height asymptote.

Because of the small number of samples, the white birch height–diameter relationship was not modeled. Among the four species, the white birch height–diameter relationship was most variable, with the shortest trees at any particular diameter (Figure 6-14).

6.6 REGENERATION SPECIES COMPOSITION, DENSITY, BASAL DIAMETER AND HEIGHT

As in the case of the canopy trees, balsam fir-dominated stand regeneration (Figure 6-15, Table 6-7) with a mean of 85,143 seedlings ha\(^{-1}\). This accounted for an average of 88% of the total number of seedlings. The densities of black spruce, white spruce and
Figure 6-14. Tree height–diameter relationships for balsam fir, black spruce, white spruce and white birch, Main River. Except for those of white birch, all relationships are modeled by four sigmoidal-type equations: Chapman–Richards, Weibull, Schnute, and modified logistic. Parameters and fit statistics are given in Table 6-6. All fitted models significant at $P < 0.0001$. 
Table 6-6. Estimated parameters and fit statistics for balsam fir, black spruce, and white spruce height–diameter (breast height) relationships, Main River. All relationships significant at \( P < 0.0001 \).

<table>
<thead>
<tr>
<th>Function</th>
<th>Species</th>
<th>Estimated coefficients (asymptotic standard error)</th>
<th>( n^a )</th>
<th>( R^{2b} )</th>
<th>( \text{RMSE}_{w}^c )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapman-Richards</td>
<td>bF( ^d )</td>
<td>\begin{align*} a &amp; = 20.4008 \quad b = 0.0603 \quad c = 1.9342 \ (0.6084) &amp; (0.0028) &amp; (0.0457) \end{align*}</td>
<td>1457</td>
<td>0.9527</td>
<td>0.4481</td>
</tr>
<tr>
<td></td>
<td>bS</td>
<td>\begin{align*} a &amp; = 20.9208 \quad b = 0.0399 \quad c = 1.2264 \ (2.1478) &amp; (0.00667) &amp; (0.0487) \end{align*}</td>
<td>453</td>
<td>0.8863</td>
<td>0.5064</td>
</tr>
<tr>
<td></td>
<td>wS</td>
<td>\begin{align*} a &amp; = 17.8554 \quad b = 0.0724 \quad c = 1.9169 \ (1.1582) &amp; (0.00972) &amp; (0.1624) \end{align*}</td>
<td>124</td>
<td>0.9524</td>
<td>0.4994</td>
</tr>
<tr>
<td>Weibull</td>
<td>bF</td>
<td>\begin{align*} a &amp; = 16.6993 \quad b = 0.00591 \quad c = 1.7078 \ (0.3417) &amp; (0.00025) &amp; (0.0226) \end{align*}</td>
<td>1457</td>
<td>0.9551</td>
<td>0.4367</td>
</tr>
<tr>
<td></td>
<td>bS</td>
<td>\begin{align*} a &amp; = 18.4102 \quad b = 0.0213 \quad c = 1.2104 \ (1.6688) &amp; (0.00158) &amp; (0.0367) \end{align*}</td>
<td>453</td>
<td>0.8872</td>
<td>0.5044</td>
</tr>
<tr>
<td></td>
<td>wS</td>
<td>\begin{align*} a &amp; = 15.5916 \quad b = 0.00766 \quad c = 1.6955 \ (0.6743) &amp; (0.00127) &amp; (0.0789) \end{align*}</td>
<td>124</td>
<td>0.9559</td>
<td>0.4806</td>
</tr>
<tr>
<td>Schnute</td>
<td>bF</td>
<td>\begin{align*} a &amp; = 0.1900 \quad b = -1.1584 \quad c = 16.2523 \ (0.0092) &amp; (0.0827) &amp; (0.2030) \end{align*}</td>
<td>1457</td>
<td>0.9596</td>
<td>0.4142</td>
</tr>
<tr>
<td></td>
<td>bS</td>
<td>\begin{align*} a &amp; = 0.0836 \quad b = 0.2297 \quad c = 17.2908 \ (0.0134) &amp; (0.1215) &amp; (1.0487) \end{align*}</td>
<td>453</td>
<td>0.8904</td>
<td>0.4973</td>
</tr>
<tr>
<td></td>
<td>wS</td>
<td>\begin{align*} a &amp; = 0.2273 \quad b = -1.3300 \quad c = 15.7916 \ (0.0338) &amp; (0.2845) &amp; (0.4282) \end{align*}</td>
<td>124</td>
<td>0.9636</td>
<td>0.4366</td>
</tr>
<tr>
<td>Modified Logistic</td>
<td>bF</td>
<td>\begin{align*} a &amp; = 23.4327 \quad b = 0.00395 \quad c = 1.7658 \ (0.8040) &amp; (0.00017) &amp; (0.0302) \end{align*}</td>
<td>1457</td>
<td>0.9533</td>
<td>0.4453</td>
</tr>
<tr>
<td></td>
<td>bS</td>
<td>\begin{align*} a &amp; = 29.6981 \quad b = 0.0134 \quad c = 1.2134 \ (4.1803) &amp; (0.00148) &amp; (0.0447) \end{align*}</td>
<td>453</td>
<td>0.8858</td>
<td>0.5074</td>
</tr>
<tr>
<td></td>
<td>wS</td>
<td>\begin{align*} a &amp; = 20.3708 \quad b = 0.00547 \quad c = 1.7735 \ (1.6969) &amp; (0.00098) &amp; (0.1115) \end{align*}</td>
<td>124</td>
<td>0.9528</td>
<td>0.4973</td>
</tr>
</tbody>
</table>

\(^a n = \text{number of trees.}\)
\(^b \text{Pseudo } R^2.\)
\(^c \text{Weighted root mean square error. Weight} = 1/\sqrt{dbh}.\)
\(^d \text{bF = balsam fir, bS = black spruce, wS = white spruce, wB = white birch.}\)
Figure 6-15. Boxplots showing tree seedling density by species for 13 Main River stands. Box limits represent the 25th and 75th percentiles of the data. Error bars represent the 10th and 90th percentiles, with dots representing the 5th and 95th percentile outliers. Mean and median values are given by the dashed and solid line, respectively.

Table 6-7. Species composition and density of tree regeneration, Main River.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Seedlings ha$^{-1}$ (Mean, standard deviation)</th>
<th>Balsam fir$^a$</th>
<th>Black spruce</th>
<th>White spruce</th>
<th>White birch</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td></td>
<td>99,304$^a$</td>
<td>3,652$^b$</td>
<td>2,000$c$</td>
<td>3,130$^{cd}$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(103,811)</td>
<td>(9,016)</td>
<td>(5,953)</td>
<td>(7,765)</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>75,600$^a$</td>
<td>10,800$^b$</td>
<td>200$c$</td>
<td>1,100$^d$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(75,776)</td>
<td>(28,486)</td>
<td>(1,407)</td>
<td>(4,691)</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>78,400$^a$</td>
<td>800$b$</td>
<td>2,100$c$</td>
<td>8,900$^d$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(104,056)</td>
<td>(3,387)</td>
<td>(5,374)</td>
<td>(33,209)</td>
</tr>
<tr>
<td>Average</td>
<td></td>
<td>85,143$^a$</td>
<td>5,016$^b$</td>
<td>1,460$c$</td>
<td>4,317$b$</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(96,196)</td>
<td>(17,492)</td>
<td>(4,831)</td>
<td>(19,673)</td>
</tr>
</tbody>
</table>

$^a$For each plot, mean values followed by the same letter are not significantly different, $P < 0.05$. 
white birch regeneration were an order of magnitude less with respective mean densities of 5,016, 1,460, and 4,317 seedlings ha$^{-1}$. Significant interaction existed among species and plots ($P < 0.0001$, $\chi^2 = 89.45$, $df = 6$). In all plots, balsam fir occurred in significantly greater frequency than any of the other species. Conclusions regarding the relative frequency of black spruce, white spruce and white birch depended on the plot being considered. Therefore, no statement can be made regarding the overall significant difference in seedling density for these three species among all plots. Relative differences for each plot are noted in Table 6-7.

The basal diameter frequency distribution for all seedlings was characterized by a reverse-J distribution that showed a somewhat regular monotonic decrease in seedling frequency across the range of seedling basal diameters (Figure 6-16). About 93% of balsam fir seedlings were < 10 mm in basal diameter and seedlings rarely attained basal diameters > 40 mm.

A similar reverse-J frequency distribution was obtained for seedling heights (Figure 6-17). Given the dominance of balsam fir among the regeneration, height distribution of balsam fir exhibited a strong reverse-J distribution as well. Among the three plots, about 90% (range = 89% to 92%) of all balsam fir seedlings were $\leq$ 40 cm in height. Both black spruce and white spruce seedlings generally occurred across the full range of heights. All white birch seedlings were $\leq$ 70 cm in height.
Figure 6-16. Seedling basal diameter frequency distribution for three Main River stands. Basal diameter classes = 1 mm.
Figure 6-17. Seedling height frequency distribution for three Main River stands. Height frequency classes = 2 cm.
6.7 REGENERATION HEIGHT–BASAL DIAMETER RELATIONSHIP

Seedling height–basal diameter relationships were characterized by the classic allometric growth curve \( Y = aX^b \) by which the ratio between increments in different-sized structures (in this case seedling height and basal diameter) remain relatively constant over the range of size structure studied (Figure 6-18).

Given the similarity among the balsam fir data and the relatively small number of samples for the other three species, all data for each species was pooled for analysis. Among the three conifers the seedling height at any basal diameter was greatest for black spruce, least for balsam fir, with intermediate values for white spruce. The height growth–basal diameter growth was similar for both white birch and white spruce, at least within the data range recorded for white birch. For all species, bivariate variability increased with seedling size.

The height–size relationships were confirmed by traditional recourse to covariance analysis of the equivalent linear form \( \log Y = \log a + b \log X \) for each power function. Bivariate log transformation linearized the allometric relationship, stabilized the error variances and normalized the error terms. All seedling height–basal diameter relationships were significant at \( P < 0.0001 \) with \( R^2 \) values ranging from 0.7322 for white birch to 0.9108 for white spruce (Figure 6-19, Table 6-8). Seedling height at any given diameter was generally greatest and most variable for black spruce.
Figure 6-18. Predicted seedling height (ht)–basal diameter (bd) relationships for balsam fir, black spruce, white spruce, and white birch, Main River. $n =$ number of seedlings. Balsam fir: $ht = 8.6667(bd^{0.7322}), R^2 = 0.9006, n = 2,644$; Black spruce: $ht = 16.9974(bd^{0.6326}), R^2 = 0.6849, n = 156$; White spruce: $ht = 13.775(bd^{0.6456}), R^2 = 0.8692, n = 46$; White birch: $ht = 12.4982(bd^{0.7044}), R^2 = 0.7135, n = 132$. 
Figure 6-19. Log–log height–basal diameter relationships for balsam fir, black spruce, white spruce and white birch seedlings, Main River. Estimated parameters, 95% confidence intervals, and fit statistics are given in Table 6-8.

Table 6-8. Simple linear regression parameters and fit statistics for the log–log height–basal diameter relationships for balsam fir, black spruce, white spruce, and white birch seedlings, Main River. All regressions are significant at $P < 0.0001$ and 95% confidence intervals are in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>$n^a$</th>
<th>Log $a$</th>
<th>$b$</th>
<th>$R^2$</th>
<th>RMSE$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsam fir</td>
<td>2,644</td>
<td>0.8661</td>
<td>0.8125</td>
<td>0.8731</td>
<td>0.1292</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.8600, 0.8721)</td>
<td>(0.8007, 0.8244)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black spruce</td>
<td>156</td>
<td>1.1460</td>
<td>0.7068</td>
<td>0.7322</td>
<td>0.1291</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.0910, 1.2009)</td>
<td>(0.6387, 0.7748)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White spruce</td>
<td>46</td>
<td>0.9767</td>
<td>0.8005</td>
<td>0.9108</td>
<td>0.1197</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.9210, 1.0323)</td>
<td>(0.7244, 0.8766)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White birch</td>
<td>132</td>
<td>0.9930</td>
<td>0.8572</td>
<td>0.7709</td>
<td>0.1912</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.9578, 1.0282)</td>
<td>(0.7761, 0.9382)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a n =$ number of seedlings.

$^b$ RMSE = root mean square error (log cm).
The black spruce regression differed significantly in slope from that of balsam fir \((P = 0.0032)\), white birch \((P = 0.0009)\), but not for white spruce \((P = 0.0867)\). A Bonferroni-adjusted \(P\) value of \(\alpha = 0.05/6 = 0.0083\) was used to test for significance. Analysis confined to the balsam fir, white spruce and white birch data confirmed homogeneity of slope for all three species. Given the homogeneity of slope assumption for covariance analysis, treatment effects (species differences in intercept) were considered. Both white birch and white spruce did not differ significantly in intercept \((P = 0.5408)\) and therefore could have been combined in a common equation. Homogeneity of slope with significantly different intercepts was recorded for balsam fir and white birch \((P < 0.0001)\) and for balsam fir and white spruce \((P < 0.0001)\). In other words, height growth at any particular basal diameter was generally of the order black spruce > white spruce = white birch > balsam fir.

6.8 CONCLUSION

Structural analysis of the diameter and height of both the tree and regeneration layer of the Main River \(Abies–Picea–Betula\) stands confirms that these stands are reverse-J (rotated sigmoid) old-growth stands. The well-defined rotated sigmoidal character of the semi-logarithmic tree dbh and height frequency distributions highlights both the structural complexity and the quasi-equilibrium character of these old-growth stands.
CHAPTER 7
CLASSIFICATION OF STAND TYPES IN AN INSECT-MEDIATED BOREAL FOREST LANDSCAPE

7.1 CLASSIFICATION OF STAND SIZE STRUCTURE

Based on visual examination of tree dbh frequency distributions and assessment of extensive field observations, all 50 sample stands were classified into four main stand structural types: (1) single-cohort, modal stands, (2) bimodal stands, (3) reverse-J stands, and (4) bistaged stands. This initial "subjective" classification was confirmed by both cluster and principal component analysis of seven diagnostic, stand structural indices based on tree diameter at breast height: (1) Shannon index of diversity, (2) 3-parameter Weibull shape parameter, (3) Lorimer's index of symmetry, (4) Gini coefficient, (5) coefficient of variation, and the two moment statistics, (6) skewness, and (7) kurtosis (Table 7-1).

Subsequently, all single-cohort stands were further classified into a chronosequence based on 10-year age classes. In this way, the structural and temporal relationships among the various stands were highlighted and permitted a greater understanding of both stand development and the landscape-level mosaic in response to recurrent insect herbivory. The use of total stand age was not meant to serve as a precise measure of stand development. It is well known that tree size is often more instructive than tree age in understanding the dynamics of stand development. The variable and sometimes long
Table 7-1. Values for seven structural diversity indices, Little Grand Lake stands

<table>
<thead>
<tr>
<th>Plot</th>
<th>(n^a)</th>
<th>Shannon index</th>
<th>Weibull (c) parameter</th>
<th>Index of symmetry</th>
<th>Gini coefficient</th>
<th>Coefficient of variation</th>
<th>Skewness</th>
<th>Kurtosis</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>521</td>
<td>1.348</td>
<td>1</td>
<td>0.064</td>
<td>0.5752</td>
<td>141.82</td>
<td>2.991</td>
<td>9.574</td>
</tr>
<tr>
<td>2</td>
<td>348</td>
<td>1.8</td>
<td>1.8</td>
<td>0.340</td>
<td>0.3194</td>
<td>57.53</td>
<td>0.819</td>
<td>1.132</td>
</tr>
<tr>
<td>3</td>
<td>142</td>
<td>2.228</td>
<td>2.04</td>
<td>0.222</td>
<td>0.2899</td>
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<td>0.685</td>
<td>0.472</td>
</tr>
<tr>
<td>4</td>
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<td>2.34</td>
<td>0.306</td>
<td>0.2548</td>
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<td>0.435</td>
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<tr>
<td>5</td>
<td>230</td>
<td>1.688</td>
<td>1.02</td>
<td>0.061</td>
<td>0.5269</td>
<td>116.31</td>
<td>2.315</td>
<td>5.334</td>
</tr>
<tr>
<td>6</td>
<td>361</td>
<td>0.322</td>
<td>1.14</td>
<td>0.364</td>
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<td>156.1</td>
<td>9.566</td>
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</tr>
<tr>
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<td>54</td>
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<td>3.66</td>
<td>0.430</td>
<td>0.1562</td>
<td>28.85</td>
<td>0.027</td>
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<tr>
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<td>0.333</td>
<td>0.3385</td>
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<td>9.580</td>
<td>108.42</td>
</tr>
<tr>
<td>9</td>
<td>690</td>
<td>1.437</td>
<td>1.57</td>
<td>0.197</td>
<td>0.3597</td>
<td>68.22</td>
<td>1.965</td>
<td>11.912</td>
</tr>
<tr>
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<td>1.957</td>
<td>2.01</td>
<td>0.237</td>
<td>0.2875</td>
<td>52.48</td>
<td>1.067</td>
<td>3.317</td>
</tr>
<tr>
<td>11</td>
<td>61</td>
<td>2.055</td>
<td>4.67</td>
<td>0.713</td>
<td>0.1304</td>
<td>23.97</td>
<td>-0.380</td>
<td>1.720</td>
</tr>
<tr>
<td>12</td>
<td>81</td>
<td>2.702</td>
<td>1.05</td>
<td>0.012</td>
<td>0.4440</td>
<td>77.57</td>
<td>0.186</td>
<td>-1.422</td>
</tr>
<tr>
<td>13</td>
<td>257</td>
<td>2.065</td>
<td>2.23</td>
<td>0.329</td>
<td>0.2639</td>
<td>47.65</td>
<td>0.834</td>
<td>0.935</td>
</tr>
<tr>
<td>14</td>
<td>260</td>
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<td>0.5022</td>
<td>100.14</td>
<td>1.667</td>
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</tr>
<tr>
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<td>169</td>
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<td>1.03</td>
<td>0.041</td>
<td>0.5025</td>
<td>117.15</td>
<td>4.189</td>
<td>25.90</td>
</tr>
<tr>
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<td>2.07</td>
<td>0.396</td>
<td>0.2810</td>
<td>51.26</td>
<td>0.949</td>
<td>1.075</td>
</tr>
<tr>
<td>17</td>
<td>163</td>
<td>1.701</td>
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<td>0.018</td>
<td>0.6285</td>
<td>138.44</td>
<td>2.039</td>
<td>3.334</td>
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<tr>
<td>19</td>
<td>315</td>
<td>1.493</td>
<td>1.729</td>
<td>0.120</td>
<td>0.3249</td>
<td>61.74</td>
<td>1.563</td>
<td>4.353</td>
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<td>100</td>
<td>1.946</td>
<td>3.254</td>
<td>0.745</td>
<td>0.1831</td>
<td>33.24</td>
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<td>0.926</td>
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<td>21</td>
<td>86</td>
<td>2.475</td>
<td>2.83</td>
<td>0.584</td>
<td>0.2065</td>
<td>37.25</td>
<td>-0.321</td>
<td>0.629</td>
</tr>
<tr>
<td>22</td>
<td>154</td>
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<td>1</td>
<td>0.016</td>
<td>0.4963</td>
<td>89.23</td>
<td>0.754</td>
<td>-0.349</td>
</tr>
<tr>
<td>23</td>
<td>321</td>
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<td>1</td>
<td>0.043</td>
<td>0.5422</td>
<td>107.64</td>
<td>1.699</td>
<td>4.072</td>
</tr>
<tr>
<td>24</td>
<td>39</td>
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<td>3.13</td>
<td>0.618</td>
<td>0.1753</td>
<td>32.88</td>
<td>1.048</td>
<td>3.396</td>
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<td>0.2239</td>
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Table 7-1. (Continued)

<table>
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<tr>
<th>Plot</th>
<th>( n^a )</th>
<th>Shannon index</th>
<th>Weibull ( c ) parameter</th>
<th>Index of symmetry</th>
<th>Gini coefficient of variation</th>
<th>Skewness</th>
<th>Kurtosis</th>
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</tr>
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<td>27</td>
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<td>-0.367</td>
</tr>
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<td>0.1946</td>
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<td>0.147</td>
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<td>130.19</td>
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<td>0.4395</td>
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<td>4.783</td>
</tr>
<tr>
<td>40</td>
<td>82</td>
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<td>2.964</td>
<td>0.502</td>
<td>0.2008</td>
<td>36.18</td>
<td>0.225</td>
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<td>42</td>
<td>247</td>
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<td>1</td>
<td>0.049</td>
<td>0.5627</td>
<td>124.68</td>
<td>2.957</td>
</tr>
<tr>
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<td>1.835</td>
<td>2.265</td>
<td>0.338</td>
<td>0.2492</td>
<td>46.31</td>
<td>1.296</td>
</tr>
<tr>
<td>44</td>
<td>461</td>
<td>1.446</td>
<td>1.132</td>
<td>0.079</td>
<td>0.458</td>
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<td>0.052</td>
<td>0.4971</td>
<td>115.87</td>
<td>3.419</td>
</tr>
<tr>
<td>46</td>
<td>155</td>
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<td>0.018</td>
<td>0.6685</td>
<td>198.2</td>
<td>3.750</td>
</tr>
<tr>
<td>47</td>
<td>336</td>
<td>1.761</td>
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<td>0.023</td>
<td>0.5300</td>
<td>116.19</td>
<td>2.393</td>
</tr>
<tr>
<td>48</td>
<td>68</td>
<td>2.697</td>
<td>2.448</td>
<td>0.185</td>
<td>0.2458</td>
<td>43.03</td>
<td>-0.245</td>
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<tr>
<td>49</td>
<td>321</td>
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<td>1</td>
<td>0.043</td>
<td>0.5885</td>
<td>144.36</td>
<td>3.133</td>
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<tr>
<td>50</td>
<td>80</td>
<td>2.367</td>
<td>3.1</td>
<td>0.555</td>
<td>0.1983</td>
<td>35.23</td>
<td>0.175</td>
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<tr>
<td>51</td>
<td>412</td>
<td>0.588</td>
<td>1.143</td>
<td>0.114</td>
<td>0.4664</td>
<td>112.1</td>
<td>4.058</td>
</tr>
</tbody>
</table>

\(^a\) \( n \) = number of trees.

\(^b\) Plots in boldface have normal dbh distributions as determined by Kolmogorov–Smirnov goodness of fit test, \( P \geq 0.02 \).
periods of suppression in shade-tolerant conifers often preclude the use of total age data as a suitable measure of the degree of stand development. Often, stand height distribution serves as a better measure of the dynamics of crown closure and self-thinning-induced stand development. Therefore, age structure was used in a heuristic sense; that is, as an aid to understanding the stand structural types within a broader temporal context. However, the relatively good relationship found between stand development and total age supported the use of a total age chronosequence in this study.

7.1.1 Cluster Analysis of Stand Structural Indices

The first level of cluster analysis successfully distinguished single-cohort stands from reverse-J stands (Figure 7-1). Within this primary division, other well-defined structural classes were identified. The single-cohort cluster comprised 28 stands (56% of total) and the reverse-J cluster included 22 stands or 44% of the total number of stands. Within the single-cohort stands three main groupings were evident: (1) younger single-cohort stands (2, 3, 4, 9, 10, 13, 16, 19, and 43), (2) older single-cohort stands (7, 11, 20, 21, 24, 25, 27, 31, 32, 34, 25, 40, and 50), and (3) old bimodal or near bimodal stands (12, 22, 29, 36, 37, and 48). Within the reverse-J stands two main clusters were identified: (1) younger reverse-J stands (6, 8, and 38), and (2) a collection of other reverse-J stands (1, 5, 14, 15, 17, 23, 26, 28, 30, 33, 39, 41, 42, 44, 45, 46, 47, 49, and 51).
Figure 7-1. Dendrogram of an agglomerative hierarchical cluster analysis (Ward’s minimum variance method) of structural indices data from 50 Little Grand Lake stands.
7.1.2 Principal Component Analysis

Interpretation of both principal component and detrended correspondence analysis gave the same results. Principal component analysis was chosen because it facilitated both ecological and practical interpretation of the ordination plot. The essentials of the cluster classification were confirmed by principal component analysis. Furthermore, ordination provided better insight into the range of structural variability among the stands. Principal component analysis of five of the seven diagnostic structural indices (Shannon index, Weibull shape parameter, index of symmetry, Gini coefficient, and coefficient of variation) confirmed that the first two eigenvalues explained 97% of the total original variance. The first component explained most of the variation at 82%. The second eigenvalue measured the variance along the second principal component at approximately 15%. Two principal components thus provided a good summary of the data and were the only two retained for interpretation (Table 7-2). Loadings for the first three principal components are given in Table 7-3.

The loadings indicate how the scoring system for each principal component is related to the original variables. For principal component 1, all scores were well correlated, with a high negative correlation for the Weibull shape parameter and the index of symmetry, and a high positive correlation for the Gini coefficient and the coefficient of variation. The Shannon index was the variable least correlated with the first component. The negative association between the couplets “Weibull shape parameter-index of symmetry” and “Gini coefficient-coefficient of variation” made sense. For each stand, a
Table 7-2. Eigenvalues of the correlation matrix from principal component analysis of Little Grand Lake stand structural indices.

<table>
<thead>
<tr>
<th>Axis</th>
<th>Eigenvalue</th>
<th>Percent of variance</th>
<th>Cumulative percentage</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>4.123</td>
<td>82.46</td>
<td>82.46</td>
</tr>
<tr>
<td>2</td>
<td>0.730</td>
<td>14.61</td>
<td>97.06</td>
</tr>
<tr>
<td>3</td>
<td>0.120</td>
<td>2.40</td>
<td>99.46</td>
</tr>
<tr>
<td>4</td>
<td>0.014</td>
<td>0.28</td>
<td>99.74</td>
</tr>
<tr>
<td>5</td>
<td>0.013</td>
<td>0.25</td>
<td>100</td>
</tr>
</tbody>
</table>

Table 7-3. Loadings on the first three principal components for each structural index, Little Grand Lake stands. Correlations are Pearson product moment linear correlations.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Loadings</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Principal component 1</td>
</tr>
<tr>
<td>Shannon index</td>
<td>-0.680</td>
</tr>
<tr>
<td>Weibull shape parameter</td>
<td>-0.987</td>
</tr>
<tr>
<td>Index of symmetry</td>
<td>-0.871</td>
</tr>
<tr>
<td>Gini coefficient</td>
<td>0.980</td>
</tr>
<tr>
<td>Coefficient of variation</td>
<td>0.984</td>
</tr>
</tbody>
</table>
smaller Weibull shape parameter or index of symmetry was associated with a larger Gini coefficient or coefficient of variation. Therefore, component 1 probably measured the relative relationship between the skewness of diameter distributions and their size inequality. In other words, principal component 1 was a measure of the modality (or nonmodality) of the diameter distributions.

The Shannon index of diversity had a significant loading of -0.721 on the second component, with all other loadings poorly correlated. Scores on principal component 2 were therefore considered closely related to the structural heterogeneity of the diameter distributions. Stands with a high Shannon index of diversity tracked negatively along component 2. In other words, the second component may be measuring the degree of bimodality in each diameter distribution.

Ordination biplots showing both indices and plots helped to describe the structural gradients found among the plots. Principal components 1 and 2 confirmed the dichotomous classification determined by cluster analysis (Figure 7-2). Both the Weibull shape parameter and the index of symmetry vectors pointed in the same negative direction confirming their positive correlation. Both the Gini coefficient and coefficient of variation were also positively correlated, but pointed in the opposite direction. In other words, non-modal or reverse-J diameter distributions (low Weibull shape parameter and index of symmetry) segregated in a positive direction along principal component 1, whereas modal single-cohort or near-modal stands (high Weibull shape parameter and index of symmetry) tracked in a negative direction along principal component 1. Plots with low scores on principal component 1 tended to be modal in character, whereas plots with high scores tended to be non-modal in character. Overlay plots clearly showed a gradual change in the
Figure 7-2. Principal component analysis joint plot using five structural indices: Shannon index of diversity, Weibull shape parameter, index of symmetry, Gini coefficient, and the coefficient of variation. Each point represents a single stand and the distances among points in ordination space are approximately proportional to the differences in modality of stand diameter (dbh) structure, Little Grand Lake.
structural character of stands from modal stands to the left of axis 1 to increasingly non-modal and reverse-J stands to the right on axis 1 (Figure 7-3).

The second principal component scores were closely related to the Shannon index of each diameter distribution (loading = −0.721) (Table 7-3). Plots with low scores on principal component 2 (high Shannon index) tended towards bimodality, whereas plots with high scores on principal component 2 tend away from bimodality (Figure 7-2, Figure 7-4). Plots having the highest Shannon index (plots 12, 22, 29, 36, 37, and 48) were generally well separated in ordination space from stands with the lowest Shannon index (plots 6, 8, 38, 39, and 51).

7.1.3 Stand Classification

Based on the initial dichotomous classification into modal (single-cohort) and non-modal (reverse-J) stands, a further breakdown was initiated based on a combined examination of the multivariate analysis, structural indices and actual field observations.

7.1.3.1 Reverse-J Stands

A total of 22 stands (1, 5, 6, 8, 14, 15, 17, 23, 26, 28, 30, 33, 38, 39, 41, 42, 44, 45, 46, 47, 49, and 51) were classified as non-modal, reverse-J stands. In all cases, Weibull shape parameters and symmetry indices indicated a reverse-J character according to the norms described by Bailey and Dell (1973) and Lorimer and Krug (1983). Both the Weibull shape parameter and symmetry indices by themselves were not able, however, to discriminate old, multi-canopied, multi-aged, reverse-J stands from young even-aged stands overtopped by a low density of veteran trees, or from young, single-cohort stands in the initiation stage of stand development.
Figure 7.3. Principal component overlay for Weibull shape parameter, index of symmetry, coefficient of variation, and Gini coefficient. Size of symbol is proportional to the magnitude of each parameter. Positive movement along axis 1 is an indication of the increase in the non-modality or reverse-J character of the stands, Little Grand Lake.
Figure 7-3. (Continued)
Figure 7-4. Principal component overlay for the Shannon index of diversity. Size of symbol is proportional to the magnitude of the index. In this case, the Shannon index is considered a measure of the structural heterogeneity or bimodality of the stands, Little Grand Lake.

Of the 22 “reverse-J” stands, nine stands (1, 5, 14, 17, 28, 30, 33, 41, and 47) had classic reverse-J diameter distributions. High Gini coefficient and coefficient of variation values, low Weibull shape parameters and indices of symmetry values and a general monotonic decline in tree diameter frequency identified these stands as negative exponential or reverse-J in character.

Thirteen of the “reverse-J” stands (6, 8, 15, 23, 26, 38, 39, 42, 44, 45, 46, 49, and 51) were classified as young, single-cohort initiation stands. Three stands (6, 8, and 38) were clustered together in the dendrogram and in ordination space, and represented the youngest single cohort stands in the initiation stage. The beginnings of a reverse-J dbh distribution found in these young stands were further developed in the young initiation
stands 15, 23, 39, 42, 46 and 51. Structural differences among these stands were, for the most part, defined by the relative presence or absence of scattered dominant relict trees. The “reverse-J” diameter distribution was distinct from that of the multicohort reverse-J stands by virtue of the absence of a general monotonic decline in tree density and an effective truncation of the oldest diameter classes.

Four “reverse-J” stands (26, 44, 45, and 49) were further classified as bistaged stands characterized as young, relatively even-aged stands overtopped by large veteran trees (particularly black spruce) that had survived historic insect outbreaks. In all cases, the relict overstory of surviving balsam fir, white spruce or black spruce accounted for the “reverse-J” indices, but it was obvious that the stands were better classified as young, modal or single-cohort stands.

It was originally thought that if only the regenerating cohorts were considered, then the bistaged stands (26, 44, 45, and 49) should be classified as young, single-cohort stands with plots 9 and 19 or with the young single-cohort stands. Recognition of stand structure as a significant determinant of stand dynamics, however, allowed for a separate bistaged category. Unlike stands 9 and 19, the four bistaged stands generally occurred on poorer sites (especially plots 44, 45, and 49) with the result that the regenerating cohorts had not achieved crown closure and self-thinning, even though the trees were chronologically older than trees on the balsam fir-dominated plots 9 and 19. Furthermore, the snag diameter frequencies and stand age structure highlighted the fundamental differences from plots 9 and 19. Despite the low values for the Weibull shape parameters (1 to 1.13) and an obvious reverse-J diameter distribution, it was considered legitimate to classify the stands
as bistaged, as relatively young regenerating cohorts overtopped by large veteran black spruce and balsam fir.

7.1.3.2 Modal or Near-Modal Stands

Twenty-eight or 56% of the total number of stands were classified as modal stands. Of the 28 stands, nine stands were classified as younger modal, single-cohort (2, 3, 4, 9, 10, 13, 16, 19, and 43), 13 stands as older single-cohort (7, 11, 20, 21, 24, 25, 27, 31, 32, 34, 35, 40, and 50) and six stands as bimodal or near-bimodal (12, 22, 29, 36, 36, and 48). Two younger and 12 older single-cohort stands were normally distributed (Kolmogorov–Smirnov goodness of fit, $P > 0.02$) with all other modal diameter distributions being slightly positively or negatively skewed (Table 7-1).

Six stands (12, 22, 29, 36, 37, and 48) were classified as "bimodal" or "near-bimodal." These stands represented old modal stands undergoing stand break-up characterized by small patch formation and release of a formerly suppressed seedling bank. Kurtosis values ranged from to $-1.422$ to $-0.326$, all indicative of actual or near bimodality (Wyszomirski 1992). Field observations confirmed that, except for stand 29, all stands had begun to break up, with gap phase recruitment of balsam fir, black spruce and white spruce. Plot 29 was considered an anomaly, with size structural features characteristic of younger 81–90-year-old single-cohort stands. The recruitment of small diameter classes leading to bimodality was either an artifact of sampling (overlap of plot with a regenerating patch), or the inclusion of densely regenerating patches within the dominant stand. The greater structural heterogeneity of these stands was confirmed by the Shannon diversity index overlay during principal component analysis. All six plots were clustered together in the
lower ordination space along the negative trajectory of principal component 2. It was along this axis that the Shannon diversity index loaded with $r = -0.721$ (Figure 7-4).

### 7.1.3.3 Final Stand Classification

Stands exhibiting single-cohort diameter distributions were classified into 10-year age classes to produce a series of 11 distinct stand age classes ranging from age class 11–20 years through to age class 111–120 years. As already indicated, classification of these stands into distinct stand age classes did not presume *ipso facto* that age class was a reliable measure of the degree of stand development of modal stands. Theoretically, stand height is a better index of the degree of stand development, especially with shade-tolerant tree species. As it turned out, however, the total age structure did provide a useful indicator of the degree of stand development, and helped as a heuristic device for modal stand classification. The only exception may be plot 13 in which stand structure, rather than age, proved to be the better criterion for classification purposes. Plot 13 had structural characteristics consistent with stands one age class younger. These differences will be addressed in detail in the appropriate sections.

Based on the tree diameter structure and age characteristics, the 50 sampled stands were classified into four categories:

1. Single-cohort (31 plots, 62% of total)
2. Bimodal (6 plots, 12% of total)
3. Reverse-J (9 plots, 18% of total)
4. Bistaged (4 plots, 8% of total) (Figure 7-5).
General size, density and age characteristics of individual stands in each stand type are given in Table 7-4. Both single-cohort and bimodal stands constitute a chronosequence of stand development, with bimodal stands expressing the most advanced stage of stand development characterized by active canopy recruitment within canopy gaps. By way of contrast, both reverse-J and bistaged stands were characterized by sites of generally lower site quality (> black spruce content) and a distinct reverse-J tree diameter distribution. Both bimodal and bistaged stands were considered to be variants of modal and reverse-J stands, respectively. The structural characteristics of each stand type and stand developmental changes are detailed in Chapters 8 and 11.
Table 7-4. Stand type classification with selected stand size and age characteristics, Little Grand Lake.

<table>
<thead>
<tr>
<th>Stand type</th>
<th>Plot</th>
<th>$n^a$</th>
<th>Quadratic mean diameter (cm)</th>
<th>Density (trees ha$^{-1}$)</th>
<th>Mean stand age (years)$^b$</th>
<th>$s^c$</th>
<th>Age range$^b$</th>
</tr>
</thead>
<tbody>
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<td>Single-cohort (0–10 yrs)</td>
<td>$^d$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Single-cohort (11–20 yrs)</td>
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<td>30</td>
<td>2.3</td>
<td>9,000</td>
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<td>9.1</td>
<td>47</td>
</tr>
<tr>
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<td>8</td>
<td>29</td>
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<td>3,925</td>
<td>15.4</td>
<td>2.9</td>
<td>9</td>
</tr>
<tr>
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<td>38</td>
<td>25</td>
<td>2.4</td>
<td>20,000</td>
<td>17.5</td>
<td>2.8</td>
<td>12</td>
</tr>
<tr>
<td>Single-cohort (21–30 yrs)</td>
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<td>24</td>
<td>5.9</td>
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<td>9.0</td>
<td>31</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>31 (32)</td>
<td>4.3</td>
<td>8,025</td>
<td>27.6 (30.8)</td>
<td>9.1 (20.5)</td>
<td>40 (118)</td>
</tr>
<tr>
<td></td>
<td>39</td>
<td>26</td>
<td>2.5</td>
<td>38,000</td>
<td>21.6</td>
<td>3.9</td>
<td>19</td>
</tr>
<tr>
<td></td>
<td>42</td>
<td>32 (33)</td>
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<td>23.7 (26.7)</td>
<td>5.9 (18.1)</td>
<td>29 (108)</td>
</tr>
<tr>
<td></td>
<td>51</td>
<td>30</td>
<td>1.9</td>
<td>13,733</td>
<td>20.8</td>
<td>4.9</td>
<td>25</td>
</tr>
<tr>
<td>Single-cohort (31–40 yrs)</td>
<td>46</td>
<td>25 (27)</td>
<td>7.5</td>
<td>3,875</td>
<td>31.1 (37.4)</td>
<td>10.5 (25.0)</td>
<td>41 (110)</td>
</tr>
<tr>
<td>Single-cohort (41–50 yrs)</td>
<td>$^d$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Single-cohort (51–60 yrs)</td>
<td>$^d$</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Single-cohort (61–70 yrs)</td>
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<td>20</td>
<td>4.2</td>
<td>30,667</td>
<td>64.8</td>
<td>8.6</td>
<td>29</td>
</tr>
<tr>
<td>Single-cohort (71–80 yrs)</td>
<td>19</td>
<td>20</td>
<td>4.6</td>
<td>31,500</td>
<td>60.5</td>
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</table>

$a$ $n$ = number of live trees sampled.

$b$ Number in parentheses include veteran trees.

$c$ $s$ = standard deviation.

$d$ No stands found in this age class.

7.2 CONCLUSION

Among the 50 stands samples in the insect-mediated Little Grand Lake boreal forest landscape, four stand structural types were recognized: (1) single-cohort (31 stands, 62%), (2) bimodal (6 stands, 12%), (3) reverse-J (9 stands, 18%), and (4) bistaged (4 stands, 8%). Multivariate cluster and principal component analysis of a suite of seven stand structural indices (Shannon index of diversity, 3-parameter Weibull shape parameter, Lorimer's index of symmetry, Gini coefficient, coefficient of variation, skewness, and kurtosis)
strengthened the initial classification based on examination of tree dbh frequency distributions and field observations. The single-cohort stands were further classified into a chronosequence of stands ranging from age class 11–20 years to age class 111–120 years. This classification provided a basis for further analysis of changes in stand structure associated with stand development.
CHAPTER 8

SPECIES COMPOSITION AND DEVELOPMENT OF STAND STRUCTURE IN AN INSECT-MEDIATED BOREAL FOREST LANDSCAPE

8.1 TREE SPECIES COMPOSITION AND DENSITY

Tree densities for individual stands varied greatly given the wide range in stand development and natural stocking levels. General species-level trends, however, were instructive. Total live tree density ranged from 864 to 38,000 stems ha\(^{-1}\) (Table 8-1).

Total live tree densities in the young stands (\(\leq 40\) years old) showed no pattern, but rather were highly variable, ranging from 3,875 to 38,000 stems ha\(^{-1}\). With the commencement of self-thinning in plots aged 61–70 years, average stocking progressively declined from a high of 31,082 stems ha\(^{-1}\) \((s = 589)\) to a low of 1,109 stems ha\(^{-1}\) \((s = 347)\) in the oldest single-cohort stands aged 111–120 years. Stem densities were of the order 31,083 \((s = 589)\), 10,862 \((s = 3379)\), 5,376 \((s = 2046)\), 2,448 \((s = 1666)\), 1,119 \((s = 204)\), and 1,109 \((s = 347)\) stems ha\(^{-1}\) for the single-cohort stands aged 61–70, 71–80, 81–90, 91–100, 101–110, and 111–120 years. Bimodal, reverse-J, and bistaged stands had mean density levels of 1,903 \((s = 1,239)\), 7,289 \((s = 1,421)\), and 17,578 stems ha\(^{-1}\) \((s = 2,732)\), respectively.

Mean tree frequencies (stems ha\(^{-1}\)) were of the order balsam fir \((\bar{x} = 6163, s = 7074.2)\) > black spruce \((\bar{x} = 1083, s = 1644.1)\) > white spruce \((\bar{x} = 563, s = 1511.7)\) > white birch \((\bar{x} = 291, s = 877.7)\) (Figure 8-1, Table 8-2).
Table 8-1. Live species composition and density of Little Grand Lake stands.

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<th>Percent of total tree density</th>
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<td>5,022</td>
<td>0</td>
<td>44</td>
<td>44</td>
<td>14,267</td>
<td>64.2</td>
</tr>
</tbody>
</table>

*a* bF = balsam fir, bS = black spruce, wS = white spruce, wB = white birch, Other = mountain maple and mountain ash.
Figure 8-1. Boxplots showing relative species composition (live and dead trees) among 50 Little Grand Lake stands. Box limits represent the 25th and 75th percentiles of the data. Error bars indicate the 10th and 90th percentiles, with dots indicating the 5th and 95th percentile outliers. The median and mean are given by the solid and dashed line, respectively.
Table 8-2. Statistical comparison of live and dead tree species composition among 50 Little Grand Lake stands.

**Live trees**

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean trees ha(^{-1})</th>
<th>Standard error</th>
<th>Balsam fir</th>
<th>Black spruce</th>
<th>White spruce</th>
<th>White birch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsam fir</td>
<td>6163.3</td>
<td>1000.4</td>
<td>–</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Black spruce</td>
<td>1083.0</td>
<td>232.5</td>
<td>&lt; 0.0001</td>
<td>–</td>
<td>0.0484</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>White spruce</td>
<td>563.3</td>
<td>213.8</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0484</td>
<td>–</td>
<td>0.0284</td>
</tr>
<tr>
<td>White birch</td>
<td>291.3</td>
<td>124.1</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td>0.0284</td>
<td>–</td>
</tr>
</tbody>
</table>

**Dead trees**

<table>
<thead>
<tr>
<th>Species</th>
<th>Mean trees ha(^{-1})</th>
<th>Standard error</th>
<th>Balsam fir</th>
<th>Black spruce</th>
<th>White spruce</th>
<th>White birch</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsam Fir</td>
<td>2883.7</td>
<td>507.5</td>
<td>–</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td>Black spruce</td>
<td>78.3</td>
<td>20.4</td>
<td>&lt; 0.0001</td>
<td>–</td>
<td>0.4137</td>
<td>0.0002</td>
</tr>
<tr>
<td>White spruce</td>
<td>54.6</td>
<td>12.3</td>
<td>&lt; 0.0001</td>
<td>&lt; 0.4137</td>
<td>–</td>
<td>0.0039</td>
</tr>
<tr>
<td>White birch</td>
<td>15.3</td>
<td>3.8</td>
<td>&lt; 0.0001</td>
<td>0.0002</td>
<td>0.0039</td>
<td>–</td>
</tr>
</tbody>
</table>

Note that the mean densities were calculated using values taken from a chronosequence of stands exhibiting a wide range of densities (864 to 38,000 stems ha\(^{-1}\)). Standard deviations were, therefore, understandably high. Mountain ash (*Sorbus americana* Marsh.), mountain maple (*Acer spicatum* Lam.) and larch were rarely present and were therefore excluded from subsequent analysis.

In most plots, balsam fir density accounted for > 85% of the total stem density (Table 8-1). Exceptions were the younger single-cohort stands 21–40 years old, and the bimodal, reverse-J and bistaged stands. In both the young single-cohort stands and the old
bimodal stands, white spruce accounted for 15% to 54% of the total stem density. By contrast, in both the reverse-J and bistaged stands, black spruce accounted for a significant proportion of the live stems, up to 60%–70% in some of the reverse-J stands. This difference in spruce densities was due, no doubt, to site quality differences, and possibly the influence of moose herbivory in the young single-cohort stands. Such departures from balsam fir hegemony were also confirmed for dead tree densities (Table 8-3).

8.2 TOTAL SNAG DENSITIES

Total dead density ranged from 375 to 17,200 stems ha\(^{-1}\) (Table 8-3). Maximum snag densities occurred in the young self-thinning, single-cohort stands (61–70 years) with successive diminution to < 1,000 snags ha\(^{-1}\) in the older single-cohort and bimodal stands. Snag densities were understandably low in the young pre-self-thinning stands (\(\bar{x} = 836\) stems ha\(^{-1}\), \(s = 376\)). Snag densities were of the order 10,666 (\(s = 9,240\)), 9,907 (\(s = 279\)), 6,923 (\(s = 2,141\)), 3,860 (\(s = 2,271\)), 1,496 (\(s = 667\)), and 2,370 (\(s = 1,677\)) stems ha\(^{-1}\) for the single-cohort stands aged 61–70, 71–80, 81–90, 91–100, 101–110, and 111–120 years, respectively. Bimodal, reverse-J, and bistaged stands had snag density levels of 1,157 (\(s = 1,033\)), 720 (\(s = 517\)) and 845 (\(s = 455\)) stems ha\(^{-1}\). Balsam fir dominated the species composition of standing dead snags, making up an average of 89.2% of snags among all sampled plots. Percentage figures for black spruce, white spruce and white birch were 6.5%, 3.3% and 1.0%, respectively. Average dead tree frequencies were of the order balsam fir (\(\bar{x} = 2,883.7, s = 3,588.5\)) > black spruce (\(\bar{x} = 78.3, s = 144.0\)) = white spruce (\(\bar{x} = 54.6, s = 87.0\)) > white birch (\(\bar{x} = 15.3, s = 26.7\)) (Table 8-2, Figure 8-1).
Table 8-3. Dead tree species composition and density of 50 Little Grand Lake stands.

<table>
<thead>
<tr>
<th>Stand type</th>
<th>Plot</th>
<th>bF</th>
<th>bS</th>
<th>wS</th>
<th>wB</th>
<th>Other</th>
<th>Total</th>
<th>Percent of total tree density</th>
</tr>
</thead>
<tbody>
<tr>
<td>Single-cohort (11–20 yrs)</td>
<td>6</td>
<td>975</td>
<td>0</td>
<td>0</td>
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<td>0</td>
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<td>100</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>1,050</td>
<td>0</td>
<td>25</td>
<td>25</td>
<td>0</td>
<td>1,100</td>
<td>95.5 2.3 2.3 0</td>
</tr>
<tr>
<td></td>
<td>38</td>
<td>1,200</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1,200</td>
<td>100 0 0 0</td>
</tr>
<tr>
<td>Single-cohort (21–30 yrs)</td>
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<td>575</td>
<td>0</td>
<td>25</td>
<td>75</td>
<td>0</td>
<td>675</td>
<td>85.2 3.7 11.1 0</td>
</tr>
<tr>
<td></td>
<td>23</td>
<td>225</td>
<td>0</td>
<td>150</td>
<td>0</td>
<td>0</td>
<td>375</td>
<td>60   0 40 0</td>
</tr>
<tr>
<td></td>
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<td>0</td>
<td>100</td>
<td>0</td>
<td>0</td>
<td>1,500</td>
<td>93.3 6.7 0 0</td>
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<tr>
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<td>50</td>
<td>0</td>
<td>0</td>
<td>625</td>
<td>92   8 0 0</td>
</tr>
<tr>
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<td>33</td>
<td>0</td>
<td>0</td>
<td>600</td>
<td>94.5 0 5.5 0</td>
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<td>Single-cohort (31–40 yrs)</td>
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<td>75</td>
<td>0</td>
<td>0</td>
<td>475</td>
<td>84.2 15.8 0 0</td>
</tr>
<tr>
<td>Single-cohort (61–70 yrs)</td>
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<td>0</td>
<td>0</td>
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<td>Single-cohort (71–80 yrs)</td>
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<td>0</td>
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<td>0</td>
<td>9,500</td>
<td>97.9 2.1 0 0</td>
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<td>25</td>
<td>0</td>
<td>9,950</td>
<td>98 0.8 1 0.3 0</td>
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<tr>
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<td>0</td>
<td>6,044</td>
<td>99.3 0.7 0 0</td>
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<td>0</td>
<td>4,575</td>
<td>96.2 1.6 2.2 0</td>
</tr>
<tr>
<td>Single-cohort (91–100 yrs)</td>
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<td>425</td>
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<td>0</td>
<td>9,125</td>
<td>92.9 2.5 4.7 0</td>
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<td>4,208</td>
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</tr>
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<td>94.1 3.9 1 0</td>
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<td>2,775</td>
<td>92.8 3.6 2.7 0</td>
</tr>
</tbody>
</table>
Table 8-3. (Continued)

<table>
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<tr>
<th>Plot</th>
<th>bF</th>
<th>bS</th>
<th>wS</th>
<th>wB</th>
<th>Other</th>
<th>Total</th>
<th>Percent of total tree density</th>
</tr>
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<tbody>
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<td>bS</td>
<td>wS</td>
<td>wB</td>
<td>Other</td>
<td>bF</td>
<td>bS</td>
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<td>889</td>
<td>75.0</td>
</tr>
<tr>
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<td>356</td>
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<td>0</td>
<td>0</td>
<td>0</td>
<td>445</td>
<td>80.0</td>
</tr>
<tr>
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<td>222</td>
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<td>0</td>
<td>0</td>
<td>578</td>
<td>61.6</td>
</tr>
</tbody>
</table>

*a bF = balsam fir, bS = black spruce, wS = white spruce, wB = white birch, Other = mountain maple and mountain ash.*
Black spruce snags were most prevalent in the bistaged and reverse-J stands, a consequence, no doubt, of the lower site quality of these stands. White spruce snags, noticeably absent in the reverse-J and bistaged stands, normally made up < 5% of snags in any stand with all bimodal and some of the young single-cohort stands being exceptions.

8.3 TREE DIAMETER DISTRIBUTION

Diagrammatic representations of the four stand structural types are given in Figure 8-2. The single-cohort and bimodal stands are presented as a chronosequence that follow the classic stand developmental sequence of stand initiation, stem exclusion, stand reinitiation, transition old-growth and old-growth (Oliver and Larson 1996). Both reverse-J and bistaged stands are each represented by unique stand diagrams. Self-thinning dynamics and development of the single-cohort–bimodal chronosequence are considered in greater detail in Chapter 11. Figure 8-3 provides photographs of the stand development stages characteristic of the single-cohort–bimodal chronosequence. Quantification of the four stand types follow.

8.3.1 Single-Cohort Stands

These stands were characterized by both truncated “reverse-J”-type diameter distributions in the younger stands (0–40 years old) and fully developed modal diameter distributions in the older stands (61–120 years old) (Figure 8-4).

Quadratic mean diameter (all live trees) increased from a low of 1.9 to 5.9 cm in the youngest stands (11–30 years old) to a range of 19 to 24 cm in the oldest stands (101–120 years old) (Table 7-4). Average tree density was variable in the younger stands, no doubt
Figure 8-2. Diagrammatic representation of stand development in balsam fir–spruce forests after insect-mediated stand disturbance, Little Grand Lake.
Figure 8-2. (Continued)
Figure 8-3. Stand development stages, Little Grand Lake. (A) Stand initiation with vigorous, released balsam fir. (B) Early stem exclusion. (C) Late stem exclusion. (D) Early stand reinitiation. (E) Late stand reinitiation–transition old-growth with well-developed seedling bank. (F) Beginning of stand breakup.
Figure 8-4. Live tree diameter distribution by species, Little Grand Lake. Stands are grouped according to one of four stand structure types: (1) single-cohort, (2) bimodal, (3) reverse-J, and (4) bistaged. Single cohort stands are further grouped according to 10-year total age classes.
Figure 8-4. (Continued)
Figure 8-4. (Continued)
Table 8-4. (Continued)
a function of variable stocking levels during stand re-initiation caused by variation in annual seed rain, germination rates, spatial pattern of suitable microsites, as well as the non-sampling of saplings < 1.3 m high. After canopy closure (61–70 years), stem density decreased steadily from a high of just over 31,000 stems ha\(^{-1}\) in the younger stands (61–70 years) to a low of 860 stems ha\(^{-1}\) in the oldest stands. Average stand age (total age) ranged from 15 to 117 years across the chronosequence.

Balsam fir dominated stand composition, with white spruce, black spruce and white birch occurring in variable amounts depending, for the most part, on site quality and history of insect herbivory. Of note is the high white spruce composition in some of the young regenerating stands (plots 15, 23, 39, 42, 46, and 51). Post-disturbance mature veteran trees were particularly evident in the youngest stands.
8.3.2 Bimodal Stands

Six stands were identified as irregular, bimodal stands (Figure 8-4). Among the oldest of all sampled stands (average age of each stand ranged from 106 to 136 years), these stands were characterized by the occurrence of stand break-up combined with release of the seedling bank in the canopy gaps. In one sense, these stands are simply the oldest “single-cohort” stands that have initiated stand break-up, and therefore could have been classified as old, single-cohort stands. However, sufficient distinction was evident to warrant a separate category. Despite the separation, it is important to understand these stands as essentially the oldest in a chronosequence.

The relative species composition of the canopy and regeneration cohorts are of interest. Whereas the mature canopy was dominated by balsam fir, a significant proportion of the regeneration was comprised of black and white spruce. White birch, uncommon in the regeneration stratum, occurred as some of the largest trees in the mature canopy. In general, these stands were beginning to break up, with mortality losses of dominant trees by windthrow, tree snap and standing death. The stands were generally open, with a mean total tree density of 1,903 stems ha\(^{-1}\) (s = 1,239).

8.3.3 Reverse-J Stands

These stands distinguished themselves by the presence of a reverse-J diameter distribution (Figure 8-4). Maximum tree diameter rarely exceeded 30 cm. Mean stand age was 93.5 years (s = 10.6). Range of tree ages was widest among the sampled stands, averaging 155 years (s = 7.0). Such structurally and spatially complex stands were generally found on poorer sites characterized by high black spruce content and ground flora.
indicative of low site quality in regional boreal forests. Some reverse-J stands were also dominated by balsam fir (especially plot 47) and probably owed their irregular structure to a history of mild insect herbivory that partially thinned the dominant canopy allowing for release of advance regeneration in the canopy gaps. Therefore, a combination of both poorer site quality, as well as tree release and recruitment in small insect-mediated canopy gaps probably contributed to the development of a reverse-J diameter distribution. Stand density was generally consistent among the plots, averaging 7,289 stems ha\(^{-1}\) (\(s = 1,421\)).

8.3.4 **Bistaged Stands**

Occurring on sites of generally poorer site quality, bistaged stands were characterized by a dense regenerating cohort overtopped by several large relict black spruce (Figure 8-5).

![Figure 8-5. Bistaged stands, Little Grand Lake. Old, veteran black spruce overtopping dense regeneration of balsam fir–black spruce.](image-url)
Diameter distributions were similar to those expressed by reverse-J stands, but the much greater frequency of regeneration < 10 cm dbh successfully distinguished bistaged stands from reverse-J stands (Figure 8-4). Quadratic mean diameter ranged from 3.9 to 4.3 cm. Diameters of veteran trees did not exceed 30 cm. Average tree density was 17,578 stems ha\(^{-1}\) (s = 2,732), with the highest percentage of stems \(\leq 10\) cm dbh. The regenerating cohort was up to four times older than comparatively sized regeneration in the single-cohort stands, this being another indication of the poorer site quality.

8.4 LIVE TREE–SNAG DENSITY BY DIAMETER CLASS

The relationship between the density of both dead and live trees helped to clarify the distinctive structural character of single-cohort, bimodal, reverse-J and bistaged stand types (Figure 8-6). Changes in the density structure of live and dead trees may be understood in terms of three identified phases: (1) post-insect disturbance–pre-self-thinning, (2) active self-thinning and density-dependent mortality, and (3) density-independent mortality.

8.4.1 Phase 1: Post-Insect Disturbance

Two stand types comprised this phase: (1) young, regenerating single-cohort stands (< 40 years of age), and (2) the bistaged stands. Inferred differences in site quality between the two stand types were no doubt significant in controlling structural differences. The relative white spruce–white birch–black spruce content in each stand grouping was instructive. In the young single-cohort stands, both white spruce and white birch accounted for an average of 67% of the total basal area. By contrast, these same two species made up only 1.2% of the total basal area of the bistaged stands; an order of magnitude smaller. The
Figure 8-6. Comparison of live and dead tree density for Little Grand Lake stands. Stands are grouped according to one of four stand types: (1) single-cohort, (2) bimodal, (3) reverse-J, and (4) bistaged. Single-cohort stands are further classified into 10-year total age classes.
Figure 8-6. (Continued)
Figure 8-6. (Continued)
Figure 8-6. (Continued)
opposite scenario occurred for black spruce, which made up 4% and 47% of the basal area of the young single-cohort stands and the bistaged stands, respectively.

8.4.1.1 Young Single-Cohort Stands (11–40 Years Old)

Characteristic of all nine stands was a dense stratum of regeneration (0–4 cm dbh, $\bar{x} = 10,737$ stems ha$^{-1}$, $s = 10,566$, range = 2,725 to 34,700 stems ha$^{-1}$, average height range of 2.7–5.0 m.) The relatively low densities of dead regeneration (0–4 cm dbh, $\bar{x} = 65.7$ stems ha$^{-1}$, $s = 67.2$, range = 0 to 200 stems ha$^{-1}$) indicated that active self-thinning had not commenced. An average of 1% of the small diameter trees (0–4 cm dbh) were counted as dead. Overtopping the regeneration was a canopy of large diameter veteran snags (dbh up to 30 + cm), legacies from historic insect outbreaks. The bark had fallen from most snags, most of which had broken tops. Large quantities of snags had fallen to the forest floor (not measured). Live veteran trees were rare, except in plot 46 that had live veteran trees exceeding 40 cm dbh.
8.4.1.2 Bistaged Stands

The bistaged stands on the poorer sites were also in the pre-stem exclusion stage. Live regeneration density (0–4 cm dbh) averaged 13,589 stems ha\(^{-1}\) (s = 1,440.3). As with the young single-cohort stands, active self-thinning had not commenced, with dead snags (0–4 cm dbh) averaging only 400 stems ha\(^{-1}\) (s = 363). An average of 2.8% of the total regeneration in the 0–4 cm dbh class was tallied as dead. Overtopping the regeneration were live dominant black spruce.

8.4.2 Phase 2. Active Self-Thinning and Density-Dependent Mortality

This period of stand development generally occurred across the age range 60 to 100–120 years. Active self-thinning increased production of dead stems, the density of which greatly surpassed live tree density, especially in the smaller dbh classes (Figure 8-6). Of note was the relative change in dead and live diameter distributions. With stand development, the diameter distribution of live trees assumed a generally modal–normal distribution, the mean of which shifted towards the right as the trees grew in diameter. In contrast, the diameter distribution of dead trees was characterized by a distinct lognormal-type distribution. During this phase, most of the dead trees were produced through self-thinning. As well, both density-dependent mortality and long-standing legacies from historic insect outbreaks contributed to the presence of larger snags.

8.4.3 Phase 3. Density-Independent Mortality and Stand Break-up

As stand development progressed, snags were increasingly present across the full range of tree diameters. In the bimodal stands in particular, both the lognormal distribution
of snags and modal distribution of live trees were no longer evident as the stands experienced break-up and increased recruitment of young, small-diameter cohorts.

The reverse-J stands also had snags across the full range of tree diameters. Notable was the absence of density-dependent mortality and generally lognormal snag distribution characteristic of the actively self-thinning stands. A possible exception was the higher site quality stand 47 that was characterized by some level of self-thinning among the small diameter trees found in canopy gaps.

8.5 BASAL AREA STRUCTURE

As with tree density, basal area distributions were classified according to the four identified stand structural types; single-cohort, bimodal, reverse-J, and bistaged. Basal area distributions of the single-cohort stands were further classified according to average stand age and provided the basis for an analysis of basal area change across a chronosequence of both single-cohort and bimodal stands. Analysis of basal area by diameter class and species was very helpful in clarifying stand structural heterogeneity.

8.5.1 Total Live and Dead Basal Area

Given the wide range of stand development stages among the single-cohort stands, both live and dead basal area were highly variable (Figure 8-7). Across the chronosequence of single-cohort stands, total live basal area ranged from a minimum of 1.5 m$^2$ ha$^{-1}$ in the youngest stands to a maximum of 60 m$^2$ ha$^{-1}$ in the 71–80-year-old single-cohort stands (Table 8-4). Mean live basal area values for the single-cohort, bimodal, reverse-J and bistaged stands were 35.5 ($s = 17.9$), 40.1 ($s = 4.3$), 26.2 ($s = 4.8$) and 31.6 ($s = 9.3$) m$^2$ ha$^{-1}$. 
Figure 8-7. Boxplots showing relative basal area accumulations for both live and dead trees in each of four stand types, Little Grand Lake. Box limits represent the 25th and 75th percentiles of the data. Error bars represent the 10th and 90th percentiles. Dots represent the 5th and 95th percentile outliers. Median and mean are given by the solid and dashed line, respectively.
Table 8-4. Total live basal area by tree species for Little Grand Lake stands. Stands are classified into four types: (1) single-cohort, (2) bimodal, (3) reverse-J, and (4) bistaged. Single-cohort stands are further classified into 10-year age classes.

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*B = balsam fir, BS = black spruce, WS = white spruce, WB = white birch, Other = mountain maple, mountain ash, larch.
Note that the basal area values for the single-cohort stands cover a wide range of stand development.

Dead basal area for the single-cohort, bimodal, reverse-J, and bistaged stands averaged 18.05 (s = 6.3), 13.82 (s = 4.7), 8.3 (s = 2.2) and 9.6 m² ha⁻¹ (s = 5.6), respectively (Table 8-5, Figure 8-7). Depending on the stage of stand development among the single-cohort stands, between 14% and 94% of the total standing basal area was dead. For the bimodal, reverse-J and bistaged stand types, dead basal area was generally consistent among all stand types, accounting for 25.6%, 24.1%, and 23.2% of the total standing basal area, respectively.

The basal area of most stands was dominated by balsam fir. This was particularly true for all single-cohort stands older than 30 years of age and for the six bimodal stands. In these stands, balsam fir basal area ranged from 70% to 95%. In the eight youngest stands (< 30 years of age), either white spruce (six stands) or white birch (two stands) had the greatest percentage of basal area, with balsam fir basal area not exceeding 43%. Both reverse-J and bistaged stands had the highest levels of black spruce basal area with little or no occurrence of either white spruce or white birch.

8.5.2 Basal Area by Diameter Class

Stand structural heterogeneity was particularly evident from an analysis of basal area distribution by tree diameter class. Unlike tree density, stand basal area provided a clearer indication of species-specific site occupancy, the relationship between disturbance history and biological legacies, and post-disturbance stand development.
Table 8-5. Total dead basal area by tree species for Little Grand Lake stands. Stands are classified into four types: (1) single-cohort, (2) bimodal, (3) reverse-J, and (4) bistaged. Single-cohort stands are further classified into 10-year age classes.

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<th>Percent dead basal area</th>
<th>% total live/dead</th>
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<td>wS</td>
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*bF = balsam fir, bS = black spruce, wS = white spruce, wB = white birch, Other = mountain maple, mountain ash, larch.
8.5.2.1 Single-Cohort Stands

In the youngest stands (6, 8, and 38, 11–20 years old) a large proportion of the live basal area was composed of dominant, veteran white birch or white spruce (Figure 8-8, Figure 8-9). Balsam fir made up most of the regeneration basal area. Balsam fir snags dominated the stand, making up an average of 93% of the dead basal area for the three stands combined. Snags made up 81% of the total standing live and dead basal area. Veteran white birch, white spruce and black spruce were not uncommon in various single-cohort stands throughout the chronosequence.

White spruce dominated the regeneration basal area of all six plots of age class 21–40 years, comprising an average of 53% of the total live basal area. As with the youngest stands, the largest live trees were veteran white spruce and white birch, with a small amount of black spruce in plot 42. An exception was stand 46 in which relict, large-diameter balsam fir comprised 71% of the live basal area. Balsam fir and white spruce snags averaged 81% and 21% of the snag basal area, respectively. Snags comprised an average of 57% of the total standing live and dead basal area in the six stands. White spruce was noticeably absent in the two stands of age class 61–70 years (9 and 19). The replacement of white spruce by black spruce in these stands was attributed simply to differences in site quality.

Stands of age class 61–70 years marked a shift in stand structure. This was indicated by the evident changes in both quadratic mean diameter and stem density. Of particular note was the development of modal basal area distributions for all single-cohort
Figure 8-8. Live tree basal area distribution by species, Little Grand Lake. Stands grouped by stand type: (1) single-cohort, (b) bimodal, (c) reverse-J, and (4) bistaged. Single-cohort stands further classified according to 10-year total age classes.
Figure 8-8. (Continued)
Figure 8-8. (Continued)
Figure 8-8. (Continued)
stands and a generally U-shaped dead basal area distribution. Self-thinning or stem exclusion promoted an increase in dead basal area in the smaller diameter trees. The minimum levels of basal area in the generally middle range of tree diameters were bracketed by dead basal area accumulations in both the smaller and larger diameter ranges. Self-thinning or stem exclusion probably accounted for the accumulations of dead basal area in the smaller dbh classes. As for the accumulations of basal area in the higher dbh classes, both relict snags and density-independent mortality were probably responsible. Such U-shaped trends occurred for the most part in stands of age class 61–100 years, after which such trends were less obvious or absent. Trees of the largest diameter in each plot tended to be either black spruce, white spruce or white birch.

8.5.2.2 Bimodal, Reverse-J and Bistaged Stands

Basal area distributions for the six bimodal stands were left skewed, with the larger trees making up the bulk of the basal area. Regeneration cohorts were identified by the left-
Figure 8-9. Live and dead basal area for all pooled species, Little Grand Lake. Stands are grouped according to stand type: (1) single-cohort, (2) bimodal, (3) reverse-J, and (4) bistaged. Single-cohort stands are further classified according to 10-year total age classes.
Figure 8-9. (Continued)
Figure 8-9. (Continued)
Figure 8-9. (Continued)
skewed basal area distribution for trees smaller than 10–15 cm dbh. Basal area
distributions for the nine reverse-J stands were divided into those stands that showed
generally equal proportions of total basal area across the dbh range (plots 5, 14, 28, 30, 33,
and 47) and those stands that showed an accumulation of basal area in the larger sized trees
(plots 1, 17, and 41). The larger proportion of dead basal area tended to reside in the larger
trees. Relatively smaller levels of dead basal area occurred for trees < 10 cm dbh.

The bistaged stands were characterized generally by the large accumulations of
basal area in dominant black spruce. Except for plot 26 in which the largest trees were
balsam fir, the largest diameter trees were almost exclusively black spruce, whereas the
smallest diameter trees were dominated by balsam fir. Generally absent were trees in the
mid-dbh range of 10–15 cm. Such relative proportions in basal area characterized two-
staged stands in which dominant, large-diameter black spruce, (or balsam fir in the case of
plot 26) overtopped a dense, regenerating stratum of mostly balsam fir. In all four plots the
largest diameter trees made up most of the snag basal area.
8.6 STAND HEIGHT

Tree height frequencies were grouped according to the initial stand classification that was based on a combination of both size (dbh) and total age structure. Note that stand total age classes were used as a proxy measure of stand development. Generally, it is better to use stand height as a measure of stand development rather than age. As trees age and increase in height, crowns tend to close. This leads to changes in stand resource dynamics and self-thinning. Furthermore, critical height levels at which self-thinning occurs are a function of the stage of stand development and not of the total tree age per se. Therefore, it is height, and not necessarily age that is the useful indicator of stand development, especially in stands dominated by shade-tolerant species. In this case, however, stand age classes proved to be adequate proxy measures of temporal stand development.

Except for the reverse-J and bistaged stands, tree height frequencies generally exhibited unimodal distributions characteristic of single-cohort stands (Figure 8-10). Seventy-five percentile heights ranged from a minimum of 2.9 m in one of the youngest stands (plot 6) to a maximum recorded value of 20.2 m in one of the oldest single-cohort stands (plot 7). The “multi-layered” nature of the canopies of the reverse-J stands was reflected in the generally right-skewed height distributions with trees rarely exceeding 15 m in height. For bistaged stands, the upper canopy stratum was dominated by veteran black spruce ranging in height from 12–17 m. Details of the height structure by species are given for each plot in Table 8-6. Both 75 and 90 percentile height figures were provided along with average stand height values for each plot. Maximum recorded individual tree heights were just over 22 m for both balsam fir and white spruce.
Figure 8-10. Tree height frequency for pooled species, Little Grand Lake. Stands are grouped by stand type: (1) single-cohort, (2) bimodal, (3) reverse-J, and (4) bistaged. Single-cohort stands are further classified according to 10-year total age classes.
Figure 8-10. (Continued)
Figure 8-10. (Continued)
Figure 8-10. (Continued)
8.7 TREE HEIGHT–DIAMETER RELATIONSHIPS

Individual tree height–dbh relationships for balsam fir were nearly equally expressed by four significant ($P < 0.0001$) asymptotic, 3-parameter, non-linear functions including Chapman–Richards, Weibull, modified logistic and Schnute (Figure 8-11). For both black spruce and white spruce, the height–dbh relationships were best expressed by significant ($P < 0.0001$) linear regressions. In general, all three species had generally similar height–dbh relationships. For all models, a weight of $1/dbh$ corrected the heteroscedasticity of the error variances. Estimated parameters, 95% confidence intervals and fit statistics for each model are given in Table 8-7.
Table 8-6. Mean tree heights and statistics for Little Grand Lake stands. Heights of veteran trees have been excluded.

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<td>( \bar{x} )</td>
<td>( s^b )</td>
<td>( n )</td>
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<td>46</td>
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<td>-</td>
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<tr>
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<tr>
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<td>0.69</td>
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<tr>
<td></td>
<td>13</td>
<td>16</td>
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<td>1.52</td>
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Table 8-6. (Continued)

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<th>Black spruce</th>
<th>White spruce</th>
<th>All species combined</th>
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<td>$n^a$</td>
<td>$\bar{X}$</td>
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<td>$s$</td>
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<td>$\bar{X}$</td>
<td>$s$</td>
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<td></td>
<td>$n$</td>
<td>$\bar{X}$</td>
<td>$s$</td>
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<td>11</td>
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<td>16.1</td>
<td>1.70</td>
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<td>1.70</td>
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<td>22</td>
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<td>13.5</td>
<td>2.92</td>
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<td>36</td>
<td>22</td>
<td>15.9</td>
<td>1.92</td>
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<td>Reverse-J</td>
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<td>5</td>
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<td>3.6</td>
<td>1.52</td>
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<td>5.4</td>
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</tr>
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<td>49</td>
<td>17</td>
<td>4.3</td>
<td>1.49</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ $n$ = number of trees.

$^b$ $s$ = standard deviation.

$^c$ 75th and 90th height percentiles.
Figure 8-11. Tree height–diameter relationships for balsam fir, black spruce, and white spruce, Little Grand Lake. Estimated parameters, 95% confidence intervals, and fit statistics are given in Table 8-7. All regressions are significant at $P < 0.0001$. 
Table 8-7. Estimated parameters, 95% confidence intervals, and fit statistics for nonlinear balsam fir height–diameter relationships, Little Grand Lake. Linear regressions are given for both black and white spruce. For all functions, weight = 1/dbh. All regressions are significant at $P < 0.0001$.

<table>
<thead>
<tr>
<th>Function</th>
<th>Species</th>
<th>Estimated parameter coefficients (95% confidence intervals)$^a$</th>
<th>$n^b$</th>
<th>$R^2c$</th>
<th>RMSE$_w$$^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Chapman–Richards</td>
<td>Balsam fir</td>
<td>$35.6753, 0.0281, 1.1982$</td>
<td>932</td>
<td>0.9596</td>
<td>0.3658</td>
</tr>
<tr>
<td>Weibull</td>
<td>Balsam fir</td>
<td>(28.7656, 42.5849), (0.0206, 0.0357), (1.1408, 1.2556)</td>
<td>932</td>
<td>0.9599</td>
<td>0.3647</td>
</tr>
<tr>
<td>Schnute</td>
<td>Balsam fir</td>
<td>$29.9764, 0.0162, 1.1890$</td>
<td>932</td>
<td>0.9609</td>
<td>0.3601</td>
</tr>
<tr>
<td>Modified-Logistic</td>
<td>Balsam fir</td>
<td>(24.8203, 35.1324), (0.0141, 0.0183), (1.1442, 1.2338)</td>
<td>932</td>
<td>0.9596</td>
<td>0.3659</td>
</tr>
<tr>
<td>Logistic</td>
<td>Balsam fir</td>
<td>$0.0650, 0.3905, 24.5799$</td>
<td>932</td>
<td>0.9596</td>
<td>0.3659</td>
</tr>
<tr>
<td>Linear model</td>
<td>Black spruce</td>
<td>$52.6141, 0.00934, 1.1877$</td>
<td>932</td>
<td>0.9596</td>
<td>0.3659</td>
</tr>
<tr>
<td></td>
<td>White spruce</td>
<td>(39.9460, 65.2822), (0.00758, 0.0111), (1.1355, 1.2399)</td>
<td>174</td>
<td>0.9518</td>
<td>0.3038</td>
</tr>
<tr>
<td></td>
<td></td>
<td>$1.2252, 0.5748, -$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>(1.1163, 1.3340), (0.5554, 0.5943)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>$1.1708, 0.601, -$</td>
<td>152</td>
<td>0.9261</td>
<td>0.3621</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(0.9606, 1.3810), (0.5741, 0.6289)</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a$ Confidence intervals are asymptotic for nonlinear functions.

$^b$ $n$ = number of trees.

$^c$ For nonlinear functions, the coefficient of determination is a pseudo $R^2$ defined as $1 – \text{sum squares residual/sum squares total}$ (corrected).

$^d$ Weighted root mean square error.
8.8 STAND HEIGHT–QUADRATIC MEAN DIAMETER RELATIONSHIP

Changes in stand height (75 percentile height) as a function of both stand quadratic mean diameter (qmd) are given in Figure 8-12. The relationship was best described by a significant sigmoidal function that showed asymptotic character in the range of 15 to 20 m stand height.

![Figure 8-12](image)

Figure 8-12. Stand 75 percentile height–quadratic mean diameter relationship for single-cohort and bimodal stands, Little Grand Lake. Estimated parameters (approximate 95% confidence intervals): \( a = 17.1524 \) (15.5439, 18.7609), \( b = 8.5191 \) (7.1921, 9.8461), \( c = 4.0887 \) (2.939, 5.2384). Sigmoidal function significant at \( P < 0.0001 \).

8.9 SEEDLING BANK REGENERATION

In single-cohort and bimodal stands, balsam fir dominated seedling composition with 91% to 100% of the seedlings in any particular plot being balsam fir. White spruce
and white birch composition ranged from 0 to 4% and 0 to 6.4%, respectively. Only one stand had black spruce regeneration that composed 1% of the total regeneration (Table 8-8). Of the 6,727 live seedlings examined, 96.8% were balsam fir, with black spruce, white spruce, white birch, and non-tree (principally *Sorbus*) seedlings making up 0.03%, 0.6%, 2.3% and 0.3% of the total seedling count, respectively. Of the 86 dead seedlings examined, 98.8% were balsam fir with white birch making up 1.2%. No dead black spruce, white spruce or other seedlings were tallied.

Balsam fir seedling density ranged from a low of 2,500 stems ha\(^{-1}\) in the 61–70 year old stands to a maximum of 482,500 stems ha\(^{-1}\) in the 91–100 year old stands. Black spruce, white spruce, white birch and *Sorbus* regeneration occurred at levels generally two orders of magnitude less than balsam fir. Black spruce seedlings were rare, occurring in only one plot. White spruce and white birch density ranged from 0 to 3,200 and from 0 to 12,400 stems ha\(^{-1}\), respectively. Except for the occurrence of white spruce in plot 4, the regeneration in all stands of age class 61–80 years was composed entirely of balsam fir. Only in stands of age class 81+ years did the other tree species occur with any consistency. Total dead seedling density ranged from 0 to 8,400 stems ha\(^{-1}\) and was dominated by balsam fir.

Seedling density variability as measured by standard deviation was high with standard deviations sometimes exceeding the mean density value. In plot 35, for example, the mean number of balsam fir seedlings m\(^{-2}\) was 37.3 (\(n = 25\) regeneration subplots) with a standard deviation of 34.7 and a range of 162. Spatial variability of seedling establishment and microsite conditions, as well as sample size, no doubt contributed to the high variability associated with mean density values.
Table 8-8. Total and species seedling density for modal and bimodal stands, Little Grand Lake. Plots are arranged in terms of increasing mean stand age.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Mean stand age (s')</th>
<th>live seedling density (s)</th>
<th>Dead seedling density (s)</th>
<th>total seedling density (s)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>bF</td>
<td>bS</td>
<td>wS</td>
</tr>
<tr>
<td>19</td>
<td>60.5 (3.2)</td>
<td>2,500</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>71.1 (7.4)</td>
<td>13,333</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>72.8 (7.7)</td>
<td>26,667</td>
<td>0</td>
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<tr>
<td>43</td>
<td>75.9 (10.1)</td>
<td>80,000</td>
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<tr>
<td>10</td>
<td>79.5 (9.4)</td>
<td>20,625</td>
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<td>0</td>
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<tr>
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<td>81.7 (6.0)</td>
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<tr>
<td>25</td>
<td>84.2 (8.5)</td>
<td>161,250</td>
<td>0</td>
<td>0</td>
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<tr>
<td>16</td>
<td>89.8 (6.8)</td>
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<td>13</td>
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<td>148,125</td>
<td>625</td>
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<td>40</td>
<td>94.6 (8.2)</td>
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<tr>
<td>32</td>
<td>95.1 (7.7)</td>
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<td>99.5 (9.0)</td>
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<tr>
<td>27</td>
<td>100.2 (5.0)</td>
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Mean total seedling density (s)

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<td>13,333</td>
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<td>27,778</td>
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<tr>
<td>80,000</td>
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<tr>
<td>161,875</td>
<td>2,500</td>
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<td>194,000</td>
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<td>235,625</td>
<td>3,125</td>
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<td>245,625</td>
<td>2,500</td>
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<td>133,814</td>
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<td>Plot</td>
<td>Mean stand age ($\bar{x}$)</td>
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<td>24</td>
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<td>(9.5)</td>
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<td>(22.2)</td>
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<tr>
<td>48</td>
<td>135.7</td>
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<tr>
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<td>(36.0)</td>
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</tbody>
</table>

$s = $standard deviation.  
$n = $number of stands sampled.  
$bf = $balsam fir, $bS = $black spruce, $wS = $white spruce, $wB = $white birch, $Sorbus = Sorbus americana Marsh.
8.10 SEEDLING ALLOMETRY

Except for plot 2 (low sample size at \( n = 12 \) seedlings), all plots displayed significant, monotonic balsam fir height–basal diameter correlations (Figure 8-13). A power function \( Y = ax^b \) best modeled the height–basal diameter relationship of the combined data set (Figure 8-14). Greatest relative height growth occurred for seedlings up to approximately 3 mm in basal diameter. For larger seedlings, height growth rate was reduced to a steady linear rate of increase. Given the small number of white spruce and white birch seedlings, all analysis was carried out on the combined data set for each species. For both white spruce and white birch seedlings, the power function best expressed the height–basal diameter relationship. In general, seedling height growth rate was of the order white birch > white spruce > balsam fir.

8.11 CONCLUSION

The structure of the four stand types identified in Chapter 7 (single-cohort, bimodal, reverse-J, and bistaged) were examined in detail. Analysis of species composition, stem density, and diameter and height characteristics of both the tree (live and dead) and regeneration layer helped to clarify the diversity of stand structure in an insect-mediated boreal forest landscape. The diversity of stand structure was a function of three processes: (1) direct insect-mediated mortality and stand initiation, (2) stand development and active self-thinning, and (3) density-independent mortality and stand break-up. The structure of
reverse-J stands growing on relatively poor sites was more a function of partial insect-mediated mortality, senescence and small-scale gap dynamics.
Figure 8-13. Balsam fir seedling height–basal diameter relationships, Little Grand Lake. Spearman rank correlation coefficient ($r_s$), significance level ($P$), and sample size ($n = \text{number of seedlings}$) are given for each plot.
Figure 8-13. (Continued)
Figure 8-14. Seedling height (ht)—basal diameter (bd) relationship for balsam fir, white spruce and white birch, Little Grand Lake. Balsam fir: $ht = 11.1745(bd^{0.6242})$, $R^2 = 0.6989$, $n = 6,588$ seedlings; White spruce: $ht = 14.9861(bd^{0.6172})$, $R^2 = 0.8811$, $n = 41$; White birch: $ht = 9.1918(bd^{0.8883})$, $R^2 = 0.6448$, $n = 154$. 
CHAPTER 9
MAIN RIVER OLD-GROWTH AGE CLASS STRUCTURE

9.1 LIVE TREE AGE DISTRIBUTION

Due to varying degrees of butt rot, not all trees provided suitable samples for determination of total tree age. Among the three sample stands, 73% to 78% of all trees provided basal ages (Table 9-1). A consistent 15% of all trees in each stand had butt rot that precluded total age determination. Of these diseased trees, from 38% to 78% were used to provide what was termed a minimum age. This was particularly helpful for estimating the minimum ages of large-diameter trees that contained only small percentages of butt rot. Dead trees comprised 6% to 11% of the total sampled stems. Of the total number of dead stems, 38% to 46% provided total ages of trees at time of death, while 48% to 60% of the dead stems were affected by butt rot. Less than 1% (0.1% to 1%) of the trees could not be aged because of sample loss and other vagaries.

Tree ages for all species ranged from 25 to 269 years for plot M1, 32 to 286 years for plot M2, and 33 to 222 years for plot M7 (Table 9-2). Except for black spruce in plot M7, all species in each plot reached maximal ages exceeding 200 years. The oldest ages recorded for balsam fir, black spruce, white spruce and white birch were 264, 264, 247, and 286 years, respectively. Trees in plot M7 were noticeably “younger” than those in the other two plots. This difference may be real or simply an artifact of sampling, given the long period of suppression commonly found in most trees. Given the slow radial growth,
Table 9-1. Number of live and dead trees sampled for age structure, Main River.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Species</th>
<th>Number of live trees</th>
<th>Number of dead trees</th>
<th>Total trees</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>Total age&lt;sup&gt;a&lt;/sup&gt;</td>
<td>Minimum&lt;sup&gt;b&lt;/sup&gt;</td>
<td>Heart rot&lt;sup&gt;c&lt;/sup&gt; (no age)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>M1</td>
<td>Balsam fir</td>
<td>568</td>
<td>63</td>
<td>75</td>
</tr>
<tr>
<td>M1</td>
<td>Black spruce</td>
<td>144</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td>M1</td>
<td>White spruce</td>
<td>54</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>M1</td>
<td>White birch</td>
<td>4</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Total (%)</td>
<td></td>
<td>770 (73.4)</td>
<td>76 (7.2)</td>
<td>82 (7.8)</td>
</tr>
<tr>
<td>M2</td>
<td>Balsam fir</td>
<td>298</td>
<td>64</td>
<td>17</td>
</tr>
<tr>
<td>M2</td>
<td>Black spruce</td>
<td>222</td>
<td>13</td>
<td>5</td>
</tr>
<tr>
<td>M2</td>
<td>White spruce</td>
<td>–</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>M2</td>
<td>White birch</td>
<td>5</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>Total (%)</td>
<td></td>
<td>525 (77.7)</td>
<td>77 (11.4)</td>
<td>22 (3.2)</td>
</tr>
<tr>
<td>M7</td>
<td>Balsam fir</td>
<td>357</td>
<td>32</td>
<td>49</td>
</tr>
<tr>
<td>M7</td>
<td>Black spruce</td>
<td>66</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>M7</td>
<td>White spruce</td>
<td>57</td>
<td>2</td>
<td>3</td>
</tr>
<tr>
<td>M7</td>
<td>White birch</td>
<td>10</td>
<td>1</td>
<td>6</td>
</tr>
<tr>
<td>Total (%)</td>
<td></td>
<td>490 (78.1)</td>
<td>36 (5.7)</td>
<td>60 (9.6)</td>
</tr>
</tbody>
</table>

<sup>a</sup> Total tree age taken at ground level.
<sup>b</sup> Minimum age of large dbh trees with heart rot.
<sup>c</sup> No age sample because of extensive heart rot.
<sup>d</sup> No age due to sample loss or other vagaries.
Table 9-2. Tree age statistics, Main River.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Species</th>
<th>$n^a$</th>
<th>Minimum</th>
<th>Maximum</th>
<th>Mean</th>
<th>Median</th>
<th>$s^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Balsam fir</td>
<td>568</td>
<td>30</td>
<td>238</td>
<td>94.2</td>
<td>84</td>
<td>38.4</td>
</tr>
<tr>
<td></td>
<td>Black spruce</td>
<td>144</td>
<td>25</td>
<td>212</td>
<td>71.7</td>
<td>65</td>
<td>33.4</td>
</tr>
<tr>
<td></td>
<td>White spruce</td>
<td>54</td>
<td>31</td>
<td>247</td>
<td>84.7</td>
<td>73</td>
<td>48.8</td>
</tr>
<tr>
<td></td>
<td>White birch$^c$</td>
<td>3</td>
<td>177</td>
<td>269</td>
<td>214</td>
<td>196</td>
<td>48.6</td>
</tr>
<tr>
<td>M2</td>
<td>Balsam fir</td>
<td>298</td>
<td>36</td>
<td>264</td>
<td>113.7</td>
<td>110</td>
<td>42.1</td>
</tr>
<tr>
<td></td>
<td>Black spruce</td>
<td>222</td>
<td>32</td>
<td>264</td>
<td>76.4</td>
<td>68</td>
<td>34.0</td>
</tr>
<tr>
<td></td>
<td>White birch</td>
<td>5</td>
<td>160</td>
<td>286</td>
<td>210.2</td>
<td>211</td>
<td>47.9</td>
</tr>
<tr>
<td>M7</td>
<td>Balsam fir</td>
<td>357</td>
<td>33</td>
<td>222</td>
<td>87.3</td>
<td>75</td>
<td>35.2</td>
</tr>
<tr>
<td></td>
<td>Black spruce</td>
<td>66</td>
<td>37</td>
<td>138</td>
<td>65.2</td>
<td>63</td>
<td>18.8</td>
</tr>
<tr>
<td></td>
<td>White spruce</td>
<td>57</td>
<td>46</td>
<td>208</td>
<td>86.4</td>
<td>78</td>
<td>37.0</td>
</tr>
<tr>
<td></td>
<td>White birch</td>
<td>10</td>
<td>135</td>
<td>210</td>
<td>174.3</td>
<td>182</td>
<td>28.8</td>
</tr>
</tbody>
</table>

$^a n =$ number of trees.

$^b s =$ standard deviation.

$^c$ One white birch tree of 25 years of age (dbh = 1.0 cm) was excluded.

Decades of suppression, and unknown number of missing rings in these trees, all ages are best considered as minimum ages.

A well-developed lognormal, all-age structure characterized each stand (Figure 9-1). When present in the stand, balsam fir, white spruce and black spruce were generally found in most age classes. A notable exception was white birch which, except for the unique occurrence in the youngest occupied age class in stand M1 (20 to 25 years), was found only in the older age classes; > 170 years for plot M1, > 155 years for plot M2, and > 130 years for plot M7. Except for age class 185 to 190 years in stand M7, all age classes were occupied up to age class 210 to 215 years after which empty age classes were more frequent, no doubt due to the higher mortality rate of the largest trees.
Figure 9-1. Total age frequency distribution for balsam fir, black spruce, white spruce, and white birch in three Main River stands.

9.2 LIVE TREE MINIMUM AGE STRUCTURE

As noted earlier, about 15% of the trees in each plot exhibited various degrees of butt rot that prevented total age determination. However, determination of minimum live ages from a number of infected trees provided further insight into the age structure of the sample stands. About 30% of the sampled, butt rot-balsam fir had minimum ages > 150 years (Figure 9-2).
Figure 9-2. Minimum ages for balsam fir, black spruce, white spruce and white birch, Main River stands. All trees had small percentages of butt rot that prevented total age determination.

For black spruce, white spruce and white birch, the percentage of trees having a minimum age > 150 years was 75%, 75% and 100%, respectively. On average, minimum ages were determined at approximately 1 m height. Given the long periods of juvenile suppression found in the majority of the shade-tolerant conifers, these trees of minimum age are certainly much older. For example, balsam fir sampled at heights of 2.4, 2.5, and 2.5 m had minimum ages of 175, 173 and 189 years, respectively. Similarly, black spruce sampled at 0.7, 1, 1.2, 1.7, and 2.3 m had minimum ages of 211, 191, 205, 184, and 171 years, respectively. Obviously, these particular trees were much older, with total ages certainly exceeding 200 years and approaching or even exceeding 250 years. Therefore, the age structures provided in (Figure 9-2) clearly underestimated the actual proportion of old trees (> 150 years) in the live canopy.
9.3 LIVE TREE DIAMETER–AGE RELATIONSHIP

Individual tree height and dbh were considered as a function of both total and breast height tree age. Given the limited number of stem analysis carried out in each stand, the data set for breast height age was considerably less than that for total age. It is well known that age at release (usually synonymous with age at breast height), and not total tree age, is the better indicator of the physiological age of shade-tolerant tree species and therefore a more useful indicator of tree and stand development. The large number of total age data in the current study, however, detailed data trends that were helpful for an understanding of overall stand dynamics.

Except for that of white birch, tree dbh–total age relationships for each species were smoothed using loess curves (Figure 9-3). Balsam fir curves for each stand are shown, with data for the other three species combined to produce a unique curve for each species. For balsam fir and the two spruces, two relatively distinct age–size relationships were recognized: (1) tree aging with relatively low rates of dbh growth, and (2) tree aging with relatively rapid increase in diameter. For balsam fir, the juncture separating the two distinct growth rates occurred around 125 years, while for both black spruce and white spruce, a similar juncture occurred shortly after 75 years. Balsam fir trees, for example, took an average of 125 years to reach 5 cm in diameter. A further 125 years, however, enabled the trees to grow from 5 to about 28 cm in diameter.

Significant Spearman rank correlation coefficients ($P < 0.0001$; ranging from 0.6 to 0.7) were noted for the dbh–age relationship of all three conifers (Table 9-3). A well-defined monotonic curvilinear relationship characterized the tree diameter–age relationship. The low sample size for white birch precluded the assignment of any confidence to the
Figure 9-3. Tree dbh–total age relationships for balsam fir, black spruce, white spruce and white birch in three Main River stands. Loess smoothing with span = 0.5. Spearman rank correlation coefficients and associated $P$ values for bivariate relationships are given in Table 9-3.
Table 9-3. Spearman rank correlation ($r_s$) and associated $P$ values for tree dbh–age bivariate relationships, Main River.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Species</th>
<th>$n^a$</th>
<th>Spearman $r_s^b$</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Balsam fir</td>
<td>568</td>
<td>0.6560</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Black spruce</td>
<td>144</td>
<td>0.5833</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White spruce</td>
<td>54</td>
<td>0.6837</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White birch</td>
<td>3</td>
<td>0.8000</td>
<td>0.2000</td>
</tr>
<tr>
<td>M2</td>
<td>Balsam fir</td>
<td>298</td>
<td>0.7128</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Black spruce</td>
<td>222</td>
<td>0.7144</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White birch</td>
<td>5</td>
<td>0.1000</td>
<td>0.8729</td>
</tr>
<tr>
<td>M7</td>
<td>Balsam fir</td>
<td>357</td>
<td>0.6043</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Black spruce</td>
<td>66</td>
<td>0.7044</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White spruce</td>
<td>57</td>
<td>0.5998</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White birch</td>
<td>10</td>
<td>0.8293</td>
<td>0.0030</td>
</tr>
<tr>
<td>All plots combined</td>
<td>Balsam fir</td>
<td>1223</td>
<td>0.6604</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Black spruce</td>
<td>432</td>
<td>0.6525</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White spruce</td>
<td>111</td>
<td>0.6330</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White birch</td>
<td>19</td>
<td>0.4374</td>
<td>0.0611</td>
</tr>
</tbody>
</table>

$^a n$ = number of trees.
$^b$ Spearman $r_s$ = Spearman rank correlation coefficient.

bivariate relationship. In fact, the vast majority of sampled white birch were large, old trees.

Despite the significant monotonic relationship between tree age and dbh for all three conifer species, only 37% to 51% of the variation in dbh was explained by tree age. In other words, due to high variability, the dbh–age correlation was not generally strong among trees. Trees at any particular age were of quite different diameters and vice-versa. For example, balsam fir trees of 5 cm dbh had ages ranging from 50 to 175 years.

Similarly, 150 year-old trees exhibited diameters ranging from 2 to 25 cm. For both black spruce and white spruce, 2 cm dbh trees had ages ranging from 30 to over 100 years.

A closer examination of conifers $\leq 5$ cm dbh revealed the general inequality between age and tree size (Figure 9-4). Balsam fir $\leq 5$ cm dbh, for example, ranged in age
Figure 9-4. Dbh–total age relationships for balsam fir, black spruce, and white spruce in three Main River stands. Balsam fir: $n = 880$, $r_s = 0.4070$, $P < 0.0001$; Black spruce: $n = 361$, $r_s = 0.4839$, $P < 0.0001$; White spruce: $n = 79$, $r_s = 0.2960$, $P = 0.0081$. $n$ = number of trees, $r_s$ = Spearman rank correlation coefficient.
from 50 to 150 years. A similar pattern occurred for black spruce and white spruce, although the age range was reduced to between approximately 50 to 100 and 60 to 100 years, respectively. Loess curves revealed a general linear relationship between size and age for balsam fir and black spruce. Note, however, that this linear relationship considered dbh growth of a maximum of only 5 cm over an age range of approximately 175 years. For white spruce, the relationship was generally flat over the data range examined. Significant Spearman rank correlation coefficients ranged from 0.3 to 0.5. Note that the loess-defined relations examined only trees ≤ 5 cm dbh. For the age range examined in Figure 9-4 there obviously existed trees > 5 cm dbh.

Stem analysis data permitted the development of tree age at breast height–dbh relationships for balsam fir, black spruce and white spruce. For all three species, significant, weighted 3-parameter sigmoidal functions best described the dbh–breast height age relationships (Figure 9-5, Table 9-4). Loess smoothing with a span of 0.5 confirmed the sigmoidal relationship. Despite the use of breast height age, bivariate variability was still high, confirming the fact that many trees were still in various degrees of height growth suppression even at breast height. With all three species, the fitted curves exhibited asymptotic limits at a dbh of approximately 25 cm and breast height ages approaching 200 years.

9.4 LIVE TREE HEIGHT–AGE RELATIONSHIP

Because both tree diameter and height were usually correlated, it was no surprise that tree height–age relationships paralleled tree diameter relationships. Evident were
Figure 9-5. Tree dbh–breast height age relationships for balsam fir, black spruce, and white spruce, Main River stands. All regressions significant at $P < 0.0001$. Estimated parameters, 95% confidence intervals, and fit statistics are given in Table 9-4.
Table 9-4. Estimated parameters, associated 95% confidence intervals, and fit statistics for a weighted 3-parameter sigmoidal fit to the dbh-breast height age relationship for balsam fir, black spruce, and white spruce, Main River. Weight used for black spruce and white spruce = 1/age. For balsam fir, weight = 1/age^2. All regressions significant at P < 0.0001.

<table>
<thead>
<tr>
<th>Species</th>
<th>Estimated parameter coefficients (95% confidence intervals)</th>
<th>n^c</th>
<th>R^2^d</th>
<th>RMSE_w^e</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>a</td>
<td>b</td>
<td>c</td>
<td></td>
</tr>
<tr>
<td>Balsam fir</td>
<td>27.6658 (22.5422, 32.7894)</td>
<td>36.2861 (27.3316, 45.2406)</td>
<td>72.5808 (56.0901, 89.0714)</td>
<td>133</td>
</tr>
<tr>
<td>Black spruce</td>
<td>27.7851 (18.0945, 37.4756)</td>
<td>37.9242 (14.4295, 61.4188)</td>
<td>89.1070 (48.1272, 130.1)</td>
<td>29</td>
</tr>
<tr>
<td>White spruce</td>
<td>27.3332 (20.4922, 34.1742)</td>
<td>30.653 (19.0131, 42.293)</td>
<td>77.8261 (55.6708, 99.9814)</td>
<td>26</td>
</tr>
</tbody>
</table>

\[ \text{dbh} = \frac{a}{1+e^{-\left(\frac{\text{age} - c}{b}\right)}} \]

\(^a\) Confidence limits are asymptotic for nonlinear functions.

\(^b\) n = number of trees.

\(^c\) For nonlinear functions, the coefficient of determination is a pseudo-R^2 defined as 1− residual sum of squares/corrected total sum of squares.

\(^d\) Weighted root mean square error.
the two contrasting height growth rates. As with diameter growth, height growth of balsam fir increased noticeably after about 125 years total age (Figure 9-6).

A similar increase in height growth for both black spruce and white spruce occurred around 75 to 100 years. Except for those of white birch, Spearman rank correlations indicted significant monotonic height growth (Table 9-5), with rank coefficient values ranging from 0.59 to 0.80. White birch data were clustered in the oldest trees.

Both fitted loess curves and Spearman rank correlations indicated significant near-linear, monotonic height–total age relationships for all conifer trees ≤ 3 m in height (Figure 9-7). Despite the significant monotonic relationships, high height–age variability was evident for all conifers, especially for the highly shade-tolerant balsam fir. Analysis of trees ≤ 3 m in height exemplified this variability. Trees of any particular height may have had quite different ages. This was in keeping with the generally poor dbh–age correlation for trees in these old-growth stands. For example, a 150-year-old balsam fir displayed heights ranging from 1.5 m to 15 m. Similarly, a balsam fir tree of 1.5 m in height had ages ranging from 30 to 150 years.

As in the case of dbh, height–breast height age relationships for balsam fir, black spruce and white spruce were best expressed by a weighted (weight = 1/breast height age) 3-parameter sigmoidal function (Figure 9-8, Table 9-6). The weight effectively stabilized the variance for both balsam fir and white spruce. The asymptotic age–height relationships for all three species were similar to each other, with height growth leveling off near 14 m over the breast height age range of 150–200 years. Bivariate variability was still high even with tree ages measured at breast height. For example, 150-year-old balsam fir (breast height age) were anywhere from 9 to 18 m in height.
Figure 9-6. Tree height–total age relationships for balsam fir, black spruce, white spruce, and white birch in three Main River stands. Loess smoothing with span = 0.5.
Table 9-5. Spearman rank correlation coefficients and associated $P$ values for tree height–total age bivariate relationships, Main River.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Species</th>
<th>$n^a$</th>
<th>Spearman $r_s^b$</th>
<th>$P$ value</th>
</tr>
</thead>
<tbody>
<tr>
<td>M1</td>
<td>Balsam fir</td>
<td>568</td>
<td>0.6044</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>Black spruce</td>
<td>144</td>
<td>0.7055</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White spruce</td>
<td>54</td>
<td>0.7994</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White birch</td>
<td>4</td>
<td>0.8000</td>
<td>0.2000</td>
</tr>
<tr>
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<td>Balsam fir</td>
<td>297</td>
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<td></td>
<td>Black spruce</td>
<td>222</td>
<td>0.6472</td>
<td>&lt; 0.0001</td>
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<tr>
<td></td>
<td>White birch</td>
<td>5</td>
<td>-0.2000</td>
<td>0.7471</td>
</tr>
<tr>
<td>M7</td>
<td>Balsam fir</td>
<td>357</td>
<td>0.5676</td>
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<td>Black spruce</td>
<td>66</td>
<td>0.6609</td>
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</tr>
<tr>
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<td>White spruce</td>
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<td>0.5934</td>
<td>&lt; 0.0001</td>
</tr>
<tr>
<td></td>
<td>White birch</td>
<td>10</td>
<td>0.4055</td>
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<tr>
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<td>0.6062</td>
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<td>Black spruce</td>
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<td>&lt; 0.0001</td>
</tr>
<tr>
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<td>White birch</td>
<td>19</td>
<td>0.1726</td>
<td>0.4798</td>
</tr>
</tbody>
</table>

$^a n =$ number of trees.

$^b$ Spearman $r_s =$ Spearman rank correlation coefficient.
Figure 9-7. Tree height–total age relationships for balsam fir, black spruce, and white spruce, Main River. Balsam fir, \( n = 918, r_s = 0.3570 \); Black spruce, \( n = 322, r_s = 0.4395 \); White spruce: \( n = 78, r_s = 0.5399 \). All Spearman rank correlation coefficients significant at \( P < 0.0001 \). \( n \) = number of trees.
Figure 9-8. Tree height–breast height age relationships for balsam fir, black spruce, and white spruce, Main River. All regressions significant at $P < 0.0001$. Estimated parameters, 95% confidence intervals, and fit statistics are given in Table 9-6.
Table 9-6. Estimated parameters, associated 95% asymptotic confidence intervals, and fit statistics for a weighted 3-parameter sigmoidal fit to the height–breast height age relationships for balsam fir, black spruce, and white spruce, Main River. All regressions are significant at $P < 0.0001$.

<table>
<thead>
<tr>
<th>Species</th>
<th>Estimated parameter coefficients (95% confidence intervals)</th>
<th>$n^b$</th>
<th>$R^2c$</th>
<th>RMSE$_w^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$a$</td>
<td>$b$</td>
<td>$c$</td>
<td></td>
</tr>
<tr>
<td>Balsam fir</td>
<td>13.1227</td>
<td>24.6343</td>
<td>71.5075</td>
<td>(11.6489, 14.5966)</td>
</tr>
<tr>
<td>Black spruce</td>
<td>13.2814</td>
<td>34.6368</td>
<td>83.2309</td>
<td>(10.7015, 15.8614)</td>
</tr>
<tr>
<td>White spruce</td>
<td>13.8708</td>
<td>23.99</td>
<td>77.4988</td>
<td>(10.8787, 16.8628)</td>
</tr>
</tbody>
</table>

\[
\text{height} = \frac{a}{1 + e^{\left(\frac{b \text{height} - c}{b}\right)}}
\]

$b$ $n = \text{number of trees.}$

$c$ For nonlinear functions, the coefficient of determination is a pseudo-$R^2$ defined as 1–residual sum of squares/corrected total sum of squares.

$d$ RMSE$_w = \text{weighted root mean square error.}$
9.5 YEARS TO BREAST HEIGHT

The frequency distribution of years to breast height were generally right skewed for balsam fir and black spruce, with white spruce defined more by a modal distribution (Figure 9-9).

Figure 9-9. Frequency distribution of minimum number of years required to reach breast height for balsam fir, black spruce, and white spruce trees, Main River.

A comparison of the different frequency distributions for the three study stands using the Kolmogorov–Smirnov test showed plot M2 to be marginally different than plot M1 ($P = 0.013$, Bonferroni $P = 0.017$). Despite this small difference, the number of years to reach breast height was pooled for each species and the resulting frequency distributions were compared. The observed distribution for balsam fir differed significantly from the distributions for both black spruce and white spruce, both of which showed no significant
difference. For all multi-way comparisons, a Bonferroni adjustment ($\alpha$/number of comparisons) set a critical level of $P = 0.0167$. Balsam fir took longer to reach breast height than either black spruce or white spruce (Tukey–Kramer, $P \leq 0.05$). Average years to breast height for balsam fir was 61.8 years ($s = 21.2$), compared to 40.4 years ($s = 11.5$) for black spruce and 48.0 years ($s = 15.0$) for white spruce. No significant differences in number of years to breast height were detected for the two spruces.

9.6 DEAD TREE AGE STRUCTURE, DIAMETER–AGE AND HEIGHT–AGE RELATIONSHIP

Age structure of the sampled dead trees was similar to that of the live trees. Total age of dead trees ranged from 45 to 232 years and produced a weak, though discernible lognormal age distribution (Figure 9-10A). Balsam fir trees were present across the entire age range, with white spruce relegated to the youngest age classes (not greater than 101 years) and white birch occurring solely in the oldest age classes (176–220 years). Of the trees sampled, minimum ages of dead trees were well represented in age classes $> 150$ years (Figure 9-10B).

The dbh–age relationship of dead trees was similar to that of live trees, exhibiting a significant curvilinear monotonic relationship ($r_s = 0.80994, P < 0.0001$) (Figure 9-11). As with the live balsam fir dbh–age curve, loess smoothing of the dbh–age scatterplot for the dead trees showed a noticeable upward shift in the relationship at around 125 years (not shown).

The height–age relationship of dead trees was similar to that of live trees, exhibiting a significant curvilinear monotonic relationship ($r_s = 0.6603, P < 0.0001$) (Figure 9-12). A
Figure 9-10. Ages of dead balsam fir, black spruce, white spruce, and white birch, Main River. (A) Total basal ages of dead trees. (B) Minimum ages of dead trees.

Figure 9-11. Dbh–age at death relationship for balsam fir, black spruce, white spruce, and white birch, Main River. $r_s = 0.8099$, $P < 0.0001$. 
loess smoothing of the height–age scatterplot revealed a noticeable upward shift in the dbh–age relationship at around 125 years. The same functional relation was indicated by the dbh–age relationship for dead trees.

9.7 SEEDLING AGE DISTRIBUTION

A reverse-J age distribution characterized the seedling population (≤ 1.3 m) for each of the three sampled stands (Figure 9-13). Emergents were included in the 0 to 5 year frequency class. Balsam fir seedlings, which dominated the seedling bank, were present in each age class up to age 70 years, after which the proportion of balsam fir decreased to minimum levels. Balsam fir had the widest range of ages with continuous presence of seedlings in nearly all age classes up to 110, 120 and 85 years for plots M1, M2, and M7,
Figure 9-13. Age class frequency for balsam fir, black spruce, and white spruce seedlings, Main River.

respectively. Despite this wide age range, most seedlings were in the younger age classes, with an average 76% of all balsam fir seedlings ≤ 20 years of age. The age range for black spruce and white spruce seedlings was narrower with ages of black spruce ranging from 6 to 70 years, and ages for white spruce ranging from 0 to 65 years of age. The oldest recorded balsam fir, black spruce and white spruce seedlings were 116, 69, and 63 years, respectively. Given the growth dynamics of these suppressed seedlings, all ages must be considered as minimum ages.
9.8 SEEDLING HEIGHT–AGE RELATIONSHIP

The height–age data from the three sampled stands were pooled for each species. All seedling height-age relationships were characterized by the sigmoidal 3-parameter Chapman equation (Figure 9-14).

\[ \hat{y} = a \left(1 - e^{-bx}\right)c \]

All seedling height–age scatterplots displayed increased height variability with seedling age. One metre high balsam fir seedlings ranged in age from 40 to over 100 years of age. Seedlings > 60 years of age were uncommon for both spruces, whereas balsam fir seedlings reached 100 years of age.

As with the seedling height–basal diameter relationships, logarithmic transformation of both variates of an allometric model \( Y = aX^b \) linearized the data, stabilized the variances and normalized the error terms, thus permitting comparison of the linear regressions by covariance analysis (Figure 9-15). All seedling height–age linear regressions were significant at \( P < 0.0001 \), with \( R^2 \) values ranging from 0.7505 for black spruce to 0.8287 for white spruce (Table 9-7).

All three regression lines were parallel (\( P = 0.4730 \)), with significantly different intercepts for all three species (black spruce > white spruce > balsam fir, \( P < 0.05 \)). Thus, for any given seedling age, each species expressed height in the order black spruce > white spruce > balsam fir. In other words, balsam fir seedlings were the oldest for any particular height, with the oldest seedlings in the 80 to 100 year range. Only rarely did black spruce and white spruce seedlings exceed 60 years of age.
Figure 9-14. Height–age relationship for balsam fir, black spruce, and white spruce seedlings, Main River. Balsam fir: height = 150.9 (1-exp\(-0.0195\text{age}\)^{1.671}, \(R^2 = 0.7874, n = 2,641\); Black spruce: height = 119.5 (1-exp\(-0.0593\text{age}\)^{2.7033}, \(R^2 = 0.7238, n = 154\); White spruce: height = 129.2 (1-exp\(-0.0516\text{age}\)^{2.6188}, \(R^2 = 0.8563, n = 46\). Emergents not included. \(n \) = number of seedlings.
Figure 9-15. Seedling height–age relationships for balsam fir, black spruce, and white spruce seedlings, Main River. Estimated parameters, 95% confidence intervals, and fit statistics are given in Table 9-7.

Table 9-7. Simple linear regression parameters and fit statistics for the height–age relationships for balsam fir, black spruce, and white spruce seedlings, Main River. Parameters are for the log-transformed equivalent of the allometric growth function $Y = aX^b$, $\log Y = \log a + b \log x$. Each equation consists of pooled data for each species. All regressions are significant at $P < 0.0001$ and 95% confidence intervals are given in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameter estimates (95% confidence intervals)</th>
<th>$n^a$</th>
<th>$R^2$</th>
<th>RMSE$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$\log a$</td>
<td>$b$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Balsam fir</td>
<td>-0.2374</td>
<td>1.1885</td>
<td>2,641</td>
<td>0.7928</td>
</tr>
<tr>
<td></td>
<td>(-0.2644, -0.2104)</td>
<td>(1.1653, 1.2116)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black spruce</td>
<td>0.1805</td>
<td>1.1047</td>
<td>154</td>
<td>0.7505</td>
</tr>
<tr>
<td></td>
<td>(0.0410, 0.3200)</td>
<td>(1.0026, 1.2068)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>White spruce</td>
<td>0.0038$^c$</td>
<td>1.1837</td>
<td>46</td>
<td>0.8287</td>
</tr>
<tr>
<td></td>
<td>(-0.1988, 0.2064)</td>
<td>(1.0202, 1.3473)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^a n =$ number of seedlings.

$^b$ RMSE = root mean square error (log cm).

$^c$ Parameter not significantly different from zero, $P = 0.9699$. 
9.9 SEEDLING BASAL DIAMETER–AGE RELATIONSHIP

As with the seedling age–height relationship, all data from the three sampled stands were pooled for each species. Monotonic relationships with increasing variability characterized the seedling basal diameter–age scatterplots (Figure 9-16). The 3-parameter asymptotic Chapman function modeled the balsam fir relationship, whereas a power function best modeled both the black and white spruce relationships.

As with the height–age scatterplots, a log–log transformation of the data permitted comparison of the least squares linear regressions using covariance analysis. All seedling basal diameter–age regressions were significant at $P < 0.0001$, with $R^2$ values ranging from 0.6327 for black spruce to 0.7767 for white spruce (Figure 9-17, Table 9-8).

All three regression lines were parallel ($F = 0.50, P = 0.6058$), with the intercept of the balsam fir curve significantly smaller than that of both black spruce and white spruce ($P < 0.0001$). The intercepts for both black spruce and white spruce were not significantly different ($P = 1.0$). Thus, for both of the spruces, the seedling basal diameter–age relationships were statistically equivalent. For any given seedling age, each species expressed basal diameter in the order (black spruce = white spruce) > balsam fir.

9.10 CONCLUSION

Main River old-growth stands are all-aged, with total tree and seedling ages exhibiting a well-defined lognormal and reverse-J frequency distribution, respectively. Ages of balsam fir are much greater than those normally reported, and may require a
Figure 9-16. Basal diameter–age relationships for balsam fir, black spruce, and white spruce seedlings, Main River. Balsam fir: basal diameter = 67.295 (1-exp^{0.0141age}^{2.0765}), R^2 = 0.7679, n = 2,641; Black spruce: basal diameter = 0.1808 (age^{1.1395}), R^2 = 0.6054, n = 154; White spruce: basal diameter = 0.045 (age^{1.5862}), R^2 = 0.8198, n = 46 seedlings.
Figure 9-17. Basal diameter–age relationships for balsam fir, black spruce, and white spruce seedlings, Main River. Estimated parameters, 95% confidence intervals, and fit statistics of the linear regressions are given in Table 9-8.

Table 9-8. Single linear regression parameters and fit statistics for the basal diameter–age relationships of balsam fir, black spruce, and white spruce seedlings, Main River. Parameters are for the log-transformed equivalent of the allometric growth curve $Y = aX^b$, $\log Y = \log a + b \log X$. Each equation is for the pooled species data from three sampled stands. All regressions are significant at $P < 0.0001$ and 95% confidence intervals are given in parentheses.

<table>
<thead>
<tr>
<th>Species</th>
<th>Parameter estimates (95% confidence intervals)</th>
<th>$n^a$</th>
<th>$R^2$</th>
<th>RMSE$^b$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsam fir</td>
<td>$\log a = -1.1794, \log b = 1.3056$</td>
<td>2641</td>
<td>0.7227</td>
<td>0.21933</td>
</tr>
<tr>
<td></td>
<td>$(-1.2153, -1.1435), (1.2747, 1.3364)$</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Black spruce</td>
<td>$\log a = -0.9143, \log b = 1.2312$</td>
<td>154</td>
<td>0.6327</td>
<td>0.18379</td>
</tr>
<tr>
<td></td>
<td>$(-1.1198, -0.7089), (1.0809, 1.3815)$</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>White spruce</td>
<td>$\log a = -1.0802, \log b = 1.3663$</td>
<td>46</td>
<td>0.7767</td>
<td>0.22584</td>
</tr>
<tr>
<td></td>
<td>$(-1.3559, -0.8044), (1.1437, 1.5888)$</td>
<td></td>
<td></td>
<td></td>
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</tbody>
</table>

$^a n =$ number of seedlings.

$^b$ RMSE = root mean square error (log mm).
century or more to reach breast height. Poor correlations exist between total tree age and tree size, and trees remain suppressed for long and widely variable periods of time. These results confirm that canopy disturbance is controlled predominantly by small-scale, stochastically-driven gap dynamics.
10.1 CLASSIFICATION OF STAND AGE STRUCTURE

Age class was based on the average age structure of the dominant conifer canopy. Age structure was given for dominant-codominant trees in structurally simple modal stands and for a wider range of tree diameters for the more structurally complex non-modal stands. In some instances, the presence of butt rot prevented the aging of dominant trees. To prevent undue skewing of the average stand age, ages of veteran trees growing above the dominant canopy were excluded from the calculation of average stand age for certain single-cohort and bistaged plots. Veteran trees were those trees whose height and age far exceeded the average tree height and age in the regenerating cohort of each particular stand. Over 70% of the 14 identified veteran trees were either black or white spruce, with the other veterans being balsam fir. Depending on the severity of any insect outbreak, some canopy trees survived and persisted into the newly regenerating stand. Age of veteran trees were excluded from plots 23, 26, 35, 42, 44, 45, 46, 49 and 50.

Total age structure of all 50 stands is given in Figure 10-1.
Figure 10-1. Total age frequency for balsam fir, black spruce and white spruce, Little Grand Lake stands. Stands are grouped by stand type; single-cohort, bimodal, reverse-J, and bistaged. Single-cohort stands are further classified into 10-year total age classes. Veteran trees excluded from calculation of age statistics. Numbers shown = mean age (standard deviation). $n =$ number of sample trees.
Tree age class (years)

Figure 10-1. (Continued)
Plot 34 (91-100 years) 99.1 (6.5) n = 15

Plot 40 (91-100 years) 94.6 (8.2) n = 20

Plot 50 (91-100 years) 99.5 (9.0) n = 19

Plot 24 (101-110 years) 103.9 (9.5) n = 13

Plot 35 (101-110 years) 108.2 (8.9) n = 14

Plot 7 (111-120 years) 110.0 (13.2) n = 20

Plot 11 (111-120 years) 117.0 (12.3) n = 21

Plot 12 (Bimodal) 122.6 (22.2) n = 17

Plot 22 (Bimodal) 112.8 (25.5) n = 29

Plot 29 (Bimodal) 109.2 (30.1) n = 25

Plot 36 (Bimodal) 106.0 (13.0) n = 19

Plot 37 (Bimodal) 121.6 (14.3) n = 14

Figure 10-1. (Continued)
Figure 10.1. (Continued)
Average single-cohort stand age ranged from 15 to 117 years of age to form a well-defined chronosequence. Stands exhibiting single-cohort diameter distributions were classified into 10-year age classes to produce a series of 11 distinct stand age classes ranging from age class 11–20 years through to age class 111–120 years. As already indicated, classification of the stands into distinct age classes does not assume *ipso facto* that age class was a reliable measure of the degree of stand development of modal stands. Theoretically, stand height is a better index of the degree of stand development, especially with shade-tolerant tree species. As it turned out, however, the total age structure did provide a useful indicator of the degree of stand development, and helped as a heuristic device for modal stand classification.

To 100 years of age, tree age range was relatively narrow with standard deviations not exceeding 13.2, with the majority of stands having standard deviations less than 10.5. Single-cohort stands with mean ages < 15 years and between 35 and 60 years were noticeably absent. The mean age of bimodal stands ranged from 106 to 136 years of age. Bistaged stands ranged in age from 47 to 81 years of age. The mean age of the nine
reverse-J stands ranged from 75.8 to 110.9 years. Reverse-J stands exhibited the highest age standard deviations, with values ranging from 26.5 to 55.5 years. The oldest recorded age for balsam fir, black spruce and white spruce was 202 years (11.0 m height, 17.6 cm dbh), 269 (15.6 m height, 25.3 cm dbh), and 182 years (15.5 m height, 22.1 cm dbh).

Differences in the average range of recorded tree ages for each stand clearly distinguished modal, bimodal and reverse-J (including bistaged) stands from each other (Figure 10-2).

Figure 10-2. Boxplots showing live tree age range for each of the four stand types, Little Grand Lake. Box limits represent the 25th and 75th percentiles of the data. Error bars represent the 10th and 90th percentiles, and the dots show the 5th and 95th percentile outliers. Mean and median age range are given by the dashed and solid line, respectively.

Age ranges were of the order single cohort < bimodal < (reverse-J = bistaged) (Tukey’s studentized range test, $P < 0.05$). Single-cohort stands, being the most even-aged, had the
smallest average tree age range ($\bar{x} = 29.6, s = 9.5, n = 31$). Bimodal stands, given the
recruitment of younger cohorts, had a significantly greater range of ages ($\bar{x} = 81.3, s = 31.6, n = 6$). Both reverse-J ($\bar{x} = 155.4, s = 21.0, n = 9$) and bistaged stands ($\bar{x} = 171, s = 34.6, n = 4$) had significantly greater ranges than either the modal or bimodal stands. In the
case of the reverse-J stands, long periods of small-scale gap disturbance (senescence, fungal
and insect mortality, windthrow) coupled with constant gap recruitment no doubt facilitated
the wide spread of ages. For the bistaged stands, longer periods of recruitment on the
poorer sites coupled with the distinct two-aged canopy supported the wide age range.

10.2 TREE HEIGHT–AGE AND DIAMETER–AGE RELATIONSHIPS

Distinct tree height–total age and tree dbh–total age relationships were used to
divide the four stand types into a set of distinct couplets; single-cohort–bimodal and
reverse-J–bistaged. In all cases, loess smoothers were used to verify the parametric
equations used to model all tree size–age relationships. Single-cohort and bimodal stands
grew on sites of greater site index compared to the reverse-J and bistaged stands. Within
each couplet, all stands were considered of sufficient equality to merit a common analysis.
Asymptotic, 3-parameter sigmoidal functions best described the relationship between
balsam fir height–dbh and total age for the single-cohort–bimodal stands, as well as the
reverse-J–bistaged stands (Figure 10-3, Table 10-1). At any particular age, both the height
and dbh of trees in the single-cohort–bimodal stands exceeded that of trees in the reverse-J–
bistaged stands. Tree height and dbh generally leveled off at an age of 125 years. For all
trees, total age of balsam fir did not exceed 200 years.
Figure 10-3. Dbh–age and height–age relationships for (A) balsam fir, (B) black spruce and (C) white spruce, Little Grand Lake. For each species, models are given for both single-cohort–bimodal and reverse-J–bistaged stands. Estimated parameters, 95% confidence intervals, and fit statistics are given in Table 10-1.
Table 10-1. Estimated parameters, 95% confidence intervals, and fit statistics for the dbh–age and height–age relationships for balsam fir, black spruce and white spruce, Little Grand Lake. Except for all balsam fir relationships and for the white spruce dbh/height–age relationship for reverse-J/bistaged trees, all regressions are significant at \( P < 0.0001 \).

<table>
<thead>
<tr>
<th>Species</th>
<th>Relationship(^e)</th>
<th>Estimated parameters (95% confidence intervals)</th>
<th>( n^b )</th>
<th>( R^2c )</th>
<th>RMSE(^d)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsam fir</td>
<td>Dbh–age (single-cohort–bimodal)</td>
<td>( a ) = 26.454, ( b ) = 22.685, ( c ) = 73.165</td>
<td>603</td>
<td>0.8192</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Dbh–age (reverse-J–bistaged)</td>
<td>( a ) = 23.318, ( b ) = 41.881, ( c ) = 125.0</td>
<td>328</td>
<td>0.6362</td>
<td>–</td>
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<tr>
<td></td>
<td>Height–age (single-cohort–bimodal)</td>
<td>( a ) = 18.386, ( b ) = 25.671, ( c ) = 65.285</td>
<td>603</td>
<td>0.8514</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Height–age (reverse-J–bistaged)</td>
<td>( a ) = 14.230, ( b ) = 48.927, ( c ) = 114.4</td>
<td>328</td>
<td>0.5802</td>
<td>–</td>
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<tr>
<td>Black spruce</td>
<td>Dbh–age (single-cohort–bimodal)</td>
<td>( a ) = 3.234, ( b ) = 0.145</td>
<td>37</td>
<td>0.5071</td>
<td>3.386</td>
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<td></td>
<td>Dbh–age (reverse-J–bistaged)</td>
<td>( a ) = 24.002, ( b ) = 42.252, ( c ) = 124.4</td>
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<td>0.7767</td>
<td>3.252</td>
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<td></td>
<td>Height–age (single-cohort–bimodal)</td>
<td>( a ) = 2.571, ( b ) = 0.0885</td>
<td>37</td>
<td>0.6711</td>
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<td></td>
<td>Height–age (reverse-J–bistaged)</td>
<td>( a ) = 17.182, ( b ) = 48.776, ( c ) = 126.691</td>
<td>137</td>
<td>0.8533</td>
<td>1.630</td>
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Table 10-1. (Continued)

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<th>( n )</th>
<th>( R^2 )</th>
<th>RMSE</th>
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<tr>
<td>White spruce</td>
<td>Dbh–age</td>
<td>-</td>
<td>142</td>
<td>0.7909</td>
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<tr>
<td></td>
<td>(single-cohort–</td>
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<tr>
<td></td>
<td>bimodal)</td>
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<tr>
<td></td>
<td>Dbh–age</td>
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<td>6</td>
<td>0.5164</td>
<td>-</td>
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<td></td>
<td>(reverse-J–</td>
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<td>Height–age</td>
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<td>142</td>
<td>0.8692</td>
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<td>bimodal)</td>
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<tr>
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<td>Height–age</td>
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<td></td>
<td>(reverse-J–</td>
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<td></td>
</tr>
<tr>
<td></td>
<td>bistaged)</td>
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</table>

*Nonlinear relationship modeled by the 3-parameter sigmoidal model: \( \text{dbh/height} = \frac{a}{1+e^{-\frac{\text{age}-c}{b}}} \)

Linear equations modeled by the simple linear regression: \( \text{dbh/height} = a + b \text{ age} \).

\( n \) = number of trees.

\( R^2 \) for nonlinear models defined as 1–residual sum of squares/corrected total sum of squares.

RMSE = root mean square error.

Both normality and variance assumptions do not hold for balsam fir. Therefore, confidence intervals and hypothesis tests based on \( t \) and \( F \) distributions are invalid. However, parameter estimates, even under non-normality and heteroscedasticity, are unbiased. The shape of the modeled sigmoidal relationship was confirmed by loess smoothing, span = 0.5.

Note the use of ordinary least squares where Model II regression is more appropriate (random variables). Estimated parameters are therefore potentially biased. Of interest is whether the slope = 0, and this test is identical for both the regression of \( X \) on \( Y \) and \( Y \) on \( X \). (Quinn and Keough, 2002, p. 104). Single linear white spruce height–age regression for reverse-J–bistaged trees significant at \( P = 0.048 \).

Single linear regression intercept is not significantly different from 0 \( (P = 0.05) \).

No model defined. Pearson correlation coefficient = 0.5164, \( P = 0.294 \).
Parametric height/dbh–total age relationships were developed for both black spruce and white spruce. As with balsam fir, black and white spruce in the single-cohort–bimodal stands were taller and larger in dbh than trees of equal total age in the reverse-J–bistaged stands (Figure 10-3, Table 10-1). A significant 3-parameter sigmoidal relationship \( P < 0.0001 \) explained the black spruce height/dbh–total age relationship for reverse J–bistaged stands. For single-cohort–bimodal stands, significant linear functions \( P < 0.0001 \) best described the black spruce height–total age and dbh–total age relationships. Maximal black spruce ages ranged from 200 to 220 years, with an exceptional age at 269 years. Trees generally did not exceed much beyond 25 cm dbh and 15 m in height.

Contrary to that used for black spruce, a 3-parameter sigmoidal function was used to describe the white spruce relationships for single-cohort–bimodal stands (Figure 10-3). Because white spruce trees rarely occurred in the reverse-J–bistaged stands, sample size was small, but the linear height–total age relationship was significant at \( P < 0.0001 \). Like black spruce, white spruce trees in the reverse-J–bistaged stands were generally shorter and smaller in diameter than white spruce trees in the single-cohort–bimodal stands of higher site quality. Maximal white spruce ages were between 120 and 140 years, with an exceptional tree at 182 years of age. The fitted regressions reached dbh and height asymptotes at approximately 30 cm and 20 m, respectively.

Stem analyses provided the data for an assessment of height/dbh–breast height age relationships for all conifer species across the chronosequence. Given the limited number of stem analysis carried out in each stand, the data set for breast height age was considerably less than that for total age. As noted earlier, age at release (usually age at breast height) and not total tree age has been traditionally accepted as the better indicator of
the physiological age of a tree and therefore a more useful indicator of tree development and stand dynamics.

A significant 3-parameter asymptotic sigmoidal function \( P < 0.0001 \) best described the height/dbh–breast height age relationships for single-cohort–bimodal balsam fir (Figure 10-4, Table 10-2).

**Balsam fir**

![Graph showing single-cohort and reverse-J stands](image)

**Black and white spruce**

![Graph showing white and black spruce](image)

**Breast height age (years)**

Figure 10-4. Dbh–breast height age and height–breast height age relationships for balsam fir, black spruce, and white spruce trees, Little Grand Lake. For balsam fir, distinction is made between single-cohort–bimodal and reverse-J–bistaged stands. Estimated parameters, 95% confidence intervals, and fit statistics are given in Table 10-2.
Table 10-2. Estimated parameters, 95% confidence intervals and fit statistics for dbh-breast height age and height-breast height age relationships for balsam fir, black spruce, and white spruce, Little Grand Lake. Balsam fir models are provided for single-cohort–bimodal and reverse-J–bistaged trees. For black spruce and white spruce, trees are pooled for each species. Except for the balsam fir reverse-J–bistaged model, all regressions are significant at $P < 0.0001$.

<table>
<thead>
<tr>
<th>Species</th>
<th>Relationship</th>
<th>Estimated parameters (95% confidence intervals)</th>
<th>$n^b$</th>
<th>$R^c$</th>
<th>RMSE$^d$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Balsam fir</td>
<td>Dbh–age (single-cohort–bimodal)</td>
<td>$a = 30.3713$ (27.2676, 33.4767) $b = 16.5970$ (11.1353, 22.0614) $c = 56.4138$ (52.5216, 60.3076)</td>
<td>92</td>
<td>0.6924</td>
<td>3.2902</td>
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<tr>
<td></td>
<td>Dbh–age (Reverse-J–bistaged)$^e$</td>
<td>–</td>
<td>15</td>
<td>0.3121</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Height–age (single-cohort–bimodal)</td>
<td>$a = 18.7708$ (17.7146, 19.8269) $b = 14.4959$ (10.9696, 18.0213) $c = 49.9730$ (47.3705, 52.5756)</td>
<td>94</td>
<td>0.7623</td>
<td>1.5388</td>
</tr>
<tr>
<td></td>
<td>Height–age (Reverse-J–bistaged)$^e$</td>
<td>–</td>
<td>15</td>
<td>0.2310</td>
<td>–</td>
</tr>
<tr>
<td>Black spruce</td>
<td>Dbh–age</td>
<td>$a = 11.4656$ (8.9197, 14.0115) $b = 0.0553$ (0.0352, 0.0755)</td>
<td>18</td>
<td>0.6799</td>
<td>2.2375</td>
</tr>
<tr>
<td></td>
<td>Height–age</td>
<td>$a = 6.2385$ (5.0315, 8.3744) $b = 0.0485$ (0.0334, 0.0601)</td>
<td>18</td>
<td>0.9017</td>
<td>0.9443</td>
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<tr>
<td>White spruce</td>
<td>Dbh–age</td>
<td>$a = 4.7004$ (-1.1997, 10.6005) $b = 0.2371$ (0.1526, 0.3215)</td>
<td>23</td>
<td>0.6185</td>
<td>4.1418</td>
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<tr>
<td></td>
<td>Height–age</td>
<td>$a = 3.8344$ (1.4966, 6.1722) $b = 0.1563$ (0.1228, 0.1898)</td>
<td>23</td>
<td>0.8178</td>
<td>1.6411</td>
</tr>
</tbody>
</table>

$^a$ Nonlinear relationships modeled by the 3-parameter sigmoidal equation: $\frac{dbh}{height} = \frac{a}{1+e^{-\frac{age - c}{b}}}$.  

Linear equations modeled by the simple linear regression: $\frac{dbh}{height} = a + b$ age.  

$^b$ $n =$ number of trees.  

$^c$ Pseudo-$R^2$ for nonlinear models = 1 – residual sum of squares/corrected total sum of squares.  

$^d$ RMSE = root mean square error.  

$^e$ No model defined for balsam fir reverse-J–bistaged trees. Pearson correlation coefficients = 0.3121 ($P = 0.2574$) and 0.2310 ($P = 0.4074$).
Sample size was much smaller for balsam fir in reverse-J–bistaged stands. For both tree height and dbh, the relationships with breast height age were horizontal linear and not significant (Figure 10-4, Table 10-2). (Pearson correlation: height: \( r = 0.231 \) (\( P = 0.4074 \)); dbh: \( r = 0.3121 \) (\( P = 0.2574 \))).

Given the small sample size for black spruce (\( n = 19 \) trees) and white spruce (\( n = 23 \) trees), trees from all plots were pooled for analysis. By far the majority of the black spruce and white spruce samples were taken from the modal–bimodal and reverse-J–bistaged stands, respectively. Significant linear height/dbh-breast height age relationships (\( P < 0.0001 \)) were noted for both black and white spruce (Figure 10-4, Table 10-2). Of note were the slower height and diameter growth and greater longevity of black spruce relative to both balsam fir and white spruce.

The height–age relationships were consistently stronger than the dbh–age relationships. This was understandable given the generally density-independent tree height growth in contrast with the generally density-dependent tree diameter growth.

10.3 YEARS TO BREAST HEIGHT

Frequency distributions showing the number of years needed to reach breast height are presented in Figure 10-5. With the exception of the single-cohort–bimodal balsam fir distribution that showed a right skewed distribution, all distributions were modal in character. The frequency distribution for balsam fir growing in the reverse-J–bistaged stands was distinct from the balsam fir (single-cohort–bimodal), black spruce and white spruce distributions (Kolmogorov–Smirnov 2 sample test, \( P < 0.0001 \)). All latter three distributions were not statistically different from one another (\( P < 0.05 \)).
There were no significance differences among balsam fir (single-cohort–bimodal), black spruce and white spruce in the time needed to reach breast height. However, balsam fir growing on reverse-J–bistaged sites took a significantly longer time to reach breast height ($\bar{x} = 56.0, s = 14.3$) than either single-cohort–bimodal balsam fir ($\bar{x} = 26.6, s = 12.0$), black spruce ($\bar{x} = 31.9, s = 11.8$) or white spruce ($\bar{x} = 26.3, s = 6.4$) ($P \leq 0.0002$).

10.4 SEEDLING HEIGHT AND BASAL DIAMETER GROWTH RATE

Balsam fir seedlings displayed significant height–age correlations in each plot (Figure 10-6). Given the general similarity among the height–age relationships, data from all plots were pooled and successfully modeled by the power function, height = $0.296(\text{age}^{1.6607})$ (Figure 10-7A).
Figure 10-6. Balsam fir seedling height–age relationships, Little Grand Lake. Spearman rank correlation coefficients ($r_s$), significance levels ($P$), and sample size ($n$) are given for each stand.
Figure 10-6. (Continued)
Figure 10-7. Height–age relationships for balsam fir and white spruce seedlings, Little Grand Lake. Data are pooled from 22 plots. (A) Balsam fir: height = 0.2960(age^{1.6607}), R^2 = 0.5490, n = 6,588; (B) White spruce: height = 0.6082(age^{1.4722}), R^2 = 0.7231, n = 41, P < 0.0001.

Seedlings rarely exceeded 25 years of age and 80 cm in height. Loess analysis of the height–age scatterplot revealed the presence of a noticeable break in the height–age relationship not evident in the monotonic increase of the fitted power function. At approximately 8 to 10 years of age, the rate of seedling height growth increased to a level that was maintained across the range of older seedlings.

Unlike height–age relationships, not all balsam fir basal diameter–age relationships were significantly correlated (Figure 10-8). This was particularly evident for the youngest stands undergoing the early stages of stand re-initiation during which the seedling basal diameter–age relationships were essentially horizontal. This was understandable, given the generally density-dependent nature of diameter growth. A power function given by basal diameter = 0.0141(age^{2.0525}) described the pooled basal balsam fir diameter-age relationship (Figure 10-9A). A loess analysis confirmed the general lack of basal diameter growth in
Figure 10-8. Balsam fir seedling basal diameter–age relationships, Little Grand Lake. Spearman rank correlation coefficient (r_s), significance level (P), and sample size (n) are given for each stand.
Figure 10-8. (Continued)
Figure 10-9. Basal diameter–age relationships for balsam fir and white spruce seedlings, Little Grand Lake. Data are pooled from 22 stands. (A) Balsam fir: basal diameter = 0.0141(age^{2.0525}), R^2 = 0.3696, n = 6,589; (B) White spruce: basal diameter = 0.9189 e^{0.0944age}, R^2 = 0.6302, n = 41, P < 0.0001. n = number of seedlings.

the early years of seedling growth. Not until after 10 years of age did seedlings begin to show consequent growth in basal diameter. Seedlings rarely exceeded 25 years of age and 15 mm in basal diameter.

Given the small number of white spruce seedlings, analysis was carried out only on the pooled data. A significant exponential functions (P < 0.0001) best expressed the height–age and basal diameter–age relationships, respectively (Figure 10-7B, Figure 10-9B). The height and basal diameter growth of the white spruce seedlings were not noticeably different from that of balsam fir.
10.5 STAND HEIGHT–AGE RELATIONSHIP

Changes in stand height (75 percentile height) as a function of stand total age is given in Figure 10-10. Relationships were best described by a significant sigmoidal function that showed asymptotic character in the range of 15 to 20 m stand height.

Figure 10-10. Stand 75 percentile height–stand age relationship for single-cohort and bimodal stands, Little Grand Lake. Estimated parameters (approximate 95% confidence intervals) are $a = 14.3464 (11.0394, 17.6533)$, $b = 78.8948 (71.8030, 85.9866)$, $c = 14.3875 (6.4593, 22.3157)$, and $d = 4.1803 (2.7156, 5.6449)$, $R^2 = 0.9112$, RMSE = 1.6647, $P < 0.0001$.

10.6 CONCLUSION

Age structure analysis of the Little Grand Lake stands confirmed the critical role played by insect herbivory in regulating stand death and re-initiation. The age structure of all single-cohort stands were modal in character, with recognizable departures from age modality expressed by bimodal, reverse-J, and bistaged stands. Stand age structure indicated that most of the sampled stands originated after insect-mediated, catastrophic
stand mortality. Lesser degrees of insect herbivory were reflected in the non-modal stand age structure, with the multi-aged, reverse-J stands expressive of both edaphic old-growth and/or varying degrees of partial insect-mediated tree mortality.
CHAPTER 11

LITTLE GRAND LAKE: SELF-THINNING AND STAND DEVELOPMENT

11.1 SELF-THINNING

Self-thinning dynamics are first presented using classic two-dimensional log–log stand attribute–stem density relationships. Attributes considered were mean tree volume, live and dead quadratic mean diameter, and mean tree height. Although self-thinning relationships are often expressed, at least in the contemporary forestry literature, in a more integrative fashion using stand density management diagrams (McFadden and Oliver 1988; Oliver and Larson 1996, Ch. 15), it was considered important to present the self-thinning data using both formats. Therefore, the self-thinning dynamics of the chronosequence of natural stands are presented in both the classic 2-dimensional format, as well as within the context of a balsam fir–spruce stand density management diagram developed for stands in the study area. The use of the classic linear log–log regressions permitted comparisons with the wealth of extant self-thinning formulations. Furthermore, the use of the self-thinning regressions permitted a check of the legitimacy of the quadratic mean diameter and height isolines of the stand density management diagram.

Stand development is best considered in terms of actual structural development (i.e. stand height and density) rather than age. This is particularly important for stands dominated by shade-tolerant tree species such as balsam fir. However, results have shown that total stand age can act as a suitable correlate of stand height and temporal indicator of
stand development. Therefore, prior to an analysis of stand size–density relations, the self-thinning rate from the density–age relationship is presented.

The negative exponential function

\[
\text{Density} = 2774020 \, e^{(-0.073 \, \text{age})}
\]

(Pseudo \( R^2 = 0.914, F = 222.38, P < 0.0001 \))
described the live density–age relationship for all single-cohort and bimodal stands of the stand chronosequence (Figure 11-1).

![Graph](image)

Figure 11-1. (A) Density–stand age and (B) log density–stand age relationship for Little Grand Lake chronosequence stands aged 60 to 120 years, plus bimodal stands. Exponential model: density = 2776876.94 e(-0.073 stand age), \( R^2 = 0.9145, \text{RMSE} = 2380.99, P < 0.0001 \); Linear model: log density = 5.5654 - 0.0215 (stand age), \( R^2 = 0.7368, \text{RMSE} = 0.2385, P < 0.0001 \); Quadratic model: log density = 8.5125 - 0.0852 (stand age) + 0.0003 (stand age)^2, \( R^2 = 0.8240, \text{RMSE} = 0.1989, P < 0.0001 \). \( n = 28 \) stands.

The decrease in stem density as a function of stand age was more or less constant until about 90 years of age, at which time the rate of density decline leveled off. The estimated exponential decay rate was given by the coefficient \( b = -0.0730 \) (asymptotic 95%
confidence intervals = -0.0848 to -0.0612). This was equivalent to an overall self-thinning rate of approximately \(1 - e^{-0.0730} = 0.0704\) or 7.04%.

This mortality rate, however, was not constant across the chronosequence. A quadratic model explained the semi-logarithmic transformation of the density–age relationship better than did a linear model (Figure 11-1B). Linear modeling of the log-transformed density data \(R^2 = 0.7368, \text{RMSE} = 0.2385, P < 0.0001, n = 28\) stands) did not fit the data to the same degree as did quadratic modeling \(R^2 = 0.8240, \text{RMSE} = 0.1980, P < 0.0001, n = 28\) stands). According to the quadratic function, the decay rate was highest in the youngest stands, but began to show appreciable signs of decline around a stand age of approximately 90 to 100 years, after which stem mortality was relatively constant over time. This quadratic trend was further confirmed by loess smoothing. For the oldest stands > 120 years, the decay rate was relatively constant. A semi-logarithmic representation fitted with a straight line would have indicated a constant decay rate with stand age.

11.2 SIZE–DENSITY RELATIONSHIPS

The size–density relationships for all single-cohort and bimodal stands ≥ 60 years of age were examined using traditional log–log linear regression analysis. Single-cohort stands < 60 years of age were located outside the zone of imminent competition mortality and had yet to undergo any appreciable degree of self-thinning. Before 60 years of age, crown closure may or may not have occurred among the sampled stands that were judged to be in the pre-stem exclusion stage of stand development (\textit{sensu} Oliver and Larson 1996). Stands older than approximately 90 years were judged to be, more or less, beyond the stage
of active self-thinning, and increasingly influenced by density-independent mortality processes.

A 75 percentile stand height of approximately 15 m (total stand age = 90 years) was identified as the point of stand development marking the juncture between actively self-thinning stands and those stands more influenced by density-independent processes (Figure 10-10). Significant changes in stand structure were evident at approximately 90 years of age. Relative to stands in the lower age class of 80 to 90 years, both stand height and quadratic mean diameter of stands > 90 years increased notably. Live stem density and live basal area decreased noticeably at this point in stand development as well. Furthermore, a slowing of the self-thinning rate was evident at approximately 90 years. Note that the bimodal plot 29 was included in the single-cohort stands for the purposes of self-thinning analysis. With a relatively high density of 4,200 trees ha\(^{-1}\), plot 29 was considered to be undergoing active self-thinning, unlike the other bimodal stands of much lower stem density (1,444 stems ha\(^{-1}\)).

Consistent with the well-known principle of self-thinning, live quadratic mean diameter, mean tree height and mean tree volume, as well as dead quadratic mean diameter displayed significant log–log linear relationships with tree density (Figure 11-2, Table 11-1). These models were constructed using data from both modal stands undergoing active, intense self-thinning as well as modal and bimodal stands experiencing increasing levels of density-independent mortality.

Comparison of the 60 to 90 years and > 90 years regression lines was made by covariance analysis of the heterogeneity of slopes estimated by ordinary least squares. Both mean tree volume and live quadratic mean diameter were best expressed by two
Figure 11-2. Log–log mean tree volume/size–density relationships for a chronosequence of primary stands, Little Grand Lake. For (A) mean tree volume and (B) live quadratic mean diameter, distinct regressions are given for stands aged 60 to 90 years and for stands > 90 years (including old bimodal stands). For (C) dead quadratic mean diameter and (D) mean tree height, only one equation is given for all stands > 60 years of age. Regression parameters, 95% confidence intervals, and fit statistics are given in Table 11-1.
Table 11-1. Regression parameters, 95% confidence intervals, and fit statistics for log–log mean tree volume/size–tree density self-thinning models for a chronosequence of primary stands, Little Grand Lake. All parameters are given in their log form. All regressions are significant at \( P < 0.0001 \).

<table>
<thead>
<tr>
<th>Variable</th>
<th>( n^a )</th>
<th>Model(^b)</th>
<th>Intercept ((95%\ CI))</th>
<th>Slope ((95%\ CI))</th>
<th>( R^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td>Mean tree volume</td>
<td>12</td>
<td>SMA</td>
<td>6.479</td>
<td>(-1.282)</td>
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<tr>
<td>(60–90 years)</td>
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<td>6.525</td>
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<td></td>
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<td>(6.024, 7.132)</td>
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<td>(5.970, 7.045)</td>
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<td>(5.882, 6.960)</td>
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<td>Correlation</td>
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<td>( -0.9886 )</td>
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<td>SMA</td>
<td>5.594</td>
<td>(-1.045)</td>
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<td>RMA</td>
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<td>Correlation</td>
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<td>Mean live quadratic mean diameter</td>
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<td>Slope (95% CI)</td>
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<tr>
<td>Mean live quadratic mean diameter (60 years–bimodal)</td>
<td>28</td>
<td>SMA</td>
<td>2.731 (2.649, 2.818)</td>
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<tr>
<td>Mean live quadratic mean diameter (60 years–bimodal)</td>
<td>RMA</td>
<td>2.736 (2.654, 2.825)</td>
<td>-0.460 (-0.486, -0.437)</td>
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<tr>
<td>Mean live quadratic mean diameter (60 years–bimodal)</td>
<td>OLS</td>
<td>2.717 (2.632, 2.803)</td>
<td>-0.455 (-0.479, -0.431)</td>
<td>0.9830</td>
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<tr>
<td>Mean tree height (60 years–bimodal)</td>
<td>28</td>
<td>SMA</td>
<td>2.058 (1.974, 2.150)</td>
<td>-0.269 (-0.295, -0.245)</td>
<td></td>
</tr>
<tr>
<td>Mean tree height (60 years–bimodal)</td>
<td>RMA</td>
<td>2.056 (1.969, 2.151)</td>
<td>-0.268 (-0.295, -0.243)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Mean tree height (60 years–bimodal)</td>
<td>OLS</td>
<td>2.032 (1.943, 2.121)</td>
<td>-0.261 (-0.287, -0.236)</td>
<td>0.9458</td>
<td></td>
</tr>
</tbody>
</table>

$^a$ $n$ = number of stands.

$^b$ SMA = standard major axis = reduced major axis (Sokal and Rohlf 1995, p. 544), RMA = ranged major axis (Legendre and Legendre 1998, p. 511-512), OLS = ordinary least squares. All regressions carried out using the Model II regression software provided by Legendre (2001).
different equations. For mean tree volume the ordinary least squares slope of $-1.267$ for the youngest range of stands was significantly less than the slope of $-0.967$ determined for the oldest stands ($P = 0.0221$). Two distinct regression lines were also identified for log live quadratic mean diameter, with the youngest and oldest stands having significantly different ordinary least squares slopes of $-0.504$ and $-0.377$, respectively ($P = 0.0142$).

Regression slopes and intercepts of the height and dead quadratic mean diameter relationships were not statistically different ($P > 0.05$) for the younger and older stands. Therefore, only one equation was presented for each of the height–density and dead quadratic mean diameter–density relationships.

Ordinary least squares parameter estimates were consistently lower than those calculated using the standard major axis (reduced major axis) and ranged major axis algorithms. Except for the average height–density regression, ranged major axis parameters were generally slightly larger than those parameters estimated using the reduced major axis regression. Note that the higher the correlation coefficient, the greater the degree of similarity among all three regression algorithms.

For both tree volume and live quadratic mean diameter, distinct standard major axis regressions were recognized for self-thinning and non-self-thinning stands. For the self-thinning tree volume–density line, the slope of $-1.282$ was significantly different from the theoretical self-thinning slope of $-1.5$ ($P < 0.05$). Older stands judged to be growing beyond self-thinning had a shallower slope of $-1.045$. The reduction in slope for the older stands indicated a reduction in mortality rate compared to the actively self-thinning younger stands. The live quadratic mean diameter–density relationship was similar, with the self-thinning slope of $-0.509$ greater than the slope of $-0.413$ for the older stands. Respective
slopes for the dead quadratic mean diameter and mean tree height regressions for all stands combined were \(-0.505\) and \(-0.269\).

Of note is the comparison between the live and dead quadratic mean diameter as a function of stand density for all stands (Figure 11-3).

Figure 11-3. Standard major axis (reduced major axis) regression for the log-log live and dead quadratic mean diameter–tree density relationship for a chronosequence of primary stands, Little Grand Lake (60 years–bimodal). Regression parameters, 95% confidence intervals, and fit statistics are given in Table 11-1.

Covariance analysis of parameters estimated by ordinary least squares analysis showed the regression lines to be parallel \((P = 0.9193)\) with significantly different intercepts \((P < 0.0001)\). For live trees, reduced major axis intercept and slope were calculated as 2.731 (95% C.I. = 2.649, 2.818) and \(-0.459\) (95% C.I. = \(-0.484, -0.435\)), respectively. For dead trees, regression slope and intercept were calculated as 2.670 (95% C.I. = 2.399, 2.990) and \(-0.505\) (C.I. = \(-0.596, -0.427\)). Across the range of stand densities examined, the live trees
had consistently larger diameters than the dead trees. In other words, smaller trees had a
greater mortality rate than larger trees.

11.3 STAND DENSITY MANAGEMENT DIAGRAM

A stand density management diagram (SDMD) developed for mixed balsam fir–
spruce stands in western Newfoundland (Sturtevant et al. 1998) was used to help situate all
chronosequence stands in terms of their relative stage of stand development (Figure 11-4).

Graphing of the sample stands on Sturtevant et al.’s (1998) SDMD produced a clear
picture of stand dynamics. The position of the stands on the SDMD was used as a measure
of each stand’s relative stage of stand development. Based on both the size and age
structure of the chronosequence stands, and their relative position on the SDMD, four types
of stand development are proposed:

(1) Single-cohort and bimodal stands undergoing intense and active self-thinning (9,
19, 2, 10, 43, 4, 16, 13, 3, 20, 29, and 25). All stands undergoing active self-thinning were
located relatively close to the upper limit of the zone of imminent competition mortality
and tracked along stem density approximately parallel to the maximum size–density line at
relative stand density = 1.0. Except for the bimodal plot 29, all stands were 60 to 90 years
old. All stands had 75 percentile height values ranging from 7.1 to 14.4 m, with > 3,000
stems ha"^1".
Figure 11-4. Relative position of 41 Little Grand Lake stands on the mixed balsam fir–black spruce stand density management diagram given by Sturtevant et al. (1998). Diagram based on a relative density index \((Pr) = 1.0\), a lower limit of the zone of imminent competition mortality (ZICM) at \(Pr = 0.5\), and an approximate crown closure (CC) line at \(Pr = 0.13\). Isolines of both tree height and quadratic mean diameter are also indicated. Relative density index is defined as the ratio of actual stand density to the maximum stand density attainable in a stand with the same mean tree volume (Drew and Flewelling 1979) and is independent of site quality.
(2) Single-cohort and bimodal stands past intense, active self-thinning and beginning or undergoing stand break-up (22, 32, 40, 27, 50, 31, 34, 21, 11, 12, 37, 36, 35, 48, 24, 7). These stands > 90 years of age were more or less located close to or outside the lower limit of the zone of imminent competition mortality. Compared to the younger self-thinning stands, these stands were of lower density (< 2,200 stems ha\(^{-1}\) except for plot 32 at 2,875 stems ha\(^{-1}\)), and taller and larger in diameter. The notable distinction between the two groups of stands occurred at an approximate density of 3,000 stems ha\(^{-1}\). For densities > 3,000 stems ha\(^{-1}\), all self-thinning stands more or less paralleled the upper maximum size–density line and exhibited a slope of –1.28. For densities < 3,000 stems ha\(^{-1}\), the rate of travel along the self-thinning line decreased and the slope of the stand development trajectory reduced notably, to reach a level of –1.04. As noted above, the slopes of both lines were significantly different at \(P = 0.05\) \((n = 28\) stands).

(3) Single-cohort stands showing no evidence of active self-thinning (8, 6, 51, 38, 39, 42, 23, 15, and 46). All nine stands were < 40 years of age and ranged in average height from 2.5 to 5.5 m. All stands were below the lower limit of the zone of imminent competition mortality. Except for plot 39 with the highest density of 39,000 stems ha\(^{-1}\), all other stands were either close to, or even below, the crown closure line.

(4) Bistaged stands (49, 45, 26, and 44). Except for plot 44, these stands were either on or below the lower limit of the zone of imminent competition mortality. Because of low stocking levels that were age and site-related (low site index), these stands were not undergoing active self-thinning.
11.4 BASAL AREA TRENDS

Chronosequence trends for basal area of live and dead trees both single-cohort and bimodal stands were defined by non-parametric loess smoothers. Basal area trends were assessed in terms of both 75 percentile stand height and total stand age (Figure 11-5). For each independent variable examined, the relationship with both stand height and stand age was similar. For both live and dead basal area trends, three distinct phases in stand development were identified (Figure 11-5A):

(1) An aggrading phase characterized by rapid accumulation of live basal area to approximately 9 to 10 m stand height (60 years total age). Live basal area increased from a minimum of 1 m$^2$ ha$^{-1}$ in the youngest stands of age class 11 to 20 years to maximum values approaching 50 m$^2$ ha$^{-1}$. Changes in total dead basal area followed an opposite trend with decreases from a peak of 23 m$^2$ ha$^{-1}$ in the youngest stands to minimum levels near 10 m$^2$ ha$^{-1}$ in stands around 60 years of age.

(2) A transition period of slightly declining, but relatively stable live basal area levels from 10 to 15 m (60 to 90 years of age). During this period of stand development, dead basal area accumulated at a steady rate to levels approximately equal to those of the early post-disturbance period.

(3) A degrading phase characterized by an increased rate of live basal area decline for stands 15 to 20 m in height and 90 to 140 years of age. Levels of dead basal area followed a similar decline to that of live basal area, but for stands approximately 2 m taller and 10 to 20 years older.
Figure 11-5. Stand basal area as a function of stand 75 percentile height and total stand age for all single-cohort and bimodal stands, Little Grand Lake chronosequence. (A) Total live and dead basal area, (B) live and dead basal area by species, and (C) relative proportion of total live and dead basal area.
Total basal area trends were mainly the result of changes in the basal area of balsam fir (Figure 11-5B). The respective quadratic and sigmoidal character of the live and dead basal area trends were similar for the basal area trends for both total and balsam fir. This similarity was understandable given the dominance of balsam fir basal area across the chronosequence.

A difference of note was the greater rate of decline for the basal area of balsam fir relative to total basal area. This was due, no doubt, to the persistence of large white birch in the older stands, a condition that would have masked the decline in balsam fir basal area in the plots showing total basal area values. Basal area levels of black spruce, white spruce and white birch showed no appreciable trends across the chronosequence. Live and dead basal area values of these species rarely exceeded 10 m$^2$ ha$^{-1}$ and 5 m$^2$ ha$^{-1}$, respectively.

Trends in the relative proportions of live and dead basal area were similar for both the height and age indices of stand development. The relative proportions of total live and dead basal area showed significant opposing linear trends across the chronosequence (Cochran–Armitage trend statistic $Z = 3.6402$, $P < 0.0001$, $n = 37$ stands). The relative proportions of live trees declined over the chronosequence whereas the relative proportion of dead trees increased (Figure 11-5C). The relative proportion of total dead basal area declined steadily from a high of approximately 80% in the youngest stands to a low of approximately 20% in 60-year-old stands and then increased to levels not exceeding an average of 30% in the oldest and tallest stands. The trend was reversed for live total basal area. The relative proportion of total live basal area increased from approximately 20% in the youngest stands, peaked at around 80% in the 60-year-old stands and then decreased to average levels not < 70% in the oldest and tallest stands. For bimodal, reverse-J and
bistaged stands, the proportions of the total dead basal area were almost equal at 23.3%,
24.3% and 23.0%, respectively.

11.5 TREE DENSITY TRENDS

Opposing trends of both percent live and dead tree density occurred across the age
and height chronosequence (Figure 11-6). Percent live tree density decreased from a
maximum of > 80% in the youngest stands to minimum levels of 40% to 50% at ages 90 to
100 years, and then increased in stands > 100 years old. Opposite trends were evident for
the density of dead trees with snag density reaching maximum levels at around 100 years of
age or a 75 percentile height of 15 m. Cross-over points occurred at 80 and 110 years of
age, and at stand heights of 11 to 19 m. These opposing changes in relative proportions of
live and dead tree density were significant (Cochran–Armitage, Z = 31.1953, \( P < 0.0001 \), \( n = 37 \) stands).

Figure 11-6. Relative proportion of total live and dead tree density as a function of 75
percentile stand height and stand age for single-cohort and bimodal stands, Little Grand
Lake. Loess smoothing with span = 0.5.
11.6 STAND DEVELOPMENT AND SIZE STRUCTURAL INDICES

Of the 37 single-cohort and bimodal stands, a chronosequence of six stands was chosen to showcase the changes in tree diameter frequency (i.e. size hierarchy) with stand development (Figure 11-7). Plots 51 to 24 represented the changes in the single-cohort stands with plot 12 representative of the bimodal stands characterized by active recruitment in canopy gaps. Evident was the shift in dbh frequency distributions from a reverse-J distribution in the youngest stands to modal stands that exhibited increasing standard deviation and flattening of the normal distribution as average tree density decreased and both average tree diameter and diameter range increased. In plot 12, the development of a distributional bimodality highlighted the recruitment of smaller diameter trees within canopy gaps as the stand began to break up. Tree densities ranged from a high of 13,733 stems ha\(^{-1}\) (plot 51) to a low of 864 stems ha\(^{-1}\) (plot 24), and total average stand age ranged from 20.8 (plot 51) to 123 years (plot 12). Concomitant decreases in the quadratic mean diameter were of the order 1.88 cm (plot 51) to 24.5 cm (plot 24).

Using average total stand age, quadratic mean diameter, and the 75 percentile stand height as measures of stand development, four stand size structure (dbh classes) indices were used to characterize stand development: Gini coefficient, coefficient of variation, skewness and the Shannon index of diversity. The four indices behaved in the same manner regardless of the measure of stand development used (Figure 11-8).
Figure 11-7. Stand structural development across a chronosequence of selected stands, Little Grand Lake. Age class (years) and tree density (stems ha\(^{-1}\)) are given for each plot.
Figure 11-8. Size (dbh) structural indices for a chronosequence of single-cohort and bimodal stands, Little Grand Lake. $r_s$ = Spearman rank correlation coefficient.
The Gini coefficient, coefficient of variation and skewness were negatively correlated with stand development, whereas the Shannon index was positively correlated with stand development. The Gini coefficient, coefficient of variation, and measure of skewness were closely correlated and expressed either a negative near-linear relationship with stand development as in the case of the Gini coefficient, or a negative curvilinear correlation with stand development as exemplified by both skewness and the coefficient of variation. In contrast, the Shannon index showed a curvilinear monotonic increase with stand development, acting, in some respect, as a reverse mirror image of the behavior of the other three indices, especially skewness and the coefficient of variation. Excluding the Gini coefficient, all indices showed rapid change in the early decades of stand development, followed by a reduced rate of increase or decrease with progression of stand development.

11.7 REGENERATION CHRONOSEQUENCE

Sampling of tree regeneration across a chronosequence of stands permitted an analysis of temporal changes in seedling age, height and basal diameter frequencies (Figure 11-9, Figure 11-10, Figure 11-11). Plots were arranged according to the average total age of each stand. Seedling age frequencies were unimodal, with the average seedling age ranging from 6.3 \((s = 2.1)\) to 13.2 years \((s = 3.8)\) (Figure 11-9). Of note is the general lack of seedlings older than 20 years. This was true for all stands, regardless of the stand age or degree of stand development. The values of the Weibull shape parameters indicated a normal or slightly negative skewness for the majority of distributions.

Average seedling height ranged from 4.4 \((s = 1.9)\) to 28.0 cm \((s = 18.0)\) (Figure 11-10). Weibull shape parameters within the range 1.4 to 2.9 indicated right-skewed,
lognormal-like distributions. Seedling basal diameter ranged from 0.6 \( (s = 0.2) \) to 4.2 mm \( (s = 3.8) \). The development of positively skewed frequencies was most pronounced with seedling basal area (Figure 11-11). Weibull shape parameters decreased from values of 3.1 to 3.7 in the youngest stands to values < 1.5 in the oldest stands.

Trends in the Weibull shape parameter, coefficient of variation, Gini coefficient and skewness were used to detect temporal changes in seedling age, height and basal diameter frequencies (Figure 11-12). All indices failed to show any significant correlation with seedling age. This was understandable given the generally stable unimodal age distributions in all stands. In contrast, the Weibull shape parameter, the coefficient of variation, and the Gini coefficient acted as significant indices of seedling size hierarchy. Skewness failed to show a correlation with either seedling height or basal diameter.

Significant changes in seedling size hierarchy were evident across the chronosequence. The mean seedling basal diameter was positively correlated with both the Gini coefficient and the coefficient of variation, whereas the Weibull shape parameter was negatively correlated with seedling basal diameter (Figure 11-12). Bivariate correlations between seedling height and the three indices (Gini coefficient, coefficient of variation, and Weibull shape parameter) were similar to those with seedling basal area, but in all cases were only marginally non-significant. In general, seedling growth increasingly strengthened a positively skewed, lognormal character for both the height and basal diameter frequency distributions. This was significant for seedling basal diameter, but weaker, though evident, for seedling height.
Figure 11-9. Seedling age distribution for a chronosequence of single-cohort and bimodal stands, Little Grand Lake. For each plot, the mean age (standard deviation), $c =$ Weibull shape parameter and $n =$ number of seedlings, are given.
Figure 11-9. (Continued)
Figure 11-10. Seedling height frequency for a chronosequence of single-cohort–bimodal stands, Little Grand Lake. Mean height ($\bar{X}$), standard deviation ($s$), 3-parameter Weibull shape parameter ($c$), and sample size ($n$) are given for each distribution.
Figure 11-10. (Continued)
Figure 11-11. Seedling basal diameter frequency distribution for a chronosequence of single-cohort–bimodal stands, Little Grand Lake. Mean basal diameter ($\bar{X}$), standard deviation ($s$), 3-parameter Weibull shape parameter ($c$), and sample size ($n$) are given.
Figure 11-11. (Continued)
Figure 11-12. Bivariate relationships between seedling attributes (height, basal diameter, and age) and selected heterogeneity indices (Gini coefficient, skewness, coefficient of variation, and Weibull shape parameter), Little Grand Lake. Spearman rank correlation coefficients ($r_s$) and probability levels are given for each distribution. $ns = not significant.$
Mean seedling bank attributes (age, height, basal diameter, density) showed significant monotonic correlations with mean canopy attributes (age, 75 percentile height, quadratic mean diameter, basal area and density (Figure 11-13, Figure 11-14, Figure 11-15, and Figure 11-16). All seedling attributes were negatively related to both stand density and basal area, but positively related to stand age, diameter and height. Seedling density–stand attribute relationships proved to be the weakest, but were characterized by significant trends equal in character to those of the other attributes. As a function of stand density, all seedling attributes exhibited monotonic curvilinear relationships, with all other seedling attribute–stand attribute relationships generally linear in character. Average seedling age, height, basal diameter and density ranged between 6.3 and 13.2 years, 4.4 to 30 cm, 0.5 to 2.9 mm, and 2,500 to 484,375 seedlings ha$^{-1}$, respectively. These mean seedling age and size ranges occurred across stands characterized by a total age range of 60 to 140 years and a height range of 8 to 20 m.

11.8 CONCLUSION

An insect-mediated chronosequence of primary stands throughout the Little Grand Lake landscape permitted an examination of post-insect disturbance stand development. The entire range of stand development from stand re-initiation to transition old-growth was examined. The balsam fir-dominated stands followed the classic pattern of self-thinning as defined by both tree size and stand density changes. A stand density management diagram designed for mixed balsam fir–black spruce forests of Newfoundland proved to be very helpful in understanding stand development in the study stands. Changes in the size and age of the established seedling bank reflected the changes in stand development. Selected
Figure 11-13. Correlation between mean seedling age and stand attributes (age, basal area, quadratic mean diameter, 75 percentile height, and stem density) across a chronosequence of stands, Little Grand Lake. $r_s = $ Spearman rank correlation coefficient. Data are means ± SEM.
Figure 11-14. Correlation between mean seedling height and mean stand attributes (age, basal area, quadratic mean diameter, 75 percentile height, and stem density) across a chronosequence of stands, Little Grand Lake. $r_s$ = Spearman rank correlation coefficient. Data are means ± SEM.
Figure 11-15. Correlation between mean seedling basal diameter and mean stand attributes (age, basal area, quadratic mean diameter, 75 percentile height, and stem density) across a chronosequence of stands, Little Grand Lake. $r_s =$ Spearman rank correlation coefficient. Data are means ± SEM.
Figure 11-16. Correlation between seedling density and mean stand attributes (age, basal area, quadratic mean diameter, 75 percentile height, and stem density) across a natural chronosequence of stands, Little Grand Lake. $r_s =$ Spearman rank correlation coefficient.
structural indices were useful in describing changes in stand and seedling bank
development. These results confirmed the significant role played by stand development
processes in determining stand structure in an insect-mediated landscape.
CHAPTER 12
LITTLE GRAND LAKE SITE INDEX

12.1 INTRODUCTION

The existence of a natural chronosequence permitted the analysis of self-thinning and stand development carried out in Chapter 11. In using the substitution of space for time in chronosequence studies, case must be taken to minimize the confounding of effects of site heterogeneity. The measured differences may not be a function of time and development, but rather a function of confounding site heterogeneity.

To confirm that the single-cohort and bimodal stands indeed formed a natural chronosequence, it was important to compare the range in site index among these stands. To accomplish this, the site index of each sample stand was approximated using graphic and arithmetic site index models developed for Newfoundland and Quebec forests.

12.2 SITE INDEX

Box plots of site indices for single-cohort, bimodal, reverse-J, and bistaged stands are given in Figure 12-1. Site index methods by Page (1968) and Newton (1992) were developed for forest stands of western and central Newfoundland, respectively, while the site index equation of Pothier and Savard (1998) was developed for balsam fir forests of Quebec. All three methods produced comparable site index values, with those calculated
Figure 12-1. Comparison of site index for single-cohort, bimodal, reverse-J, and bistaged stands, Little Grand Lake. Site index data included site index curves (Page 1968) and equations (Newton 1992; Pothier and Savard 1998) developed for the balsam fir and black spruce forests of Newfoundland and Quebec. Box limits represent the 25th and 75th data percentiles. Error bars represent the 10th and 90th percentiles, with the dots representing the 5th and 95th percentile outliers. Mean and median site index are given by the dashed and solid line, respectively.
using Newton’s (1992) site index equation having the greatest range. Mean site index for single-cohort stands ranged from 12.4 to 13.7 m (Table 12-1). Bimodal stands had higher mean values that ranged from 13.2 to 17.1 m. Reverse-J and bistaged stands had the lowest mean site index values. Both stands types had similar site index ranges; 9.5 to 11.6 m for reverse-J stands, and 9.4 to 11.1 m for bistaged stands.

Table 12-1. Statistical comparison of site index among four stand types, Little Grand Lake.

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<tr>
<th>Stand type</th>
<th>Mean site index&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Standard error</th>
<th>n&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Single-cohort</th>
<th>Bimodal</th>
<th>Reverse-J</th>
<th>Bistaged</th>
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<td></td>
<td></td>
<td></td>
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<td></td>
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<td>Single-cohort</td>
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<sup>a</sup> Sites indices determined using site index curves (Page 1968) and site index equations (Pothier and Savard 1998; Newton 1992). One-way analysis of variance with Tukey–Kramer adjusted <i>P</i> values for unbalanced data.

<sup>b</sup> <i>n</i> = number of plots. Total number of trees analyzed = 152.

<sup>c</sup> Based on two-way analysis of variance of site indices, with Tukey–Kramer adjusted <i>P</i> values for unbalanced data.

<sup>d</sup> Based on one-way analysis of variance of site indices for each method.
Two-way analysis of variance confirmed a non-significant ($P = 0.139, n = 132$) "stand type x site index method" interaction. Therefore, tests for individual factors were valid. There were no overall significant differences among the three methods used to calculate site index ($P = 0.1696, n = 132$). Significant differences, however, occurred for the site indices among stand types ($P < 0.0001, n = 132$). Site indices (standard error) were calculated as 15.1 (0.66) for bimodal stands, 13.0 (0.34) for single-cohort stands, 10.4 (0.33) for reverse-J stands, and 10.2 (0.51) for bistaged stands. This corresponded to a statistically significant order ($P < 0.05$) \((\text{bimodal} > \text{modal}) > (\text{reverse-J} = \text{bistaged})\) (Table 12-1). Note, however, that when each stand type was analyzed separately, no significant difference was found between the site index of the single-cohort and bimodal stands. The unbalanced nature of the data and consequent interpretation difficulties contributed to this discrepancy (Keough and Quinn 2002, p. 187–188; Littell et al. 2002, p. 141–146).

12.3 CONCLUSION

All three methods produced comparable site index values. The site index values for the modal and bimodal stands exceeded those for the reverse-J and bistaged stands. The range of site index values for the single-cohort and bimodal stands were such that these stands were considered to form a legitimate chronosequence study.
CHAPTER 13

COMPARATIVE LANDSCAPE ANALYSIS OF MAIN RIVER AND LITTLE GRAND LAKE STUDY AREAS

The Little Grand Lake (106 km$^2$) and Main River (225 km$^2$) study areas represent primary forest landscapes whose structure and function are determined for the most part by natural disturbances. Only 2% of the Little Grand Lake area and 0.4% of the Main River area consisted of regenerating cutovers (Figure 13-1).

The Little Grand Lake area is now part of the provisional Little Grand Lake ecological reserve, a system of ecological and wilderness reserves managed by the Government of Newfoundland and Labrador. The Main River watershed, much of which is under timber license to Corner Brook Pulp and Paper Limited (Kruger Inc.), has undergone increased forest road construction and clear-cut logging over the last five years. In March 2001, Corner Brook Pulp and Paper announced a “no clearcut” policy for the Main River watershed. In June 2001 the Main River was granted Heritage River status based on its significant natural, recreational and wilderness values (Government of Newfoundland and Labrador 2001).
Figure 13-1. Landtype composition, (A) percent and (B) total area for both the Main River and Little Grand Lake study area.

13.1 LANDTYPES

Commercial forest stands and scrub forest stands comprised the largest part of both landscapes (85.8% for Main River and 86% for Little Grand Lake) (Figure 13-1). The
terms "commercial" and "scrub" are based on criteria of economic forest accessibility. Commercial forests are defined as capable of producing $\geq 30 \text{ m}^3$ gross merchantable volume ha$^{-1}$ at rotation age. The Main River study area had 1.3 times more of its area under commercial forests relative to scrub forests. This ratio was 3.0 for the Little Grand Lake area. Percentage of peatland was similar for both areas, with the proportion of rock and soil barren 5.4 times greater in the Little Grand Lake area. The percentage of the Main River area classified as water was almost 2.5 times that recorded for the Little Grand Lake area. The amount of cleared land was very small, consisting, for the most part, of roads and former landings in the Little Grand Lake area.

13.2 TREE SPECIES COMPOSITION AND SITE QUALITY

Little Grand Lake's forests were generally more productive than those of the Main River watershed. The former had 16% more productive forest and 16% less scrub forest compared to the Main river forests. Another indication of the comparative site conditions was the relative tree species composition. The following figures describe the percentage of stands having the stated tree species as the primary tree species. Both sites were dominated by balsam fir (89.7% and 83.6% for Main River and Little Grand Lake, respectively), but Little Grand Lake had lower percentages of black spruce-dominated stands (3.2% vs. 10.3%) and higher percentages of both white spruce- (3.5% vs. 0.03%) and white birch-dominated stands (9.6% vs. 0%), all indicating the generally higher site quality of the Little Grand lake forests (Figure 13-2A).
Figure 13-2. Comparison of forest landscape parameters for the Main River and the Little Grand Lake study area. Parameters considered include (A) tree species, (B) site class, (C) age class, (D) height class, and (E) density class. Tree species, age class, height class and density class codes are described in Table 5-1.
A similar conclusion on relative site quality was supported by the site class
distribution (Figure 13-2B). The percentage of medium sites was generally similar,
comprising over 60% of each study area. However, Little Grand Lake had 3.5 times the
percentage of good sites and less than half the percentage of poor sites compared to Main
River.

13.3 LANDSCAPE DISTRIBUTION OF TREE SPECIES

13.3.1 Little Grand Lake

The spatial arrangement of dominant forest types in the Little Grand Lake area is
given in Figure 13-3. Of special interest was the presence of large, old-growth white pine
on the warm, south-facing slopes of Little Grand Lake (Figure 13-4). White pine patches
were also evident in the sheltered, north-facing valley of the river draining the western
region of the study area. The relict white pine overtopped a balsam fir–white spruce–white
pine understory. White pine blister rust symptoms and mortality were evident among
young white pine. Minimum breast height ages for the dominant white pine were 250 to
300 years. White pine was absent from the higher altitude plateau of the study area.

Dominating the slopes of the study area were mature stands of white birch with a
regenerating stratum of balsam fir, white spruce, and white birch. Much of the formerly
mature conifer component of these stands was killed during recent insect outbreaks of the
spruce budworm and hemlock looper.
Figure 13-3. Forest cover type map of the Little Grand Lake study area. bF = balsam fir, bS = black spruce, wS = white spruce, wB = white birch, and wP = white pine. Non-forested areas include peatlands and heathlands (rock and soil barrens), as well as scrub forests not capable of producing 30 m$^3$ gross merchantable volume ha$^{-1}$ at rotation age.
Recently killed conifer-dominated stands had well-established balsam fir regeneration mixed with a lesser density of white spruce and white birch. These regenerating forests covered the sheltered river valleys in both the southern and northern sections of the study area. On these particular sites, plant species indicating good site quality were common and included raspberry, red elderberry (*Sambucus pubens* Michx.) and mountain ash (Meades and Moores 1989).

Of particular interest were the so-called “moose-meadows,” relatively small (usually < 3 ha or so, but can be larger) killed patches surrounded by older forest. Due to the generally good fertility of these sites, the presence of relict, seed-bearing, mature white spruce and the constant browsing of balsam fir by a high-density moose population, white
spruce regeneration and development were enhanced. Open, park-like, pre-crown closure stands of almost pure white spruce developed under these circumstances (Figure 13-5).

Most of the upland areas were characterized by almost pure balsam fir stands or balsam fir–black spruce mixtures. Wet areas, depressions, and areas of low site quality were dominated by old, layered black spruce.

![Figure 13-5. Post-insect disturbance “moose meadows.” Preferential browsing of balsam fir regeneration by moose on good sites have created open-grown white spruce with full crowns to the ground. Residual live white birch and conifer snags and logs are evident.](image)

13.3.2 Main River

Of the commercial forest of the Main River study landscape, 97.5% was dominated by balsam fir and black spruce; balsam fir (54.3%), black spruce (2.6%) or mixtures thereof (40.6%) (Figure 13-6). White pine was absent, the study area being north of the range of
Figure 13-6. Forest cover type map of Main River study area. bF = balsam fir, bS = black spruce, tL = larch, and wS = white spruce. Non-forested areas include peatlands and heathlands, as well as scrub forests not capable of producing 30 m³ gross merchantable volume ha⁻¹ at rotation age.
white pine. Scrub stands, composed mostly of layered black spruce, or balsam fir growing on interior forest fens, were well-dispersed and comprised 37.5% of the study area.

Patches of softwood–white birch mixtures were scattered throughout the study area, often in areas prone to windthrow, especially areas at the westerly end of river or lake valleys. White spruce usually occurred as a minor component in balsam fir stands, especially on the lower reaches of seepage slopes. Exceptions were the rare meadowlands and islands of the “Big Steady,” a 15 km² section of the Main River dominated by grasses (Calamagrostis inexpansa A. Gray) and Agrostis borealis Hartm.), sedges (e.g. Carex vesicaria L.), and other species including bulrushes (Scirpus cyperinus (L.) Kunth), blueflag (Iris versicolor L.) and ferns (e.g. Onoclea sensibilis L.). On these alluvial islands the continuous deposition of sediment combined with annual ice scouring have created open, park-like conditions with mature forests of large white spruce and balsam fir.

13.4 AGE CLASS DISTRIBUTION

All 20-year stand age classes were represented throughout the Little Grand Lake landscape (Figure 13-2C). Age classes 2 and 3 (21 to 60 years) were poorly represented, accounting for only 8.8% of the total landscape. Age class 5 (81 to 100 years) dominated at 36.3%, while each of the remaining age classes constituted between 11.6 and 16.5% of the commercial forest landscape. Of note was the 64.3% of the commercial forests classified as stands > 80 years of age. Patch size was not examined in detail, but the range in age patch size varied from approximately 0.5 to 150 ha.

The youngest forest generally occurred along the southern and northern slopes of the study area, and throughout three river valleys draining the study area; one to the
northwest draining into Grand Lake (especially the southern aspect of the drainage), and the other two draining to the southwest and the southeast into Little Grand Lake. The relief and aspect conditions of these areas no doubt provided the microclimatic conditions conducive to the development of insect outbreaks that are characteristic for the study area (Figure 13-7). In contrast to Little Grand Lake, 98% of the Main river landscape was covered by stands of age class 7 (121+ years) (Figure 13-8). The 2% of the landscape in age class 4 was certainly anomalous and was not field checked because of its relative inaccessibility.

13.5 HEIGHT AND DENSITY CLASS DISTRIBUTION

Due to the absence of regenerating stands in the Main River area, stand height classes 1 and 2 (stands ≤ 6.5 m) did not exist (Figure 13-2D). Well over half of the commercial stands (58.9%) had dominant tree heights between 9.6 and 12.5 m (height class 4), with 27.8% of height class 5 (12.6 to 15.5 m). Maximum heights were in height class 7 (18.6 to 21.5 m) which represented only 0.05% of the study area.

In the Little Grand Lake area, height class distribution mirrored age class distribution. As in the Main River area, height class 4 was well represented, covering 41.4% of the study area. The proportion of the landscape in stands of height class ≥ 5 (23.3%) was less than that recorded for the Main River (30.6%).

Given the old-growth nature of the Main River forests, there were almost no stands with crown closure ≥ 75% (crown class 1) (Figure 13-2E). This compared with 12.6% of the Little Grand lake forests in crown class 1. In both areas, stands of crown class 2 dominated, with substantial areas in generally open stands of crown class 3 (26% to 50%).
Figure 13-7. Map of Little Grand Lake study area showing landscape-level stand age class structure. Age class 1 (0–20 years), 2 (21–40 years), 3 (41–60 years), 4 (61–80 years), 5 (81–100 years), 6 (101–120 years), and 7 (121+ years). Non-forested areas include peatlands and heathlands (rock and soil barrens), as well as scrub forests not capable of producing 30 m$^3$ gross merchantable volume ha$^{-1}$ at rotation age.
Figure 13-8. Map of Main River study area showing landscape-level stand age class structure. Age class 4 (61–80 years), and age class 7 (121+ years). Non-forested areas include peatlands and heathlands (rock and soil barrens), as well as scrub forests not capable of producing 30 m$^3$ gross merchantable volume ha$^{-1}$ at rotation age.
13.6 CONCLUSION

Selected forest landscape parameters of the Main River and Little Grand Lake study areas were compared. Distinct differences in forest landscape structure between the two study areas are a function of different disturbance regimes. The Main River forest landscape is characterized by a contiguous forest canopy, the structure of which is determined by fine-scale individual tree mortality caused predominantly by root rots and butt rots. In contrast, the Little Grand Lake forest landscape is characterized by a mosaic of patches or stands of varying ages and stages of stand development, the structure of which is determined by recurrent insect herbivory.
CHAPTER 14
DISCUSSION

Comparison of the structural characteristics of the Main River forests with those of the Little Grand Lake forests is a study in contrasts. Characteristic of each forest ecosystem is a distinct size and age structure on both a stand and landscape level. These distinctive forest structures reflect, in turn, unique disturbance regimes operative within each forest region.

The Main River forests are fungal-mediated, gap-dynamic forests. Butt rot- and root rot-mediated mortality on a fine-scale tree or neighbourhood level has created an ostensibly long-continuity, old-growth forest landscape. The old-growth stage of stand development characterizes the entire landscape. In contrast, the Little Grand Lake forests are insect-mediated, patch-dynamic forests. Insect-mediated mortality and modification on a stand (or landscape) level has created a patch mosaic of stands in diverse stages of stand development. The entire landscape is composed of stands that span the full spectrum of stand development from stand initiation to transition old-growth (and possibly true old-growth) stage of stand development (Oliver 1981; Oliver and Larson 1996).
14.1 MAIN RIVER OLD-GROWTH FORESTS

From a structural perspective, old-growth forests generally have the following classic characteristics (adapted from Oliver and Larson 1996; Franklin et al. 1981; Kneeshaw and Burton 1998; Franklin and Spies 1991a):

1. Reverse-J (rotated sigmoid) tree diameter distributions
2. Trees at maximal ages for the species
3. Standing dead trees (snags) in various stages of decomposition
4. Accumulation on the forest floor of coarse woody debris in all stages of decomposition
5. Relatively continuous vertical distribution of foliage (complex, "multi-storied" tree canopies)
6. Quasi-equilibrium standing tree biomass
7. Spatially heterogeneous, clumped regeneration in response to canopy gaps

Appreciation of the old-growth character of boreal forests is increasing. Boreal forests were long considered the product of catastrophic, stand-replacing disturbance that included fire in the continental boreal forest and insect outbreaks in the more humid eastern boreal forests. A contemporary understanding of boreal forests, however, must include small-scale gap dynamics (and associated old-growth stand structures) as a significant disturbance regime in boreal forests protected from periodic, large-scale disturbance (Liu and Hytteborn 1991; Hofgaard 1993a; Kuuluvainen 1994; Syrjänen et al. 1994; Kuuluvainen et al. 1998; McCarthy 2001; Bartemucci et al. 2002; Wallenius 2002; Kneeshaw and Gauthier 2003). Old-growth boreal forests are even extensive in forest regions characterized by relatively high fire frequency (Harper et al. 2003).

The Main River old-growth forests share many of the structures and processes considered characteristic of old-growth forests. The following structural features (and associated processes) are worthy of note:

14.1.1 Rotated Sigmoid Diameter Distributions

All stands expressed well-developed rotated sigmoid tree diameter distributions (semi-logarithmic presentation). Size distributions have a steep negative slope for trees < 10 cm, a leveling off or only a slight decline for trees in the diameter range 10 to 30 cm, followed by a precipitous decline for trees > 30 cm dbh (Figure 14-1). A stand-level view of a rotated sigmoid distribution is given in Figure 14-2.
Figure 14-1. Idealized rotated sigmoid diameter structure of old-growth boreal forest stands. Shown are the three phases common to stands undergoing small-scale gap dynamics (adapted from Goff and West 1975).

Figure 14-2. Main River old-growth rotated sigmoid stand. Note the range of tree diameters. As is usual in old-growth stands, trees show poor size-age correlation.
Viewed as an expression of tree mortality rate, a reverse-J tree diameter distribution described by the exponential function $Y = aX^b$ has been traditionally viewed as characteristic of a stable or steady-state forest (Meyer and Stevenson 1943; Meyer 1952; Meyer et al. 1961; Leak 1964, 1965). It is important to note that a reverse-J diameter distribution may not be indicative of uneven-aged status, particularly for mixed stands composed of tree species with different growth rates (Oliver and Larson 1996), or for stands that have undergone slow, long-term establishment after catastrophic stand mortality.

First described by de Liocourt (1898) for uneven-aged silver fir forests growing in the French Vosges mountains, the progressive decrease in stem diameter frequency became the basis for the uneven-aged or “plenter system” developed in the late 1880s by the Swiss forester Henri Biolley (Biolley 1980; Schütz 1990, 1997a).

The exponential function assumes that the geometric progression in the ratio of the number of trees in adjacent diameter classes is a constant. This ratio of the number of trees in adjacent diameter classes is termed the $q$ ratio that has become the basis for describing target residual stand structures in uneven-aged forest management (Knuchel 1953; Kostler 1956; Alexander and Edminster 1977; Frank and Blum 1978; Nyland 1996).

A semi-logarithmic representation of the exponential function normally produces a straight line. This assumes that the natality rate is constant, and that the mortality rate is constant for all diameter classes. However, mortality rate is generally not constant throughout the life history of long-lived tree populations, but actually changes with diameter class and is a function of tree age (Hett 1971; Hett and Loucks 1971, 1976). In fact, a semi-logarithmic presentation of diameter class frequency for old-growth forests
generally produces not a straight line, but a well-defined semi-logarithmic rotated sigmoidal diameter relationship (Schmelz and Lindsey 1965; Goff and West 1975; Jones et al. 1981; West et al. 1981; Leak 1987; McCarthy et al. 1987; Busing and Wu 1990; Goodburn and Lorimer 1999; Leak 2002).

Mortality is high in the understory, decreases and levels off for the dominant, vigorous overstory, and then increases again for the senescent overstory. This U-shaped mortality function is biologically consistent with rotated sigmoid size distributions. Studies have consistently reported U-shaped mortality rates for old-growth forests (Harcombe 1987; Platt et al. 1988; Nakashizuka et al. 1992; Kubota and Hara 1995; Runkle 2000; Lorimer et al. 2001). This scenario fits well with the hypothesized gap dynamic disturbance regime of the study stands. Suppressed understory trees die from interspecific competition among the clumped regeneration common in the gaps of old-growth forests (Moeur 1997). Furthermore, long periods of seedling and sapling regeneration would only enhance mortality-inducing physiological stresses. The high incidence of moose herbivory in Newfoundland forests (Bergerud and Manuel 1968; Thompson et al. 1992; Thompson and Curran 1993), especially in tall forests conducive to winter yarding, would further promote the mortality rate of the understory in these particular forests.

Mortality rates would be relatively low for vigorous released trees that had attained the co-dominant or dominant canopy position. Dendrochronological data (unpublished) indicated that most (if not all) of the sampled canopy trees had experienced long periods (up to 100 to 120 years) of juvenile suppression, only to experience relatively rapid and sustained growth once they were released (Figure 14-3).
Figure 14-3. Gap-filler in old-growth Main River stand. Balsam fir gap-filler growing into the canopy. (B) Close-up of the vigorous crown of tree in (A) showing the relatively rapid height growth rates possible in trees released from decades of suppression.

Due to the absence of large-scale canopy disturbance, old senescent trees are common in the dominant canopy. At the same time, these old, large trees have a higher mortality rate than the mid-diameter, faster growing trees. The old, large trees generally have a high incidence of root and butt rots (unpublished data), and therefore a greater disposition to stem snap. Stem snap was the dominant cause of tree fall in these stands (unpublished data).

Under historic climatic conditions, the Main River old-growth stands may have existed in an equilibrium or quasi-equilibrium state. Long periods of constant seedling recruitment, no evidence of exogenous disturbance and a tree-size–dependent mortality rate have probably created near-equilibrium stand conditions. A simulation study of
equilibrium diameter distributions in shade-tolerant sugar maple deviated markedly from both the negative exponential and negative power functions to closely resemble rotated sigmoid curves (Lorimer and Frelich 1984). Modeling of stand equilibrium in plenter forests was attained only under conditions of a rotated sigmoid diameter distribution (Schütz 1975, 1997b, 1997c). Successful modeling of the non-logarithmic form of the rotated sigmoid diameter distribution has been carried out using a finite mixture of two Weibull distributions (Zhang et al. 2001; Liu et al. 2002).

14.1.2 Longevity of Balsam Fir

Total balsam fir ages recorded in this study exceeded assumed maximum ages for the species. Trees > 150 years of age were abundant, while trees > 200 years of age were common. Several trees were aged > 250 years (Figure 14-4).

Figure 14-4. Structural heterogeneity of old-growth balsam fir–black spruce canopy. Most of the canopy trees are > 200 years of age. Note the abundance of arboreal lichens.
Balsam fir is traditionally considered a short-lived tree species, not generally exceeding 200 years of age (Bakuzis and Hansen 1965; Frank 1990; Hardin et al. 2001). Due to its proclivity to infection by root rots and butt rots (Spaulding and Hansbrough 1944; Basham et al. 1953; Davidson 1957; Redmond 1957; Whitney 1976, 1989, 1995; Lavallée 1986), balsam fir is generally prone to early mortality. So pervasive is the incidence of decay, especially with increases in age and dbh, that the pathological rotation age for balsam fir has been set at 70–80 years (Bakuzis and Hansen 1965, p. 140) or even < 65 years of age (Whitney 1976, 1989).

The great age of balsam fir in the upper watershed of the Main River is reflective of a number of factors. First, is the relatively high elevation (350 to 500 m) at which the trees were sampled. In this region of the Long Range Mountains, tree line occurs at approximately 500 to 550 m, so the sampled stands are relatively close to their ecological limits. Under such climatic and edaphic conditions, slow-growing trees may be less prone to fungal decay and will therefore live longer. Balsam fir growing in the White Mountains of New Hampshire had much lower incidence of root and butt rots than fir trees growing at lower elevations (Worrall and Harrington 1988). Trees growing on productive sites usually have higher mortality rates, with an acceleration of stand break-up (Franklin et al. 1987; Robichaud and Methven 1993). This can be attributed to the rapid height growth on more productive sites. Relative to slow growing trees on poor sites, faster-growing trees will reach critical windthrow heights at a younger age, thus promoting the risk of earlier windthrow (Smith et al. 1987; Ruel et al. 2000).

Tree mortality from windthrow (tip-up mounds) was uncommon, with fungal decay-mediated tree snap being by far the dominant reason for tree mortality (unpublished data).
The slow height growth of balsam fir in these forests would minimize windfall-induced mortality. It was noted as well that the taper of the mature trees seemed much greater than that found in fast-growing, even-aged stands farther to the south. The cessation of height growth and the continued stem diameter growth in these old trees may act as an evolutionary survival mechanism in these relatively harsh site conditions (King 1990).

At its northern limit in the James Bay area, balsam fir was aged at a maximum value of 212 years (≥ 30 cm core height) (Sirois 1997). Leak (1985) reported a maximum age of 202 years for balsam fir growing in a virgin spruce–fir stand in the White Mountain National Forest, New Hampshire. Maximum recorded age (at the stump) for balsam fir in Labrador and western Newfoundland were 220 and 222 years, respectively (Wilton 1965; Jardon and Doyon (in review)). It has been suggested that slow-growing trees growing under “adverse” conditions can display enhanced longevity (Schulman 1954; Loehle 1987; Mueller-Dombois 1987; Larson 2001). Significant examples includes centuries-old cliff-edge white cedar (Kelly and Larson 1997) and 1800-year-old clonal black spruce growing in subarctic environments (Laberge et al. 2000).

Secondly, the seedling bank of balsam fir and other species of *Abies* are known to undergo decades of juvenile suppression (Morris 1948; Hatcher 1960; Zarnovican 1981; Kohyama 1983; Antos et al. 2000). In the present study many trees required over 60 to100 years to reach breast height (Figure 14-5).

It seems that the long periods of juvenile suppression experienced by most balsam fir has promoted trees of great chronological age. The physiological age of a balsam fir that has been suppressed for a century is much less than its chronological age. In fact, Morris (1948) noted that “it is rather surprising to see that a balsam fir tree 200 years old, when
Figure 14-5. Suppressed balsam fir trees of this type range in age from 80 to 150 years old. Mortality rates of such trees are not known. Note the low crown length on a well tapered stem.

severely suppressed for the first 100 years, is not more susceptible to rot than a 100-year-old balsam fir in the same stand” (See also Crossley 1976). Schütz (1969) confirmed that suppression does not influence physiological aging by showing that spruce trees suppressed for more than 100 years showed the same growth potential as trees that were not
suppressed. Or, as Oliver and Larson (1996, p. 137) have quipped, trees, when released “act their size, not their age.”

14.1.3 Size–Age Structure

Long and differential periods of suppression in individual balsam fir and spruce promoted another characteristic of primary, old-growth forests – the generally poor relationship between tree age and size (dbh and height). Trees of equal height and diameter differed in age by as much as 120 years. Tree size, therefore, provided minimum indication of the actual chronological age of trees in these old-growth forests. Tree growth is best understood on an individual tree basis, as trees respond to the stochastic release of growing space, or by simply growing slowly upward into the canopy. This is in contrast to the release of seedling bank regeneration in response to complete or partial canopy removal. In these situations, tree age–size relationships are better correlated. This wide variability in the tree age–size relationship found in old-growth forests comprised of shade-tolerant tree species is well known (Gates and Nichols 1930; Gibbs 1963; Hatcher 1963; Tubbs 1977; Szwagrzyk et al. 1995; Parish et al. 1999; Antos and Parish 2002b, 2002b). This general lack of relationship between tree age and size in old forests confirms the established notion that size is generally more important than actual chronological age in assessing reproductive development and stand dynamics (Harper and White 1974; Harper 1977; White 1980; Peet 1981). Foresters have long understood this by using a tree’s physiological age at breast height, rather than the chronological age, when assessing, in particular, the growth of shade-tolerant trees.
14.1.4 Age Structure and Stand Stability

The well-established reverse-J, uneven-aged structure of both trees and regeneration for all three stand reconstruction plots confirmed that these stands represent stable, self-perpetuating systems. Under current climatic and small-scale gap disturbance regime, balsam fir, black spruce and white spruce are well adapted to maintain continuous canopy cover for long periods of time:

1. Once established, the high shade tolerance of fir and spruce (especially balsam fir) (Logan 1969) confer the ability to persist for decades in a suppressed state under the high canopy (Morris 1948; Antos et al. 2000).


3. Vegetative reproduction of all three species, especially in continuously moist, moss-rich boreal forests (Cooper 1911; Bannan 1942; LeBarron 1945; Bakuzis and Hansen 1965).

4. The ability of both seedlings and layers to respond vigorously in height growth in response to released growing space upon the death of a neighbouring tree or trees (Baskerville 1961a; Richardson 1975; Crossley 1976; Davis 1991; Paquin and Doucet 1992a).
5. The ability of both *Abies* and *Picea* to germinate on moss-covered and coarse woody debris microsites commonly found in humid, old-growth boreal and subalpine forests. Compared to *Picea*, the robust morphology of *Abies* seedlings allow them to germinate and establish on a wider variety of microsites. *Picea* will often preferentially germinate on suitably decomposed coarse woody debris microsites (Bedell 1948; Place 1955; Rowe 1955; Horton 1959; Day 1964; Wagg 1964; Knapp and Smith 1982; Takahashi 1994; McLaren and Janke 1996; DeLong et al. 1997; Hörnberg et al. 1997; Simard et al. 1998, 2003; Takahashi et al. 2000; Nakagawa et al. 2001; Narukawa and Yamamoto 2002; Ruel and Pineau 2002; Brang et al. 2003; Nakagawa et al. 2003; Narukawa et al. 2003) (Figure 14-6).

Figure 14-6. Preferential establishment of white spruce regeneration on moss-covered coarse woody debris. Balsam fir seedlings are also well-established.
These well-known life history traits of fir and spruce permit the development of stable, reverse-J age distributions in the absence of large-scale canopy disturbance. Similar reverse-J age distributions have been documented for old-growth Engelmann spruce–subalpine forests (Day 1972; Hanley et al. 1975; Whipple and Dix 1979; Veblen 1986a; Aplet et al. 1988; Rebertus et al. 1992; Roovers and Rebertus 1993; Parish et al. 1999; Antos and Parish 2002a, 2002b), as well as Scandinavian old-growth boreal Pinus (Kuuluvainen et al. 2002), Pinus–Picea (Engelmark et al. 1994) and Picea forests (Kullman 1996). Stable, reverse-J tree age structures have also been documented for old-growth, cliff-face eastern white cedar (Thuja occidentalis L.) (Kelly and Larson 1997).

The late successional, “climax” character of balsam fir (particularly in combination with spruce-birch on mesic sites in the long-term absence of fire) is well documented for Canadian boreal forests (Wilton 1959; Hatcher 1963; Damman 1964; Dix and Swan 1971; Carleton and Maycock 1978; Viereck 1983; Bergeron and Dubuc 1989; Zoladeski and Maycock 1990; Frelich and Reich 1995; Kenkel et al. 1998; Bergeron 2000; De Grandpré et al. 2000; Gauthier et al. 2000; Lesieur et al. 2002). In south-east Labrador, a fire cycle of approximately 500 years has permitted the creation of old, multi-aged spruce and fir forests > 300 years of age that reproduce predominantly by vegetative layering (Foster 1983, 1984).

14.1.5 Fungal-Mediated Tree Mortality

As we have seen, balsam fir, as well as black and white spruce, is particularly well-adapted to self-perpetuation under a small-scale, fungal-mediated gap disturbance regime. Under such a gap disturbance regime, old-growth forests persist on the landscape.
No studies have been conducted on the role of fungi in determining tree mortality and gap dynamics in these old-growth stands. That fungi in the form of root and butt rots do play a role is obvious from a preliminary assessment of the mode of tree mortality. In the absence of fire and insect herbivory, fungal-mediated tree mortality predominates. Preliminary data indicate that an average of 13.4% of all trees > 1.3 m was standing dead in the Main river old-growth stands (Figure 14-7).

As well, tree snap was the main cause of treefall and associated coarse woody debris accumulations in these stands (unpublished data). Stem breakage occurred at the ground level and up the length of the bole to a height of approximately 1 to 2 m. This form of etiology is common in trees that are affected by root and butt rots that kill lateral roots and decay structural heartwood of the major roots and butt sections of conifers (Warren and English 2001) (Figure 14-8).

Decay fungi of greatest importance in primary Newfoundland forests are indeed butt and root rots that normally extend 1 to 2 m up the stem (Whitney 1995; Gary Warren, Forest mycologist, Atlantic Forestry Centre, pers. comm.). According to Warren (pers. comm.), fungal species probably responsible for butt snap in the early stages of stand decline include *Coniophora puteana* (Schumach.:Fr.) P. Karst., *Tyromyces balsameus* (Peck) Murrill, and *Poria subacida* (Peck) Sacc., whereas *Inonotus tormentosus* (Fr.:Fr.) S. Teng, *Scytinostroma galactinum* (Fr.) Donk and *Resinicium bicolor* (Albertini & Schwein.:Fr.) Parmasto are more prevalent in the decline of older stands. Both live and dead trees are able to snap, but most snapped trees had probably died before subsequent stem weakening and breakage, especially given the common occurrence of *Armillaria ostoyae* (Romagn.) Herink, a moderate to aggressive root pathogen responsible for the
Figure 14-7. Snags, Main River. (A) Balsam fir snag showing former recovery after top damage. (B) White spruce snag with woodpecker cavities. (C) White birch snag. (D) Clump of balsam fir snags.
Figure 14-8. Two examples of fungal-mediated stem snap (butt rots).


In the absence of fire and other stand-replacing disturbance, the importance of pathogenic fungi as mediators of stand structure and composition grows in importance. Fungi become the main agents of tree mortality, stand structural and compositional heterogeneity and the ultimate mediator of gap dynamics (Hubert 1918; Worrall and
During collection of tree spatial data in the stand reconstruction plots, it was evident in the generally open stands that large trees (and therefore trees with butt and root rot) tended to be clustered. These clusters may be arranged randomly in the stand, but the spatial data remains to be analyzed. Tree mortality in fungal-mediated forests is not random, but rather is spatially clustered (van der Kamp 1995; Lundquist and Klopfenstein 2001). These clusters may range from large root disease centres up to 10s of hectares in size in Pacific Northwest coniferous forests (Nelson and Hartman 1975; McCauley and Cook 1980; Tkacz and Hansen 1982; Bloomberg and Reynolds 1985; Boone et al. 1988; Dickman and Cook 1989; van der Kamp 1991; Holah et al. 1993, 1997) to dead tree clustering at the scale of 10 to 20 m (Dobbertin et al. 2001). This random arrangement of fungal clusters probably explains the generally complex or “chaotic” structural heterogeneity or gap structure commonly associated with high-elevation old-growth forests.

14.1.6 Why This Gap Disturbance Regime and Old-Growth Structure?

The upper Main river watershed has no recorded history of stand-replacing disturbance from fire or insect outbreaks. Data are scarce, but research based on written records has shown that the east side of the Great Northern Peninsula is a region of low fire hazard (Wilton and Evans 1974) with no known large-scale outbreaks of either the hemlock looper nor the spruce budworm (Corner Brook Pulp and Paper Limited 2001).

The forests of insular Newfoundland have a long history of spruce budworm and hemlock looper outbreaks that have caused extensive forest stand mortality (Carroll 1956;
Figure 14-9 outlines the range of historical insect outbreaks for insular Newfoundland. What is obvious is the lack of insect outbreaks along the entire length of the east side of the Great Northern Peninsula from the Cloud River watershed in the north to the Main River watershed in the south. Equally evident is the occurrence of insect outbreaks along the entire west coast of the Great Northern Peninsula and across the top of the Peninsula south of Hare Bay. These distributional patterns point to an elevational barrier, not a latitudinal barrier to insect dispersion and distribution.

The geographical distribution of insect outbreaks reflects very closely the extent of the coastal plain formation along the Great Northern Peninsula. This poorly drained, low elevation (0 to 150 m) region runs the entire length of the west side of the Great Northern Peninsula and includes the northern section of the peninsula as well. This low elevation region lies in stark contrast to the neighbouring high elevation (200 to 600 m with some peaks rising to nearly 800 m) Long Range Mountains to the east and south. Insect outbreaks (principally of the hemlock looper) occur regularly throughout the coastal plain and across the northern region of the Great Northern Peninsula. Even though the Great Northern Peninsula was considered highly vulnerable to the spruce budworm, the little damage from the budworm was attributed to the climate and to the stochastic factors associated with budworm moth flights (Raske 1986).

It seems that the Long Range Mountains effectively shelter the eastern slope forests from extensive invasion by moths from the coastal plain region. This is not to say that insects may not enter the east coast forests. In the past several years, low levels of hemlock
looper herbivory resulting in some tree mortality has been detected in sheltered sections of the lower Main River valley (2001–2002 maps of hemlock looper defoliation within the Main River watershed provided by H. Crummey, Newfoundland and Labrador For. Serv.). No herbivory, however, has been detected in the higher elevation regions of the watershed. The wet, cool climatic conditions of the upper watershed may prevent the development of insect populations to levels that can cause tree and stand mortality.

The forests of western Newfoundland form part of the humid, balsam fir-dominated forests of eastern Canada that have notably longer fire cycles compared to the more pyrogenic forests of the continental boreal forest south of the tundra. Cycles may range from 50 to 150 years in the western boreal forest and black spruce boreal forests to more than 200 to 500 years in the eastern boreal forests (Heinselman 1981; Yarie 1981; Foster 1983; Payette 1992; Bergeron et al. 2001; Bergeron et al. 2002). Note that the forests of central Newfoundland are predominantly composed of black spruce, the result of a relatively higher fire frequency under a continental climate regime of warm, dry summers.

The fire history of the Main River watershed is unknown. However, given the predominance of balsam fir and the fact that the region has been classified as having a low to very low risk of fire (Wilton and Evans 1974; Johnson 1995), it is reasonable to assume that fire cycles are at least centuries long. Considerable orographic enhancement of precipitation (rain, drizzle, snow) during moist east-northeast flows off the North Atlantic and the southward-flowing Labrador Current give generally cool, damp–wet conditions over the upper Main River watershed (C. Banfield, retired, Memorial University of Newfoundland, pers. comm.) A relatively long fire cycle, therefore, is reasonable.
14.1.7 Temporal and Spatial Continuity of Old Growth

The temporal continuity of the Main River old-growth forests is unknown. Only detailed pollen and soil charcoal analysis can provide estimates of long-term disturbance history in these forests (Bradshaw and Zackrisson 1990; Bradshaw 1993; Segerström et al. 1994). Paleoecological studies have showed that old-growth boreal forests may show century-scale (Hörnberg et al. 1995) and millennial-scale periods of fire-free continuity (Payette et al. 1989; Segerström et al. 1996; Ohlson and Tryterud 1999; Jasinski 2002). Studies in British Columbia old-growth temperate rainforests have identified sites that have not burned for over 6000 years (Lertzman et al. 2002; Gavin et al. 2003; Hallett et al. 2003). Dendrochronological and palynological studies have also shown that boreal forests have responded rapidly to climatic changes. In response to climatic variability, boreal forests, particularly those in tree-line or high-altitude environments respond with dynamic shifts in reproductive strategies, phenotypic expression, and stand structural features (Payette et al. 1985; Hofgaard et al. 1991; Lavoie and Payette 1992, 1994; Payette and Lavoie 1994; Zackrisson et al. 1995; Kullman 1996). Conclusions as to whether the Main River old-growth forests represent the product of long-term, millennial-scale continuity, or whether they are recent phenomenon can only await further study. However, given the current uneven age distribution, canopy trees > 200–250 years, suppression periods of up to 100 years, and complex structural heterogeneity, it is reasonable to presume that old-growth forests driven by gap dynamics have been continuous for at least 500 to 1000 years.

The geographical extent of old-growth forests in insular Newfoundland is not known. Any conclusions regarding distribution are hindered by the lack of empirical definitions for old-growth of different forest types. A survey of the provincial forest
inventory data for the Great Northern Peninsula (Forest management districts 16, 17, and 18), however, estimated that the old-growth forests identified in the Main River watershed most certainly extend the entire length of the east side of the Great Northern Peninsula from the Main River watershed in the south to Hare Bay in the north (Figure 14-10) (Corner Brook Pulp and Paper Limited 2001).

Figure 14-10. Map of Newfoundland showing the potential old-growth boundary on the Great Northern Peninsula. (Adapted from Corner Brook Pulp and Paper Limited, 2001, Figure 3.8).
An age limit of 150 years and a reverse-J dbh distribution were used as old-growth criteria in this classification. This region essentially corresponds to that region known not to have incurred large-scale insect outbreaks. Included within this region is the Soufflets River watershed whose primary forests are exclusively old-growth (> age class 120 +) (Government of Newfoundland and Labrador 1996).

14.1.8 Forest Equilibrium

The upper Main river forest landscape may be considered as a quasi-equilibrium forest of natural disturbance type 1; “ecosystems with rare stand-initiating events.” (Province of British Columbia 1995). Under current climatic controls and small-scale gap dynamics, the demographic age and size evidence points to the continued, long-term maintenance of stable, balsam fir-dominated old-growth forests. Continuous reverse-J age distributions for both the seedling bank and tree layer, and semi-logarithmic rotated sigmoid diameter distributions, are strong primae facie evidence of a forest landscape under equilibrium or quasi-equilibrium conditions. Equilibrium conditions, of course, depend on general climatic stability. Climate change may necessarily induce shifts in temporal and spatial patterns of fire and insect herbivory. The old-growth forests will then respond accordingly and shift into a new disturbance regime, with consequent changes in stand composition, age and size structure.

14.2 LITTLE GRAND LAKE: INSECT-MEDIATED FOREST STRUCTURE

The Little Grand Lake forest landscape is a complex heterogeneous landscape composed of a fine-scale mosaic of stands of diverse age, structure and developmental
sequence. This landscape heterogeneity is controlled by both recurrent hemlock looper and spruce budworm outbreaks and in situ edaphic conditions. On one level is the insect-mediated natural chronosequence of relatively homogeneous even-aged stands in all stages of stand development from stand initiation to transition old-growth and old-growth (sensu Oliver 1981; Oliver and Larson 1996). On a second level, are changes in endogenous site quality across the study area that either promote or temper the impact of the exogenous insect-mediated disturbance. The influence of site quality is mediated primarily through control on stand species composition, specifically on the relative composition of balsam fir and black spruce. Partial canopy mortality and species-specific mortality are the result of this disturbance–edaphic interaction.

Periodic insect outbreaks over long periods of time (centuries) have crafted a structurally diverse boreal forest landscape (Figure 14-11). The landscape-level mosaic patch structure of the relatively small landscape (106 km²) has provided a unique opportunity to examine the relationship between insect herbivory and stand and forest structure. In most other forest areas of Newfoundland, such an opportunity does not exist because of the confounding effects of forest harvesting.

Four main stand structural types were identified: (1) single-cohort stands, (2) bimodal stands, (3) bistaged stands, and (4) reverse-J stands. Single-cohort and bimodal stands form a well-defined chronosequence that provides insight into balsam fir stand dynamics over a 100 to 120 year period. Bistaged stands include those lower site quality stands characterized by a regenerating stratum (generally pre-self-thinning stage) overtopped by large, old black spruce veterans. Reverse-J stands are generally all-aged stands created by periodic insect-caused partial canopy mortality and subsequent gap or
Figure 14-11. Insect-mediated patch mortality, Little Grand Lake. (A) Small patch mortality that is being regenerated with vigorous white spruce, age class 2 (20–40 years). (B) Note the leave patches within a large patch kill. (C & D) Large patch mortality with well-defined edge separating affected and unaffected stands. (E) Residual white birch, with abundant conifer logs on ground. (F) Entire background slope in age class 3 (40–60 years) following stand replacement. Bleached snags are evident throughout the stand undergoing stem exclusion.
patch regeneration, or they are simply low site, edaphic reverse-J strands dominated by layered black spruce and slow-growing balsam fir. Among the single-cohort–bimodal stands, the four classic stages of stand development were identified: (1) stand initiation, (2) stem exclusion, (3) stand re-initiation, and (4) transition–true old-growth. Each stage will be examined in detail.

14.2.1 Stand initiation


Of note was the variability in stand density and species composition of the young stands. Stand densities differed by an order of magnitude, ranging in value from 3,800 to 38,000 stems ha\(^{-1}\). It is interesting to note that, in his study of production in immature balsam fir stands, Baskerville (1965b) was able to locate stands of variable density (700 to 5,000 stems acre\(^{-1}\); 1,729 to 12,350 stems ha\(^{-1}\)) within an area of constant site. Equally-aged stands of six densities were the product of a 1913–1919 spruce budworm outbreak. MacLean (1988) reported a range of 9,750 to 79,000 stems ha\(^{-1}\) for regeneration released during the spruce budworm outbreak of the late 1970s.
In addition to the expected factors regulating such density (seed production, microsite variability, competition), is it hypothesized that moose browsing help to regulate post-disturbance density (Bergerud and Manuel 1968; Thompson et al. 1992; Thompson and Curran 1993). On the richer sites, it was not uncommon to find areas, locally known as "moose meadows," where much of the advanced balsam fir regeneration was browsed to the benefit of the generally unpalatable white spruce that grew with well-developed open-grown branch systems. On the better sites as well, especially sites with close to 100% stand removal, raspberry grew in profusion and no doubt increased the competitive pressure on the released regeneration (Ghent et al. 1957; Batzer and Popp 1985; MacLean 1988; Osawa 1994).

14.2.2 Stem Exclusion

Self-thinning in *Abies* forests has been traditionally examined in high-altitude *Abies* wave forests located in Japan, the United States and Newfoundland (Oshima et al. 1958; Kuroiwa 1959; Tadaki et al. 1977; Mohler et al. 1978; Kohyama and Fujita 1981; Sprugel and Bormann 1981; Sprugel 1984, 1985; Moloney 1986; Kohyama et al. 1990; Robertson 1993b). The special wave pattern of these true fir forests provides a unique opportunity to examine stand development across a well-defined chronosequence (Figure 14-12).

Self-thinning in a spruce budworm-mediated chronosequence of balsam fir was examined by Vincent (1962). Recent development of stand density management diagrams for balsam fir, spruce–fir and fir–spruce forests relied on a series of regional-level second-growth plots (except for primary stands > 80 years old in Sturtevant et al. 1998) that
showed no sign of insect damage (Sturtevant et al. 1998; Wilson et al. 1999; Solomon and Zhang 2002). A recent study of self-thinning in Quebec balsam fir forests used a series of regional growth plots from second-growth forests protected for the most part from spruce budworm outbreaks (Bégin et al. 2001). This study examines a 120-year period of stand development, including self-thinning dynamics, in a primary forest landscape periodically subject to herbivory from both hemlock looper and the spruce budworm.

My results confirmed that the post-disturbance developing stands followed the classic sequence of self-thinning. Increased inter-tree competition due to crown closure and light extinction produced classic changes in tree plasticity and mortality as defined by the

Table 14-1 compares the self-thinning slope and intercept found in this study with those determined for other *Abies* stands undergoing self-thinning. The slope of -1.282 differs significantly from the assumed self-thinning slope of -1.5, comparing favourably to that determined by Mohler et al. (1978), Sprugel (1984), and Wilson et al. (1999). Early formulations of the self-thinning rule focused on the seeming law-like inviolability and universality of the -3/2 asymptotic self-thinning slope (White and Harper 1970; White 1980). Subsequent research, however, has shown that the self-thinning exponents can be more variable than originally assumed, and that the exponent value may differ from the theoretical value depending on species, site quality, and plant allometric relationships, for example (Zeide 1985, 1987, 1991; Weller 1987a, 1987b, 1989, 1990; 1991).

Other authors, while recognizing that slope values may indeed change, prefer to focus on the upper -3/2 boundary rule as a robust, general way to view the dynamic relationship between plant density and size (Osawa and Sugita 1989; Sackville Hamilton et al. 1995). Recent empirical and theoretical research on allometric scaling and mass properties in plants affirms that the self-thinning slope should be -4/3 and not -3/2 (Lonsdale 1990; Enquist et al. 1998; Franco and Kelly 1998), thus making the study slope of -1.282 of greater theoretical acceptability. A number of other forest tree and chaparral self-thinning studies have also found slope coefficients significantly less than the theoretical -1.5 (Schlesinger and Gill 1978; Verwijst 1989; Osawa and Allen 1993; Kenkel et al. 1997; Guo and Rundel 1998).
Table 14-1. Comparison of balsam fir self-thinning in the Northeast United States, eastern Canada and Japan.

<table>
<thead>
<tr>
<th>Location</th>
<th>Stand history</th>
<th>Species</th>
<th>n</th>
<th>Dependent variable</th>
<th>Slope</th>
<th>Intercept</th>
<th>Regression algorithm</th>
<th>Self-thinning line</th>
<th>Reference</th>
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<td>23</td>
<td>Mean weight</td>
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<td>-</td>
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<td>Dynamic thinning line</td>
<td>Kuroiwa 1959</td>
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<td></td>
<td></td>
<td><em>Abies mariesii</em></td>
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<td></td>
<td></td>
<td><em>Abies balsamea</em></td>
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<tr>
<td>Whiteface Mountain, New York</td>
<td>Wave forest</td>
<td><em>Abies veitchii</em></td>
<td></td>
<td>Mean tree mass</td>
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<td>3.94</td>
<td>OLS</td>
<td>Dynamic thinning line</td>
<td>Mohler et al. 1978</td>
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<td><em>Abies veitchii</em></td>
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<td>Dynamic thinning line</td>
<td>Kohyama and Fujita 1981</td>
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<td></td>
<td></td>
<td><em>Abies mariesii</em></td>
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<td>4.52</td>
<td>RMA</td>
<td>Maximum boundary line</td>
<td>Wilson et al. 1999</td>
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<td><em>Abies balsamea</em></td>
<td></td>
<td>Mean stem volume (ft³)</td>
<td>-1.441</td>
<td>4.114</td>
<td>Robust PCA</td>
<td>Maximum boundary line</td>
<td>Bégin et al. 2001</td>
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<td>Northern Maine</td>
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<td><em>Picea rubra</em></td>
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<td>$n$</td>
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<td>Intercept</td>
<td>Regression Algorithm</td>
<td>Self-thinning line</td>
<td>Reference</td>
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<td>6.479</td>
<td>RMA</td>
<td>Dynamic self-thinning</td>
<td>This study</td>
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</tbody>
</table>

$^a$ OLS = ordinary least squares.
$^b$ PCA = principal component analysis.
$^c$ RMA = reduced major axis.
Regardless of the accepted theoretical allometric model, it is important to realize that slope estimates may differ simply because of sample size, the volume equations and regression algorithms employed, and whether the self-thinning data set actually included stands representing maximum combinations of size and density (Zeide 1991; Sackville Hamilton et al. 1995; Bi et al. 2000). Furthermore, despite the population biology debates regarding the validity of the self-thinning rule, it provides a viable heuristic for understanding the relationship between forest stand density and tree size, and for providing the theoretical foundations to stand density management diagrams, an efficient tool for the operational management of forest stand density (Drew and Flewelling 1979; Smith 1989; Newton and Weetman 1993, 1994; Archibald and Bowling 1995; Farnden 1996; Jack and Long 1996).

14.2.2.1 Self-Thinning, Tree Mortality, and Size Distribution

The good fit of the empirical chronosequence data with the mixed balsam fir–black spruce stand density management diagram (SDMD) for western Newfoundland (Sturtevant et al. 1998) allows some statement to be made about self-thinning stand dynamics in these insect-driven forests. The good fit of the study data with the SDMD provide the first independent test of the general validity of the SDMD for balsam fir forests of western Newfoundland. Sturtevant et al. 1998 proposed their SDMD as a first approximation. Given the effective congruence between my data set and the SDMD, however, one may propose the SDMD as a good reflection of stand dynamics in balsam fir–black spruce stands, and therefore an effective operational tool for control of stand density in forest management.
Empirically-derived stand density management diagrams provide a framework by which to understand the dynamics of self-thinning and interspecific competition in even-aged stands. The yield, density and mortality at various stages of stand development are defined for any particular stand. Self-thinning benchmarks include the crown closure line, the lower limit of the zone of imminent competition mortality (ZICM) and the maximum size density line or upper boundary of the zone of imminent competition mortality. Prior to crown closure, trees are essentially independent of stand density and grow as isolated individuals. Following crown closure, trees begin to compete with each other, with onset of self-pruning and crown class differentiation. Within the ZICM stands undergo active and accelerated self-thinning. The upper limit of the ZICM defines a maximum size-density line at which point developing stands experience a reduction in density and an increase in stem diameter as they track relatively parallel to the maximum size-density line. (Long and Smith 1984; Jack and Long 1996).

The young single-cohort plots (plots 6, 8, 38, 15, 23, 39, 42, 51, and 46) all lie outside the ZICM. As well, plots 8 and 6 lie below the crown closure line. Prior to crown closure, the site is not fully occupied, competition among the trees is limited, and tree growth is essentially independent of stand density.

Stands located within the ZICM tracked parallel to the upper self-thinning boundary line. In these stands, self-thinning began once stands had reached quadratic mean diameters of 4 to 5 cm, 75 percentile heights of 7 to 8 m, and stem densities of approximately 31,000 stems ha\(^{-1}\) (plots 9 and 19). These stand conditions were reached around 60 to 65 years of age (total age). The beginning of self-thinning corresponds to maximum stand volume conditions. Yield curves for balsam fir stands (medium site, crown density 50%–75%) of
the study area have maximum volumes of 140–150 m³ ha⁻¹ developing in stands of stump age > 60 years (Boyd Pittman, *pers. comm.*)

With increase in stand height, the size–density relationships closely followed the -3/2 power self-thinning rule. The trajectory of the chronosequence stands along the upper boundary thinning line, however, slowed as the stands developed. At a particular section of the self-thinning curve, the stands began to fall away from the self-thinning upper boundary line and to follow a line with slope approximating unity. This decease in the size–density slope from a self-thinning line of -1.5 to a non-self-thinning line of -1.0 has been observed in other plant size–density relationships (White and Harper 1970; Peet and Christensen 1980; Hutchings and Budd 1981; White 1981; Westoby 1984; Nakashizuka 1984b; Peet and Christensen 1987; Kohyama 1992). This decrease in size–density slope was also evident for balsam fir thinning relationships given by Sturtevant et al. (1997) and Bégin et al. (2001).

The breaking point seems to occur in stands > 90 years old, having densities of 2,000 to 3,000 stems ha⁻¹ and growing at approximately 15 to 17 m in height. Along this new shallow slope trajectory, stands exhibit less and less self-thinning mortality, with density-independent processes such as butt rots and root rots, windthrow, and particularly in these stands, mortality related to insect herbivory, increasing in importance. Note that the 75 percentile stand height–stand age relationship for both single-cohort and bimodal stands begins to level off at heights approaching 15 to 17 m, corresponding in effect to the self-thinning breakpoint for these stands. During self-thinning and a gradient of -1.5, total stand volume increases despite the decrease in stem density. However, with the change in the self-thinning slope to -1, the total yield becomes constant (White and Harper 1970),
with net biomass production approaching or matching mortality loss. Given the noticeable beginnings of decline in basal area at around 90 years and stand heights of 15 to 17 m, it seems that the stands have entered the stand breakup stage at this point.

14.2.2.2 Self-Thinning, Size Hierarchy and Tree Mortality

Three distinct phases in tree mortality were evident across the chronosequence: (1) post-insect disturbance, (2) active self-thinning and density-dependent tree mortality, and (3) post self-thinning and density-independent mortality. Idealized tree diameter distributions characteristic of even-aged stand development are given in Figure 14-13.

1. Post-insect disturbance (Pre-self-thinning): Prior to self-thinning, mortality among the 11 to 20 year old regeneration was minimal or non-existent. At this stage of stand development, a distinct hierarchy of dominance and suppression had not yet developed. Trees are slowly differentiating in height growth and diameter because of microsite, genetic and stochastic events, a differentiation that will attenuate after crown closure and the onset of competition mortality. Furthermore, the truncated reverse-J shaped diameter distributions (Figure 14-13) may simply be an expression of the exponential growth of saplings growing free of competition (Koyama and Kira 1956). Dead volume was dominated by snag legacies still standing after historic insect outbreaks, and comprised up to 80% of the total live and dead tree basal area.

2. Active self-thinning: Prior to and during the process of self-thinning, stands undergo significant structural change. First, is the production of dead trees that die during the intense, light-driven, asymmetric competition and secondly, is the dramatic shift in the dbh frequency of live trees. Changes in tree size hierarchy and skewness of diameter
Figure 14-13. Idealized representation of post-disturbance stand development in the balsam fir forests of the Little Grand Lake area.
distributions with stand development creates the conditions necessary for self-thinning. The skewness and size hierarchy of tree diameter distributions are in turn fashioned by the changes determined by self-thinning.

Pre-self-thinning distributions are generally truncated reverse-J structures, with the L-shaped distribution characteristic of the youngest age class of saplings (11 to 20 years) (Figure 14-13). Even before the onset of self-thinning, there is some degree of tree size differentiation due to local neighbourhood effects that include microsite effects, differential emergence effects, and genetic differences that establish, right from the beginning, a dominance hierarchy that can influence the future development of each individual (Ross and Harper 1972; Watkinson et al. 1983; Weiner 1984).

As stands move into self-thinning, the skewness of the diameter distribution becomes increasingly positively skewed (Ford 1975; Mohler et al. 1978; Schlesinger and Gill 1978; Westoby 1981; West and Borough 1983; Benjamin and Hardwick 1986; Newton and Smith 1988; Xue and Hagihara 1999). This increase in skewness is caused both by the higher mortality rate of the smaller trees, a measure of the increasing competitive advantages of the taller trees. Canopy differentiation has promoted an increasingly positively skewed diameter distribution, with many smaller trees and few larger trees. With an increase in tree height, the degree of competitive interaction increases until the development of intense interspecific competition during the self-thinning process per se (Long and Smith 1984; Peet and Christensen 1987). Inter-specific competition during self-thinning is generally one-sided, asymmetric (resource pre-emption) competition in which individuals share limited resources disproportionate to their relative size (McMurtrie 1981; Weiner 1985, 1986, 1988, 1990; Hara 1986; West et al. 1989; Newton 1990; Kohyama
In other words, the larger trees out compete the smaller trees, especially for limited light resources. The larger trees depress the relative height growth rates of the smaller trees (Cannell et al. 1984) resulting in the preferential death of the relatively smaller diameter classes. Many studies have confirmed the greater probability of death for the lower proportion of plant size distributions during self-thinning (Lee 1971; Pollard 1971; Ford 1975; Yarranton and Yarranton 1975; Mithen et al. 1984; Gibson and Good 1986; Peet and Christensen 1987; Kikuzawa 1988; Kenkel et al. 1989; Kenkel et al. 1997; Ogawa and Hagihara 2003).

3. Post self-thinning: After the period of intense self-thinning and during the early period of density-independent mortality, diameter distributions are generally symmetric in character (Mohler et al. 1978; Lorimer and Frelich 1998). With stand development and increased density-independent mortality, bimodality develops in response to the release of advance regeneration in the created canopy gaps.

14.2.3 Patterns of Dead Wood Accumulation

In these insect-mediated stands, three main processes promote the accumulation of dead wood: (1) partial or complete stand mortality during insect outbreaks, (2) self-thinning-induced competition mortality, and (3) post-thinning density-independent processes including fungal-mediated tree snap, and windthrow. The combined action of these three processes is often best described by a sigmoidal relationship, a relationship that was clearly evident during post-disturbance stand development of the balsam fir stands. U-shaped patterns of coarse woody debris accumulation have been described for a number of forests (Agee and Huff 1987; Spies and Cline 1988; Spies et al. 1988; Clark et al. 1998;

Post-disturbance snags are abundant (Figure 14-14). With time, snags deteriorate *in situ*, are blown to the ground or simply fall to the ground as roots succumb to decay. Then begins the process of decay and incorporation into the forest floor and upper mineral soil (Figure 14-15).

The onset of competition-induced self-thinning begins the production of snags among the smaller diameter classes. Self-thinning mortality eventually terminates with tree mortality increasingly determined by density-independent processes such as windthrow and senescence. Collected data did not permit an assessment of snag or log longevity. Storaunet and Rolstad (2002) estimated a mean residence time of 22 years (range = 0 to 91 years) for Norway spruce snags, and log residence times in subalpine and boreal *Abies–Picea* forests have been approximated to range from 70 to 200 years (Lambert et al. 1980; Foster and Lang 1982; Hytteborn and Packham 1987; Liu and Hytteborn 1991; Hofgaard 1993a; Siitonen et al. 2000).

Study results compared favorably with those of Sturtevant et al. (1997) who examined coarse woody debris changes across a chronosequence of secondary and primary balsam fir stands in western and central Newfoundland. Residual decay of coarse woody debris ended near 58 years, with the accumulation period lasting between ≈50 and 90 years (bh age + 8yrs). I did not examine coarse woody debris *per se*, but rather the basal area of standing snags, precursors to coarse woody debris. The basal area of snags declined by almost 50% in the first 60 years of stand development followed by accumulation from 60 to
Figure 14-14. Post-insect disturbance snags, Little Grand Lake. (A) Well-developed balsam fir–white spruce sapling bank under snags. (B) Note the mature residual white spruce that often survive insect herbivory. (C) Remains of old snags within stand in the stem exclusion stage of stand development. (D) If not blown over after loss of root stability, snags will eventually deteriorate into stubs.
Figure 14-15. Post-insect disturbance coarse woody debris, Little Grand Lake. (A) What looks to be a white birch with the root mat still recognizable. (B) Conifer coarse woody debris in stage undergoing stem exclusion. 100% moss coverage of coarse woody debris is common in these stands.

100–110 years. Self-thinning mortality was first evident in 60 year-old stands. Older stands showed declines in dead basal area as stands began to break up.

14.2.4 Stand Structural Indices

Stand structural indices (Gini coefficient, Shannon index of diversity, skewness, coefficient of variation, and Weibull shape parameter) successfully characterized the changes in diameter distribution with self-thinning. The decrease in skewness during self-thinning and its leveling out at zero (with slightly negative values for bimodal stands) recorded the change in diameter frequency outlined in Figure 14-13. A skew value of zero implies a normal distribution, to which all diameter distributions tended during the period of late self-thinning.

All other indices successfully recorded the same diameter distribution changes as did skewness. Both Gini coefficient and coefficient of variation decreased with increase in stem density (Weiner and Thomas 1986; Weiner and Whigham 1988). Maximum
differences in tree size hierarchy (> Gini) were expressed in the early reverse-J, lognormal stands compared to the later modal stands. It should be noted that better correlations would have been obtained if the data for the more complex bimodal stands had been excluded from the data set. Bimodal stands had higher Gini coefficients than the late self-thinning stands.

Shannon index increased with development of self-thinning. Maximum values of the Shannon index occur when the proportions are equal over the range of tree diameters. This would occur to a greater degree for modal stands compared to reverse-J or lognormal distributions. Finally, the Weibull shape parameter is less for high density stands because of the reverse-J-lognormal character of stands in the early stages of self-thinning. An increase in the modality of diameter distributions (later self-thinning) would show an increase in the Weibull shape parameter.

14.2.5 Understory Re-initiation

A seedling bank has three main characteristics: (1) regeneration that persists through time under the shade of an overstory canopy, (2) remains suppressed on a decadal level within a restricted range of sizes, (3) and is capable of rapid release in height growth upon removal of the mature canopy (Grime 1979; Marks and Gardescu 1998). Balsam fir has all these characteristics and is able to form persistent seedling banks under mature forest canopies (Greene et al. 1999; Johnson et al. 2003).

The study stands are characterized by high seedling bank densities. Chronosequence stands ranging in age from 80 to 120 years hosted balsam fir seedling banks with mean densities ranging from 55,000 to 482,000 stems ha⁻¹, with all plots except
one having mean balsam fir seedling densities > 124,000 stems ha\(^{-1}\).\(^1\) In all cases, balsam fir accounted for 91% to 100% of all seedlings in any one plot. The very high densities for balsam fir advance growth may not be too unusual for Newfoundland. Densities of balsam fir advance growth have been recorded at high values ranging from 377,000 to 460,000 seedlings ha\(^{-1}\) (Page and Robinson 1969).

Studies in Quebec have recorded maximum mean balsam fir densities of > 90,000 (Bélanger et al. 1991), > 60,000 (Côté and Bélanger 1991), 34,000 (< 1 m in height) (Kneeshaw and Bergeron 1996), 39,000 (Doucet 1988), and 205,000 seedlings ha\(^{-1}\) (Morin and Laprise 1997). In primary (overmature) balsam fir forests in New Brunswick, Baskerville (1965a) recorded balsam fir densities of 90,000 stems ha\(^{-1}\) (all seedlings < 1.3 m). Under old primary balsam fir stands on the Cape Breton Highlands, balsam fir seedling density ranged from 7,400 to 74,000 seedlings ha\(^{-1}\) (Wile 1979). Note that these figures represent simply a slice in time as densities will change in response to both seeding and seedling recruitment, and seedling mortality. The mast seeding ability of balsam fir (Houle 1999) and the high mortality of balsam fir seedlings within the first months and years of germination (Hett and Loucks 1968; Duchesneau and Morin 1999) make comparisons tenuous. Nevertheless, the maximum densities recorded in Quebec and New Brunswick generally fall short of the densities recorded for the western Newfoundland sites.

Why the high densities on the Newfoundland sites? Obviously, the relationship between recruitment and mortality determine seedling survival. Little is known about the amount and periodicity of seed production in these forests. However, given the proliferate

\[\text{The dense pole-stage stands that often develop from these initial densities are often referred to in French-Canada as "bois du Saint Michel," a reference, no doubt, to the dense thickets through which the early traveler ventured only after calling upon Saint Michael, the patron saint of lost travelers, for guidance.}\]
seedling bank and the winter-transient seedbank nature of balsam fir (Houle 1992), seed production must have been quite regular during the preceding years (Morris 1951; Ghent 1958).

In these forests, seed germination and seedling survival are probably facilitated by both the humid climate devoid of periods of moisture stress, and by the almost complete coverage of the forest floor with suitable germination sites (Figure 14-16).

Figure 14-16. Typical forest floor in a primary balsam fir stand, Little Grand Lake. Note the complete coverage by feathermosses and the abundance of coarse woody debris. Balsam fir regeneration is abundant on such forest floor microsites. The fern *Dryopteris spinulosa* (O.F.Mull.) Watt is an indicator of medium to good site quality.

Each chronosequence plot had close to 100% feathermoss coverage (unpublished data).

Feathermoss coverage of abundant decayed coarse woody debris from past insect outbreaks, root swells, the general absence of hardwood litterfall, and mineral soil-laden
tip-up mounds produced by the blowdown of large snags has created a diversity of microsites well suited to seedling germination, particularly of balsam fir (Bélanger et al. 1991; Kneeshaw and Bergeron 1996; McLaren and Janke 1996; Duchesneau and Morin 1999; Raymond et al. 2000; Parent et al. 2003; Simard et al. 2003) and other Abies species (Day 1964; Knapp and Smith 1982; Nakamura 1992; Takahashi 1994; Szewczyk and Szwagrzyk 1996; Takahashi et al. 2000; Nakagawa et al. 2001; Narukawa and Yamamoto 2002; Nakagawa et al. 2003; Narukawa et al. 2003; Narukawa and Yamamoto 2003). Balsam fir seedlings, and Abies seedlings in general, are robust with sufficiently long radicles that permit germination on a variety of diverse microsites and that minimize desiccation, an important factor in early seedling mortality (Place 1955; Zobel and Antos 1991).

Stand re-initiation did not seem to occur before stands reached 60 years of age (8.1 m = 75 percentile height). Assuming an average period of 27 years to reach breast height (includes pre-and post-canopy disturbance), this corresponds to a breast height release age of 33 years for the 60-year-old stand. Average age of seedlings in this stand was 7 years, which corresponded to a stand release age of 27 years at the time of seeding. This matches the observation that balsam fir sexually matures at 20 to 30 years (Frank 1990). In Japanese Abies forests, seed-producing trees were absent in stands younger than 32 years of age (Kohyama 1982).

Seedling density was significantly positively correlated with both total stand age and stand height across the chronosequence. It seems, therefore, that balsam fir seeding was regular over the life of the oldest stands. It was not until stands were about 85 years of age and 12 to 14 m in height that balsam fir seedling densities began to exceed 100,000
stems ha$^{-1}$ and that other tree species, especially white birch and white spruce, began to appear. It was possibly at this stage of stand development that sufficient quantities of moss-covered decayed logs and tip-up mounds (with mineral soil) were available to act as germination sites. Moss-covered, suitably decayed logs and tip-up mounds are known to act as preferential microsites for both *Betula* and *Picea* (Bedell 1948; Rowe 1955; Wagg 1964; Harmon and Franklin 1989; Perala and Alm 1990; Safford et al. 1990; DeLong et al. 1997; Hörmberg et al. 1997; McGee and Birmingham 1997; Carlton and Bazzaz 1998; Ruel and Pineau 2002). The probable increase in subcanopy light levels with stand development may have also contributed to the increase in regeneration diversity.

The development of the seedling bank does not seem to have been detrimentally affected by insect herbivory. This is despite the fact that the preferential feeding of second instar spruce budworm larvae on the flower megasporangiate stroboli of balsam fir and black spruce is well known (Blais 1952; Greenbank 1963; Powell 1973; Schooley 1978, 1980; Crummey and Otvos 1980). Appearing about two weeks before the flushing of vegetative buds (Powell 1970), the flower buds provide excellent food for the second instar larvae. Definitive claims regarding the impact of historic insect herbivory in the study area on seed production and seedling bank development, however, cannot be made given the lack of knowledge on the synchrony of insect feeding and flower production in these stands, and the impact of insecticide spraying within the study area over the past 35 years.

Zelazny and Hayter (1991) suggested that 30,000 seedlings ha$^{-1}$ are required to achieve adequate stocking (>$60\%$) following harvesting operations. Given the densities of the seedling bank for mature stands > 80 years of age (total age), it is clear if these stands are disturbed, either by logging or insect outbreak, there will be more than adequate
seedling numbers to assure the development of the future stand. There exists a generally held belief that mature balsam fir stands present no future regeneration stocking problems after disturbance, especially in the absence of logging damage and moose herbivory. This conclusion was based on early work that showed the excellent regenerative ability of primary balsam fir forests after insect disturbance (assuming no serious defoliation of regeneration by insects) (Vincent 1956, 1962; Baskerville 1975) and clear-cut logging (assuming minimal advance regeneration damage by the logging operation (Hatcher 1960; Hughes 1964). The study sites dominated by mature and old primary stands would fall under this rubric.

This assumption of adequate regeneration, however, is currently being questioned, especially for second-growth balsam fir stands that are logged on rotations of 50 to 60 years (Coté and Bélanger 1991; Dery et al. 2000). Seedling banks can be immature with small seedlings and a poor spatial arrangement of established seedlings. Competition from ferns and herbs can also prevent adequate tree regeneration on richer sites.

14.2.6 Old-Growth in Little Grand Lake?

Does old-growth forest occur in the Little Grand Lake study area? The answer will depend, in part, on the definition of old-growth that is used. If we consider the strict, developmental definition of “true old-growth” offered by Oliver and Larson (1996, p. 270), i.e. “stands composed entirely of trees which have developed in the absence of allogenic processes,” (e.g. insect outbreaks), then the answer is probably “no or not very much.” Given the 17-year insect outbreak periodicity in this region of western Newfoundland (Jardon and Doyon, in review), and the well-known history of hemlock looper (Otvos et al.
1971; Otvos et al. 1979; Hudak 1996) and spruce budworm outbreaks (Otvos and Moody 1978; Hudak and Raske 1981) in the study area, the entire landscape has probably experienced some degree of canopy mortality due to insect herbivory. The frequency of stand-replacing insect outbreaks is such that stand development is effectively truncated at the stand re-initiation stage of stand development. The development of old-growth is effectively prevented by recurrent insect herbivory. Maximum ages of balsam fir did not exceed 200 years.

Despite the high frequency of insect herbivory in the study area, however, the range in severity of stand-level mortality across the landscape may be quite variable. It is well-known that spruce budworm-caused mortality has been found to be greater for balsam fir than for black or white spruce and that the greater the spruce and white birch content in balsam fir stands, the less their vulnerability to spruce budworm (Blais 1957, 1968, 1981; MacLean 1980; Seegrist and Arner 1982; Blum and MacLean 1984; MacLean et al. 1984; Lynch and Witter 1985; Raske and Alvo 1986; MacLean and Ostaff 1989; Ostaff and MacLean 1989; Bergeron et al. 1995; Su et al. 1996; MacLean and MacKinnon 1997). Fifty-five percent of the commercial forests found in the study area are currently pure balsam fir, 13.2% are balsam fir–black spruce mixtures, with 15.1% dominated by balsam fir at 50%–75% of basal area. About 7% of the commercial forests are dominated by pure and mixed black and white spruce. Of course, this says nothing of the 21% of the entire landscape covered by scrub stands, most of which are dominated by black spruce. About 10% of the commercial forests are composed of white birch-dominated stands.

Given this variability in stand species composition, it is reasonable to conclude that the severity of insect-caused mortality may be quite variable throughout the landscape. The
differing degrees of stand vulnerability resulting in partial stand mortality, as well as periodic light or moderate insect outbreaks, would have created a range in the degree of stand-level tree mortality. This may have ranged from catastrophic, complete stand mortality in good site index balsam fir stands growing in protected valleys or on warm slopes, to partial mortality in poor site index, imperfectly- or poorly-drained black spruce–balsam fir forests.

On a small enough scale and over sufficiently long periods of time, partial insect mortality may be considered “autogenic” in character; autogenic in the sense that long-term, small-scale partial or moderate mortality may actually promote the development of true old-growth (or transition old-growth) in these forests. Jardon and Doyon (in review), in their study on the relationship between forest structure and insect disturbance in western Newfoundland, noted that 66% of their study sites experienced only low to moderate mortality from insect outbreaks. This created forests whose stands were dominated by reverse-J (33%) or irregular-shaped diameter distributions (37%). Only 30% of the sampled stands were described as bell-shaped in character. Jardon and Doyon (in review) did not indicate that these percentages accurately represented the actual structural makeup of the landscape. In fact, the forest landscape in which they sampled has a long history of both clearcut harvesting and stand-replacing insect disturbance. Their sampled stands were primary growth with no history of harvesting. Sampling may have actually favoured stands of generally poorer site quality than the norm for the region as all the better stands would have been targeted for logging. No indication was given of site quality, but the stands were older than expected (maximum age for balsam fir and black spruce is 222 and 236 years,
respectively), a possible indication of the poorer site quality. Under these circumstances, irregular and reverse-J diameter distributions would not be unusual.

Stands described as bimodal stands (> 100 years of age) may qualify as “transition old-growth” (Oliver and Larson 1996, Ch. 11). Not affected by catastrophic insect herbivory, for example, the stands are beginning to break up through partial insect herbivory, windthrow and butt and root rots, and show irregular tree diameter distributions. The stands are essentially old, multi-aged, with heterogeneous, multi-layered canopies, and gap dynamics as the dominant form of tree re-initiation. Given time and the absence of stand-replacing insect disturbance, these stands will develop into “true old-growth.”

Some of the old reverse-J stands and all of the irregularly structured bimodal stands are probably the product of this process. As well, a number of the reverse-J stands may be true “edaphic” old-growth stands that have been under gap dynamics for long periods of time, with spruce (and fir) layering the dominant form of reproduction (Figure 14-17).

The high black spruce composition of the reverse-J stands further confirms their relatively low vulnerability to complete stand replacement, especially low- and moderate-level outbreaks, and the subsequent development of transition old-growth or old-growth status.

The notion of “old-growth” may best be viewed within the context of what has been termed “primary, natural heritage value forests” – forests characterized by a continuous heritage of natural disturbance and regeneration (Frelich and Reich 2003). This definition is process-based and does not require the development of often arbitrary old-growth thresholds with respect to tree species, age or size, but instead allows for all stages of stand development and forest succession as stands move in and out of the old-growth stage of
stand development. Given the high frequency of stand-level disturbance in the Little Grand Lake area, such a notion of "primary forest" is more holistic and all-encompassing than an emphasis on any particular stage of stand development or forest succession.

14.2.7 Stand Break-up Dynamics

Figure 14-18 gives the yield curves for both balsam fir and black spruce growing under different site qualities for western Newfoundland and the Main River watershed. For western Newfoundland, maximum merchantable volumes usually occur in stands of
Figure 14-18. Yield curves (net merchantable volume m$^3$ ha$^{-1}$) for balsam fir and black spruce, western Newfoundland and the Main River watershed. All curves are for stand density class 2 (51% to 75% crown closure) and for good, medium and poor site quality stands. Permission to use granted by the Newfoundland and Labrador Forest Service.
approximately 60- to 70-year-old balsam fir and 100- to 110-year-old black spruce. Catastrophic stand breakup, at least in terms of gross merchantable volume, was around 130 years for balsam fir and 160 to 180 years for black spruce.

While my study did not examine the break-up of stands per se, the stand chronosequence examined in the Little Grand Lake area provides some insight into the later stages of stand development. No evidence was found of catastrophic stand break-up (other than insect kill) as depicted in the modeled yield curves. Data on stand break-up in Newfoundland is sketchy and is the least known stage of stand dynamics (Boyd Pittman, Newfoundland and Labrador For. Serv., pers. comm.) (Figure 14-18). Other than catastrophic stand kill by insects, evidence points to a more gradual and prolonged break-up, if indeed that is what actually happens. If old stands are not subject to insect-induced mortality, then stands may eventually shift to transition old-growth into the old-growth stage of stand development with the maintenance of significant crown cover and standing volume.

Surprisingly, in the western Newfoundland curves, there were equal break-up ages for stands of good, medium and poor site quality. It is well known that stand break-up and tree longevity is proportional to site quality, with stands growing on the better sites breaking up earlier than stands growing on the poorer sites (Robichaud and Methven 1993). This propensity to faster break-up is often attributed to the relationship between tree height and stability (Smith et al. 1987). All poor study sites had reverse-J diameter distributions, complex canopy structure, and lower tree height–age ratios compared with stands growing on better sites that had modal diameter distributions, relatively homogeneous canopy structure and higher height–age ratios. These relative stand characteristics would give the
poorer site quality stands greater mechanical stability, therefore promoting greater stand longevity.

If decline in basal area may be used as a proxy measure of the beginnings of stand breakup (volume loss), then results of this study agree well with established understanding of balsam fir stand dynamics in Newfoundland. Gross merchantable volume normally declines at around 70 years of age (breast height) (Figure 14-18) which is close to that documented in the present study that showed declines in basal area at 90 years of age (total age). These periods are equivalent given the roughly 20 years needed for balsam fir to reach breast height in these stands. The onset of stand break-up for forests of northern Newfoundland was determined to be over 100 years (Page et al. 1970). Maximum mean annual increment in western and northern Newfoundland forest stands have been calculated to be not more than 50 to 65 years (Bajzak et al. 1968; Page et al. 1970).

Note that the yield curves for the old-growth forests of the Main River area have been modified to indicate no catastrophic stand break-up, but rather are extended to indicate no change in merchantable stand volume with time. The yield curves given in Figure 14-18 are based on thousands of permanent and temporary sample plots maintained by the Newfoundland and Labrador Forest Service. The inherent error of these curves is unknown, but less confidence is attributed to the break-up dynamics of the old stands compared to that of the young and middle-aged stands.

14.2.8 Landscape Structure and Dynamics

The 106 km² Little Grand Lake study area is a complex patch mosaic of stands of varying ages, structural types and stages of stand development. Four main structural types
were identified: (1) single-cohort, modal (or truncated reverse-J) stands, (2) bimodal stands, (3) bistaged stands, and (4) reverse-J stands. Single-cohort stands were of two structural types; young, truncated, reverse-J types in the stand initiation stage of stand development, and older, modal structural types in the stem exclusion and stand re-initiation stages of stand development. Bimodal stands were characterized by a more complex stand structure caused by increased stand break-up and recruitment and release of regeneration in the developing canopy gaps. Bimodal stands were in either the late stand re-initiation stage or the transition old-growth stage. Bistaged stands occurred on poorer sites and consisted of a regenerating layer overtopped by old, dominant black spruce. All bistaged stands were in the late stand initiation stage–very early stem exclusion stage. Relative to the single-cohort stands, stand development in the bistaged stands was slower, with older trees growing in an earlier stage of stand development. Reverse-J stands generally grew on poor sites with the greatest densities of black spruce. Stands may be either transition old-growth or true old-growth.

Of significance is the level of structural complexity in a landscape that has a long history of insect herbivory. Preliminary examination of dendrochronological data from the study area revealed that, during the 19th and 20th centuries, the study area experienced a series of recurrent insect outbreaks. Using tree-ring data, Jardon and Doyon (in review) have provided the first use of dendrochronology to document historic insect outbreaks in Newfoundland. Their results record a high outbreak disturbance frequency of 17 years. Given the close proximity of their study area to the Little Grand Lake study area, it is assumed that the study stands have been subject, more or less, to the same frequency of insect outbreaks.
This disturbance related complexity is no doubt confounded by the complexity determined by tree species and edaphic variability. As we have seen in the old-growth discussion section, all stands do not have equal probability of being damaged or killed by insect herbivory. At this juncture, however, such confounding effects will be simply noted but will not be fully considered. Of importance here is simply a consideration of the four identified stand structures and their relative importance on the landscape, regardless of provenance.

The relative proportion of the four structural types is not necessarily a reflection of the actual structural composition of the landscape. Sampling was not random, but rather stratified so as to sample a good cross section of the various age classes identified by the forest inventory. An estimate of the landscape-level proportions of the four main structural types can be made, however, by using the interpreted stand age classes as a proxy measure of stand structural type. Table 14-2 presents the estimated frequency of each stand structural type in each interpreted age class.

Table 14-2. Estimation of the percent of stand structure types in the Little Grand Lake study area.

<table>
<thead>
<tr>
<th>Interpreted age class</th>
<th>Interpreted % of commercial forest</th>
<th>Number of plots in each interpreted age class</th>
<th>Frequency of stand structure types in each age class (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Single-cohort</td>
</tr>
<tr>
<td>1</td>
<td>14.6</td>
<td>7</td>
<td>100</td>
</tr>
<tr>
<td>2</td>
<td>3.4</td>
<td>5</td>
<td>40</td>
</tr>
<tr>
<td>3</td>
<td>5.4</td>
<td>6</td>
<td>100</td>
</tr>
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<td>9</td>
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<tr>
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<td>7</td>
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</tr>
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<td>7</td>
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</tr>
<tr>
<td>7</td>
<td>11.6</td>
<td>9</td>
<td>11.1</td>
</tr>
</tbody>
</table>

*a One bimodal plot was interpreted as age class 4. However, given it actual mean stand age of 109 years, it was included in stands of age class 6 for this exercise.
These frequencies were determined by multiplying the percent commercial forest area in each age class by the respective frequency of occurrence for each structural type among the 50 sample stands of known age and structure. This gave an estimate of the proportion of the landscape in each structural type. Two-thirds of the nine interpreted age class 7 stands were determined to be reverse-J and multi-cohort in character. Bimodal stands were generally old as well, and were concentrated in the stands interpreted as age class 6 and 7. Bistaged stands were rare and concentrated in the age classes 2 and 4.

Using the photo-interpreted age structure of the landscape (commercial forests only), the following breakdown of the various structural types is proposed: single-cohort (73%), bimodal (10%), bistaged (4%) and reverse-J (13%); total irregular stands = 14%. Figure 14-19 compares the current study with two other studies that have reported the frequency of stand structural types in an insect-disturbed landscape.

![Figure 14-19](image_url)

Figure 14-19. Comparison of landscape-level frequency of stand structure types in three balsam fir-dominated, insect-mediated landscapes.
Leblanc and Bélanger (2000) used photo-interpretation of 1929 aerial photographs of a 55 km$^2$ primary coniferous forest sector in Forêt Montmorency to show that single-cohort, irregular and reverse-J stands occupied 59%, 39%, and 2% of the forest landscape. Photo-interpretation was aided by the use of early inventories and forest management plans for the area. A dendrochronological study of historic insect outbreaks and stand structure in western Newfoundland proposed a relative frequency of 30%, 37%, and 33% for single-cohort, irregular and reverse-J stands Jardon and Doyon (in review). These results were obtained from the measurement of 27 primary forest stands in the region of western Newfoundland and did not involve the use of landscape-level photo interpretation.

The current study compares favourably well with that of Leblanc and Bélanger (2000). Single-cohort stands dominated landscapes with an appreciable coverage by irregular and reverse-J stands. Irregular and reverse-J stands were equally present in the Little Grand Lake area, with the Quebec study showing much greater coverage by irregular stands compared to reverse-J. The two landscapes are similar in terms of broad species composition with balsam fir and balsam fir-dominated stands making up 88% and 84% of the Quebec and Newfoundland areas, respectively. Caution must be exercised in any comparison because of the differences in data quality, study methodology, insects involved (hemlock looper as well as spruce budworm in Newfoundland), insect outbreak histories experienced by the two landscapes, and of course climatic and landscape physiography. Furthermore, my study only considered commercial forest stands defined as capable of producing $\geq 30$ m$^3$ gross merchantable volume ha$^{-1}$ at rotation age. Comparisons with the study by Jardon and Doyon (in review) are even more tenuous given that the structural
percentages are not based on an assessment of an entire landscape, but rather 27 subjectively chosen plots throughout a 3,000 km² region of western Newfoundland.

All three studies, however, show that insect-mediated landscapes are not composed solely of single-cohort, even-aged stands. A significant percentage of the landscape is made up of irregular and reverse-J stands. The provenance of such stands may be linked to both edaphic factors and to the significance of partial insect herbivory. Despite the relatively high frequency of insect herbivory in these forests, some stands may simply escape tree-killing mortality, with senescence from other mortality factors being of greater significance. Partial mortality may also be common, especially given the outbreak severity, spatial patterns of tree mortality, stand variability and other stochastic factors not related to stand characteristics (Baskerville and MacLean 1979; MacLean 1980; MacLean and Piene 1995).

Of interest is the relatively high percentage of the commercial forest in old age classes. Seventy-seven percent of the forest is ≥ 60 years of age, a figure that decreases to 64% for stands ≥ 80 years of age. This compares favourably with the 63% to 75% in mature (> 50 years) and overmature (> 90 years) stands in the Montmorency Forest study site of Leblanc and Bélanger (2000). Sixty year-old stands (total age) are not mature in the study site, so the figure of 64% may more realistically indicate the amount of old forest across the study area.

Landscape analysis of both contemporary and historic primary forests has shown the degree to which old forests can dominate the landscape under natural disturbance regimes of wind, fire, and insect herbivory (Table 14-3). Regardless of the stand developmental
Table 14-3. Landscape-level age class and stand development distribution for selected primary forests. Percentages based on both empirical analysis of contemporary forest landscapes and reconstruction of historic forest landscapes.

<table>
<thead>
<tr>
<th>Study</th>
<th>Stand development stages</th>
<th>Percent of landscape</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Lorimer (1977)</strong></td>
<td>Recently burned land and large windfalls (0–10 years)</td>
<td>2</td>
</tr>
<tr>
<td>(Mixed conifer-northern hardwood forests,</td>
<td>Birch-aspen forest and young regrowth on windfalls (10–75 years)</td>
<td>14</td>
</tr>
<tr>
<td>northeastern Maine, land survey records of</td>
<td>Immature climax forest (75–150 years)</td>
<td>25</td>
</tr>
<tr>
<td>presettlement forests, disturbance regime =</td>
<td>Mature, uneven-aged climax forest (150-300 years)</td>
<td>32</td>
</tr>
<tr>
<td>fire, wind, spruce budworm herbivory)</td>
<td>All-aged climax forest (300+ years)</td>
<td>27</td>
</tr>
<tr>
<td><strong>Frelich and Lorimer (1991b), Frelich (2002)</strong></td>
<td>Sapling (stand initiation)</td>
<td>1.9</td>
</tr>
<tr>
<td>(Hemlock-hardwood forests, Upper Michigan,</td>
<td>Pole (early stem exclusion)</td>
<td>2.3</td>
</tr>
<tr>
<td>simulation study, disturbance regime =</td>
<td>Mature (late stem exclusion)</td>
<td>5.0</td>
</tr>
<tr>
<td>windstorms)</td>
<td>Multi-aged break-up (demographic transition)</td>
<td>9.5</td>
</tr>
<tr>
<td></td>
<td>Multi-aged pole</td>
<td>8.4</td>
</tr>
<tr>
<td></td>
<td>Multi-aged mature</td>
<td>19.0</td>
</tr>
<tr>
<td></td>
<td>Old multi-aged</td>
<td>50.4</td>
</tr>
<tr>
<td></td>
<td>Steady-state</td>
<td>3.6</td>
</tr>
<tr>
<td><strong>Leblanc and Bélanger (2000)</strong></td>
<td>Young</td>
<td>10–20</td>
</tr>
<tr>
<td>(Balsam fir-white birch forests, Quebec,</td>
<td>Mature and overmature (≥ 50 years)</td>
<td>63–75</td>
</tr>
<tr>
<td>historical reconstruction of primary fir</td>
<td>Overmature (≥ 90 years)</td>
<td>24–60</td>
</tr>
<tr>
<td>forests, disturbance regime = spruce budworm and windthrow)</td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Present study</strong></td>
<td>0–20 years</td>
<td>14.6</td>
</tr>
<tr>
<td>(Primary balsam fir forests, western</td>
<td>21–40 years</td>
<td>3.4</td>
</tr>
<tr>
<td>Newfoundland, disturbance regime = hemlock</td>
<td>41–60 years</td>
<td>5.4</td>
</tr>
<tr>
<td>looper and spruce budworm herbivory)</td>
<td>61–80 years</td>
<td>12.2</td>
</tr>
<tr>
<td></td>
<td>81–100 years</td>
<td>36.3</td>
</tr>
<tr>
<td></td>
<td>101–120 years</td>
<td>16.5</td>
</tr>
<tr>
<td></td>
<td>120 + years</td>
<td>11.6</td>
</tr>
</tbody>
</table>
classification used, or the forest type examined, each landscape was dominated by old forests. It should be noted that, for the Upper Michigan hemlock–hardwood forests as well as for the forest regions of eastern Canada and the northeastern United States, catastrophic fire disturbance is relatively rare (Wein and Moore 1977, 1979; Fahey and Reiners 1981; Whitney 1986; Frelich and Lorimer 1991a; Clark and Royall 1996). Furthermore, rotations of catastrophic windthrow events in the hemlock–hardwood forests of the Lake States region normally exceed 1000 years (Canham and Loucks 1984; Whitney 1986; Frelich and Lorimer 1991a). These disturbance regimes would promote the development of old forest on the landscape, a result clearly seen in Table 14-3. However, even in insect-mediated landscapes that experience recurrent insect outbreaks, old stands (mature and overmature) are abundant.

In a region of relatively high insect frequency, why this relatively high percentage in old forest? Firstly, the actual percentage may be lower because of the confounding effects inherent in the methodology of photo-interpretation. All pure white birch stands and white birch–white pine stands, that make up about 4% of the total commercial forest area, were interpreted as > age class 5. Much of the balsam fir in these stands was killed during the spruce budworm outbreak of the late 1970s. Exclusion of these non-host species would reduce the old forest cover to 60%.

Of probably even greater significance in explaining the high proportion of old forest on the landscape are the three periods of insecticide spraying carried out against the hemlock looper since 1969. In 1969, small northwestern and southeastern sections of the study area were sprayed with two applications of fenitrothion. Much of the eastern section of the study area was sprayed in 1987 (two applications of fenitrothion) and 1995 (two
applications of *Bacillus thuringiensis var kurstaki* (B.t.) (Hubert Crummey, Newfoundland and Labrador Forest Service, *pers. comm.*). These aerial spray programs corresponded to the 1966–1971 and the 1983–1995 hemlock looper outbreaks (Otvos et al. 1971; Hudak 1996). During the late 1970s–early 1980s spruce budworm outbreak, areas of dead, moribund, and very severely damaged stands were mapped in the study area, particularly along the steep slopes facing Grand Lake and Little Grand Lake (Hudak and Raske 1981; Raske et al. 1982). At this time, no spray program was carried out against the spruce budworm in the study area. Therefore, it is reasonable to conclude that, if such protection treatments had not been applied, the study area would currently support a greater percentage of younger forest. It is impossible to tell by how much.

Even-aged patch size varied between 0.5 and 150 ha. This compares well with the 1–100 ha patch size range as reported by the Newfoundland and Labrador Forest Service (cited in Sturtevant et al. 1996) and the fine-scaled mosaic of virgin forests of the Montmorency Forest in Quebec (Leblanc and Bélanger 2000), although larger patch sizes do occur (Thompson et al. 2003). The range in patch sizes would obviously depend on the severity of historic insect outbreaks, the vulnerability (relative species mix and stand age) and natural heterogeneity (peatlands, water bodies, physiography) of the forest landscape.

Almost all the single-cohort stands seem to be the product of historic catastrophic insect outbreaks. Stands are dominated by balsam fir (or white spruce for a couple of the stands in the stand initiation stage) with well-developed modal diameter distributions. Except for steep-sided slopes and well-developed valleys of the study area, where stand replacement occurred on the scale of 100 to 150 ha, the small-scale patch structure of stands of variable ages was evident. A striking characteristic of hemlock looper outbreaks
is their localized nature (Carroll 1956). Commonly observed in the study area were pockets of totally-killed stands directly bordering virtually uninjured mature stands. This is in contrast to the late 1970s prolonged, severe spruce budworm outbreak that killed or severely damaged extensive areas of the province’s forests.

Within the study area, the hemlock looper has probably exerted greater long-term influence on forest-level structure of the Little Grand Lake area than has the spruce budworm. The earliest recorded spruce budworm outbreaks in Newfoundland (1942–1954, 1952–1956, and 1960–1971) were small in size, of short duration and resulted in little or no appreciable tree mortality (Otvos and Moody 1978; Hudak and Raske 1995). These outbreaks were not recorded in the study area. It was not until the beginning of the 1970s that the Island of Newfoundland experienced an unprecedented spruce budworm outbreak that resulted in extensive areas of dead, moribund and very severely damaged forests throughout the entire province, including the Little Grand Lake study area (Otvos and Moody 1978; Hudak and Raske 1981). Part of the extensive regional spruce budworm outbreak across eastern Canada and neighbouring regions of the United States, the outbreak was the first one to cause extensive, severe tree mortality in Newfoundland (Hudak 1991), as well as extensive mortality in young stands (Raske et al. 1986) and the delayed mortality of black spruce stands (Raske and Sutton 1986). The current patch structure of the Little Grand Lake study area is the result of structuring by both the hemlock looper and the spruce budworm. The long-term, fine-scale patch mortality caused by the hemlock looper has been supplemented by the coarser-scale patch mortality from the 1970s spruce budworm outbreak.
14.2.9 **Landscape Forest Equilibrium**

Balsam fir forests of eastern Canada have experienced periodic stand-replacing spruce budworm outbreaks for centuries (Blais 1954, 1961, 1965, 1983; Brown 1970; Kettela 1983; Hardy et al. 1986; Morin and Laprise 1990; Morin et al. 1993; Krause 1997; Morin 1998; Simpson and Coy 1999; Fleming et al. 2000). Many of these outbreaks have been synchronized across Ontario, Quebec, and New Brunswick (Blais 1985; Candau et al. 1998; Williams and Liebhold 2000). Jardon and Doyon *(in review)* have confirmed the occurrence of the major continental outbreaks in Newfoundland. The forests of Newfoundland have also experienced a long history of hemlock looper outbreaks (Carroll 1956; Otvos et al. 1979).

Consideration of the long-term insect herbivory history and the landscape-level age and size structure mosaic confirms the existence of tightly coupled links between the forest and the insect herbivore. The study area forests may be considered to be in a form of quasi-equilibrium on the landscape level. The spruce budworm and hemlock looper disturbance regimes, combined with the characteristic ability of balsam fir to form a persistent seedling bank that is responsive to canopy disturbance, have produced a dynamic, disturbance-based, self-perpetuating forest ecosystem (Baskerville 1975; MacLean 1984, 1988; Holling 1992; Morin 1994).

The landscape may be described as a shifting mosaic steady state (Bormann and Likens 1979, 1981), or a mosaic-cycle (Remmert 1991) in which the forest is composed of patches in all stages of stand development in a more or less constant state. This forest “stability” may be described in terms of “constancy” (staying essentially unchanged),
“resilience” (returning to the reference state after a temporary disturbance), and “persistent” (persistence of an ecological system through time) (Grimm and Wissel 1997).

It is important to view this constancy, resilience, and persistence on the forest level. On the stand level, the forests are extremely unstable. Stands with bell-shaped, modal age distributions are inherently unstable and indicate that the probability of disturbance is not the same over time (Frelich 2002, p. 124–126). This corresponds to the periodic stand-replacing outbreaks. However, on the forest level, forest patterns are more or less constant, persistent, and resilient. In other words, low stability has introduced high resilience (Holling 1973).

While the proportion of the commercial forest occupied by the four age classes 1, 4, 6, and 7 is reasonably equal (range = 11.6%–16.5%), age classes 2 and 3 total only 8.8%, with age class 5 occupying a high of 36.3% (Figure 13-2C). The low percentage of age classes 2 and 3 (20 to 60 years) is probably a feature of high stand mortality experienced during the severe spruce budworm outbreak of the late 1970s, as well as the hemlock looper outbreaks from 1966 to 1971 and from 1983 to 1995. This low percentage of the landscape in age class 2 and 3 forest is also evident in regional forests that have experienced a long history of insect herbivory (Figure 14-20). An obvious difference with the “working forests” is the low relative percentage of young forest. Forest Management Districts 14, 15 and 16 have large percentages of the landbase in young forest, attributable, most likely, to the extensive clear-cut harvesting in all three districts. District 16 has a significant proportion of its forest landbase occupied by old forest > 120 years of age. This district has less insect-related tree mortality than the other two districts and includes the Main River watershed, most of which is covered by old-growth forest. The high percentage
of age class 5 forest could be a product of the three spray operations carried out in 1969, 1987, and 1995. Even without protection, however, the forests might still have been characterized by high percentages of old forest.

Despite the general “equilibrium” of the landscape, it seems that exogenous disturbances may “momentarily” inflict “destabilizing” forces. In this case, such “destabilizing” forces may assume a dual character; relatively high levels of insect-induced mortality extending over several decades (1960s to 1990s), as well as relatively high levels

Figure 14-20. Age class structure for Forest Management Districts 14, 15, and 16 in western Newfoundland.
of anthropogenically-induced protection from mortality over those same decades. The landscape equilibrium is periodically punctuated by pulses of mortality that in turn determine the dynamics of coarse woody debris production, litter, bole and branch fall, seedling bank release, forest floor decomposition, and shifts in biogeochemical cycling (Lovett et al. 2002).
CHAPTER 15
SUSTAINABLE FOREST MANAGEMENT IMPLICATIONS

Research results point to a number of forest management implications. A select list is enumerated.

15.1 NATURAL DISTURBANCE REGIMES AND FOREST MANAGEMENT

The Main River forests may be viewed as NDT (natural disturbance type) 1 forests; “ecosystems with rare stand-initiating events.” In contrast, the Little Grand Lake forests may be classified as NDT 3 forests; “ecosystems with frequent stand-initiating events” (Province of British Columbia 1995). This difference in natural disturbance regime presents opportunities and constraints for operational forest management. These differences may be related to what one could term the “volatility” of the forest landscape. Because of the long history of recurrent insect outbreaks, the Little Grand Lake forests are best described as volatile forests, whereas the Main River forests are just the opposite, being relatively stable or non-volatile, at least certainly over several “rotations.”

Insect-driven landscapes are never effectively “managed” in a traditional sense of the term. Forestry often responds to the rapidly defined, pulsed events that never assume characteristics suitable to planned forest landscape planning, at least in the traditional sense of the term. Forest managers will often find themselves responding to the volatility of the forest landscape, whether it be in terms of salvage operations, protection measures, supply
and market problems, disruption of management plans, etc. Insect outbreaks, governed by essentially unpredictable stochastic events, essentially frustrate forest-level planning and inject a degree of indeterminateness that must be accepted. This general instability is manifested as well in the modal age structure of stands derived from historic insect disturbance. If managed for fibre, such stands must be acknowledged as relatively unstable, and therefore, strict harvesting scenarios must be undertaken if the forest is to be effectively managed.

The current wood shortage on the Island of Newfoundland is due to the general absence of forest in the 40- to 60-year-old age class, a situation that is currently imposing constraints on the annual allowable cut. This age gap is attributed to both past cutting practices as well as to insect outbreaks (Government of Newfoundland and Labrador n.d., p. 83). An extensive pre-commercial thinning program and emphasis on the cutting of the oldest forest have been initiated to carry the forest industry along through the period of wood shortages. This situation is a good example of the need to consider insects as "co-harvesters" in this type of landscape. Despite a well-established forest protection program in Newfoundland (Crummey 1995), periodic extensive forest mortality is characteristic of much of Newfoundland’s forests, particularly in western Newfoundland (Hudak and Raske 1995).

Insect-disturbed landscapes are often different from clearcut landscapes, especially in terms of post-disturbance stand structural diversity, deadwood structure and dynamics, and the frequency of patch sizes across the landscape. The greater structural diversity of insect-killed patches, many of which are more dispersed and smaller (usually from 0.5 to 100 ha patch size in the study area) than traditionally-sized Newfoundland clearcuts, has
significant implications for maintenance of biodiversity in managed forests (Payer and Harrison 2000, 2003; Thompson et al. 2003). Furthermore, the link between post-disturbance coarse woody debris accumulations and protection of released regeneration (Ripple and Larsen 2001; Turner et al. 2003) and the provision of future regeneration microsites in the form of moss-covered, decayed logs is being recognized. This may be extremely important in these forests where advance regeneration density may decease by as much as 75%, three to five years after clearcut logging (Page and Robinson 1969).

Insect-driven landscapes also pose opportunities. Given the co-evolution of the balsam fir forests and insect outbreaks, the forest ecosystem is generally robust and resilient to disturbance, including human-mediated logging disturbance. Therefore, long-term forest harvesting may be carried out, especially if due attention is given to both stand- and landscape-level impacts on biodiversity. Clearcut harvesting may be part of long-term sustainable forest management in these insect-driven forests. This may be so, but only if clear-cutting is tempered with various degrees of variable retention, coarse woody debris management, and maintenance and protection of natural regeneration at the stand level, stand structural diversity at the landscape level, as well as consideration of various habitat supply models.

On the other extreme, the Main River watershed poses different opportunities and challenges. First, the long-term stability of the forest landscape provides the forest manager with much temporal flexibility. The gap disturbance regime poses no immediate threat to significant volume loss. Rather, standing volumes may exist in a quasi-equilibrium condition, with the forest effectively acting as a “reservoir” of large volumes of merchantable timber.
A significant challenge is related to the long-term forest continuity and small-scale disturbance, both of which are well beyond any scale of disturbance traditionally assumed by even-aged forest management (Figure 15-1).

Figure 15-1. Clearcut logging by Corner Brook Pulp and Paper Limited (CBPP) in Main River old-growth forests. (A) Pre-logging, year 2000 and (B) Post-logging, year 2001. In March 2001, CBPP initiated a “no-clearcut” policy for the Main River watershed.

Inexperience in managing such old-growth forests, plus the high biodiversity and conservation and wilderness values associated with these forests, has introduced significant restraints on traditional even-aged management in the Main River watershed.

Partially as a result of this study and a deeper appreciation of the unique and special character of these old-growth forests, Corner Brook Pulp and Paper Limited changed its cutting policy. In March 2001, the pulp and paper company announced a “no-clearcut” policy for the Main River watershed. Alternative harvesting strategies are currently being considered and include various forms of selection and variable retention systems (Corner Brook Pulp and Paper Limited 2001).
These harvest trials and further landscape considerations were assessed by the Main River Advisory Group composed of forestry and environmental scientists jointly appointed by both Corner Brook Pulp and Paper Company and the Sierra Club of Canada. The Advisory Group recently submitted their report consisting of 10 recommendations that focused on the three areas of management actions, information acquisition, and analysis of alternatives (Bélanger et al. 2003). Stand-level harvest recommendations included testing of single-tree or narrow, irregular strip harvesting as well as forms of variable retention, clear-cutting systems.

15.2 FOREST HOMOGENIZATION

Increased attention is being paid to the loss of structural diversity in commercially managed forests and the consequent negative impact on biodiversity and community resilience (Kohm and Franklin 1997; Bunnell and Johnson 1998; Voller and Harrison 1998; Hunter 1999; Lindenmayer and Franklin 2002). Large-scale clearcutting, pre-commercial thinning, reduction of rotation ages, and an “oldest-first” cutting priority are significant factors leading to possible increasing homogenization of the balsam fir landscape of western Newfoundland (Sturtevant et al. 1997; Thompson et al. 2003). The impact of such practices on both forest biodiversity and forest resilience are largely unknown, but increasing evidence is pointing out the possible unsustainable nature of such practices, especially when carried out across forest regions (Siitonen 2001; Kuuluvainen 2002; Lindenmayer and Franklin 2002; Haeussler and Kneeshaw 2003).
15.3 LANDSCAPE-LEVEL FOREST STRUCTURE

A first level of consideration is the forest-level structure. The contiguous old-growth character of the Main River watershed and the fine mosaic heterogeneous patch structure of the Little Grand Lake area underscore the diversity of forests on a landscape basis. Radically different disturbance regimes have created clearly differentiated forest- and stand-level structures. In an ecosystem-based approach to forest management, these differences in forest structure and dynamics call for appropriately devised silvicultural and forest management practices. The application of traditional, large-scale, even-aged management in both areas fails to acknowledge the possible negative consequences for biodiversity associated with loss of forest structures associated with these disturbance regimes. A continual reduction in the amount of old-forest across the landscape is a concern.

15.4 OLD FORESTS

The loss of old forest in western Newfoundland is a concern, not only in terms of a loss of forest structural and process diversity, but because of the significance of older forests as habitat for a host of species including invertebrates, birds and mammals (Thompson et al. 1999; Setterington et al. 2000; Thompson et al. 2003). Of particular concern has been the decline of the endangered endemic subspecies of Newfoundland marten. The decline to less than 300 animals on the island (Forsey et al. 1995) has been attributed to loss of suitable old forest habitat primarily from logging, as well as insect outbreaks (Thompson 1991; Thompson and Curran 1995), and non-target capture in traps.
and snares. It is no surprise that the two study areas, both of which are characterized by extensive old forest, should be the two main areas on the island of Newfoundland that continue to support significant populations of Newfoundland marten. Both stand-level and landscape-level habitat requirements for the Newfoundland marten seem well-provided by both old-growth forests (Sturtevant et al. 1996) and insect-mediated heterogeneous landscapes (Chapin et al. 1997; Payer and Harrison 2000, 2003).

15.5 STAND DENSITY MANAGEMENT DIAGRAMS

In response to the general 40- to 60-year-old age gap in Newfoundland’s forests and a predicted wood deficit of 602,750 m$^3$ year$^{-1}$ (Government of Newfoundland and Labrador n.d.), an ambitious precommercial thinning program has been conducted in young, dense regenerating stands between 10 and 20 years of age. The average annual commitment has been in excess of 5,000 ha during the period 1979 to 1996 (Government of Newfoundland and Labrador n.d.). Regardless of this commitment to pre-commercial thinning, stand density management diagrams have not been employed in planning density reduction during pre-commercial thinning, despite the availability of developed stand density management diagrams for both Newfoundland black spruce (Newton and Weetman 1993, 1994) and mixed balsam fir–black spruce stands (Sturtevant et al. 1998). The stand density management diagram developed by Sturtevant et al. (1988) proved to be very useful in understanding stand dynamics in the Little Grand Lake stand chronosequence. Data confirmed the congruency of the stand density management diagram to stand dynamics of primary, natural stands. For operational pre-commercial thinning, it is clear that stand
density management diagrams would provide a robust, operational tool that would ground stand tending on a firm grasp of self-thinning dynamics.

15.6 STAND RE-ESTABLISHMENT SUCCESS

Newfoundland forestry has traditionally relied on natural regeneration following clearcut harvesting. For the most part this has proven to be very successful, especially given the high densities of healthy seedlings that make up the well-established, persistent seedling bank (Richardson 1974). Except for some Ericaceous-dominated black spruce sites, almost all Newfoundland and Labrador forest types (especially balsam fir types) possess this inherent regenerative capacity after canopy disturbance from cutting or insect outbreaks (Bajzak 1962; Bajzak et al. 1968; Page et al. 1970; Page and van Nostrand 1970; Richardson 1975).

However, because of the current wood shortage, increased pressure is being placed on the forest resource. Shortened rotations, the decrease in operability limits from 35 to 30 m³ ha⁻¹, and the unknown impact of extensive precommercial thinning on regeneration success, may lead to regeneration problems, especially in second- and third-growth stands. Our current understanding of the resilience of balsam fir forests vis-à-vis canopy disturbance has been formulated exclusively in terms of primary, naturally-thinned forests. In second-growth balsam fir stands in Quebec, early indications point to the potential regeneration problems in future stands, especially given the current practice of 55 to 60 year commercial rotations (Déry et al. 2000). In balsam fir stands intensively managed under short rotations, a persistent seedling bank (as opposed to a transitory seedling bank)
may not be able to develop, resulting in stand initiation failure following logging (Johnson et al. 2003).

15.7 PROTECTED AREAS POLICY

Both the Main River watershed and the Little Grand Lake area are high conservation value forests. Both forest areas provide important habitat for the endangered Newfoundland marten and represent extensive areas of primary forest that have not been appreciably altered by human activity. These forests act as significant baseline areas essential for proper understanding of the impact of industrial forestry on the forest landscape and biodiversity habitat supply. Furthermore, the forests of the Main River watershed represent an extensive area of rare or uncommon Abies–Picea old-growth boreal forest ecosystem. The Little Grand Lake study area represents a structurally heterogeneous insect-mediated forest landscape, something that is becoming increasingly rare in the intensively managed forests of western Newfoundland.

The Little Grand Lake study area lies within the 1,496 km² provisional Little Grand Lake reserve system that includes an ecological reserve (742 km²), a wildlife reserve (575 km²) and a public reserve (178 km²). Reserve boundaries have been established, but the reserve system has yet to be formally designated. Within the Main River watershed, a 200 km² protected area has been established along the length of the Main River as a Waterway Provincial Park and Canadian Heritage River. A management plan has been written for the protected area (Government of Newfoundland and Labrador 2001). Operational implementation of the no-clear cut policy promulgated by Corner Brook Pulp and Paper Limited remains to be determined (Bélanger et al. 2003). Given the high conservation
value of these old-growth boreal forests, concerns persist regarding extensive road-construction and harvesting within the watershed.
CHAPTER 16

CONCLUSIONS

This study is a first assessment of the relationship between natural disturbance regimes and stand- and landscape-level structure of primary boreal forests in Newfoundland, Canada. The structure of two primary forest landscapes were compared: (1) the old-growth, fungal-mediated Main River forest landscape composed of a continuous cover of all-aged forest, and (2) the insect-mediated Little Grand Lake forest ecosystem composed of a chronosequence of stand developmental stages. Chronosequence, retrospective spatial and aspatial stand structure and dendrochronological studies, and aerial photo interpretation were employed to study the role of disturbance regime and stand developmental processes on both the stand and forest structure. The study’s main conclusions are as follows:

1. The stand- and landscape-level structure of boreal forests in western Newfoundland is a function of disturbance regime. Main River forests are governed by a Natural Disturbance Type 1 (NDT 1) disturbance regime in which stand-initiating events are rare. Little Grand Lake forests are governed by an NDT 3 disturbance regime in which stand-initiating events are frequent.
2. The Main River forests are primary old-growth boreal forests whose stand and forest structure is determined by small scale (< 100 to 200 m²) gap disturbance mediated by fungal pathogens that cause root and butt rots.

3. The Little Grand Lake forests are primary boreal forests that are not dominated by the old-growth stage of stand development. Rather, the forest and stand structure are determined by large-scale (0.5–100 ha) patch disturbance mediated by recurrent insect herbivory by the hemlock looper and the spruce budworm. This creates a landscape-level mosaic of stands in all stages of stand development.

4. Under current climatic and disturbance regimes, both *Abies–Picea* forests are “constant,” “resilient,” and “persistent.” However, this “stability” is manifested at radically different temporal and spatial scales. Long-term (> 500–1000 years) stand- and landscape-level forest continuity describes the Main River forests. Rotated sigmoidal dbh distributions and reverse-J age distributions exemplify this long-term stability.

5. In the Little Grand Lake area the modal, even-aged and irregular stands are unstable, whereas the landscape may be termed stable. Catastrophic canopy disturbance perpetuates tree species composition and therefore stand vulnerability to future insect-mediated canopy disturbance. Stand instability creates a “pulsed” landscape characterized by significant, periodic changes in standing biomass, and associated resource pools and fluxes.

6. An NDT 3 landscape may include transition and true old-growth stands, whose frequency are a function of stochasticity and edaphic-mediated old-growth stands.
7. This research confirms that long-term, old-growth forest continuity in boreal forests is much more common than previously assumed. Furthermore, even insect-mediated landscapes are more complex than simply a collection of even-aged stands.

8. This research has shown the significant implications of disturbance regimes for stand and forest structure and dynamics. Forest management that recognizes these spatial and temporal patterns can only progress in sustainability. The results of this study should help forest land managers to promote the emulation of natural disturbance as a current paradigm for sustainable forest management in Newfoundland boreal forests.
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