

**Sapling growth and mortality in contrasting light environments for four
predominant tree species across the Canadian boreal forest**

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Presented to the University of Manitoba in partial fulfillment of the requirements for the
degree of Master of Science in the Faculty of Graduate Studies

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**Sapling growth and mortality in contrasting light environments for four
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BY

Lisa A. Matthias

**A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University of
Manitoba in partial fulfillment of the requirement of the degree
Of
MASTER OF SCIENCE**

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TABLE OF CONTENTS

TABLE OF CONTENTS	i
ABSTRACT	v
ACKNOWLEDGEMENTS	vi
LIST OF FIGURES	vii
LIST OF TABLES	x
LIST OF APPENDICES	xii
CHAPTER 1. The function of advance regeneration in boreal forest stand dynamics	1
1.1 Introduction	1
1.2 Succession in the North American boreal forest	2
1.2.1 Defining characteristics of the North American boreal forest	2
1.2.2 Fire disturbance	4
1.2.3 Additional forms of disturbance	5
1.2.4 Succession theory	6
1.2.5 Canopy replacement following gap formation	8
1.3 Growth and mortality of advance regeneration	10
1.3.1 The ecological process of mortality	10
1.3.2 The relationship between sapling growth and mortality	12
1.3.3 Shade tolerance in juvenile trees	12
1.3.4 Factors in addition to shade tolerance and light availability that contribute to variation in sapling growth and mortality	16
1.4 Summary	18
1.5 Justification for study and overall objectives	19
CHAPTER 2. Analytical approaches to characterize growth and mortality of juvenile trees	23
2.1 Introduction	23

2.2 Plant growth analysis: an historical sketch and its application to juvenile trees	24
2.2.1 Introduction	24
2.2.2 The evolution of plant growth analysis	26
2.2.3 Relative growth rate	27
2.2.4 An alternative standardized growth rate for woody plants	29
2.2.5 Applications of growth analysis to saplings	31
2.3 Survival analysis: introductory methodology and applications in plant ecology	33
2.3.1 Background: conventional mortality rates	33
2.3.2 Introduction to survival analysis	34
2.3.3 Descriptions of survival time distribution	35
2.3.4 The Kaplan-Meier estimate of survivorship	37
2.3.5 Estimating percentiles from a survivorship curve	38
2.3.6 Comparing the overall survival of two or more groups	38
2.3.7 Cox's Proportional Hazards model	39
2.3.8 Applications of survival analysis in plant ecology	40
2.4 Summary	42
CHAPTER 3. Data Collection	45
3.1 Study area	45
3.2 Field methods	46
3.2.1 Plot establishment	46
3.2.2 Sapling measurements	47
3.3.3 Site-level measurements	50
CHAPTER 4. Sapling mortality in contrasting light environments for four predominant tree species across the Canadian boreal forest	57
4.1 Introduction	57
4.2 Analytical methods	58
4.2.1 Finite mortality rates	58
4.2.2 Survival analysis	60
4.3 Results	63
4.3.1 Survival tables	63
4.3.2 Finite mortality rates	64
4.3.3 Survival analysis	67

4.4 Discussion	69
4.4.1 Interspecific differences in sapling mortality	70
4.4.2 The season of mortality	71
4.4.3 Differential mortality between high and low light environments, and among regions	72
4.4.4. Light, size, and crown morphology as predictors of survival time	75
4.4.5 Manion's conceptual model of the tree mortality process applied to saplings	76
4.4.6 Summary	77
CHAPTER 5. Sapling growth and crown morphology in contrasting light environments for four predominant tree species across the Canadian boreal forest	95
5.1 Introduction	95
5.2 Analytical methods	97
5.2.1 Mean height over time	97
5.2.2 Derived response variables	98
5.2.3 Distribution of relative growth rates	99
5.2.4 Height distribution at study onset and after several years of exponential growth using empirical growth rates	100
5.2.5 Summary statistics and discrete analysis of growth rates and crown morphology	100
5.2.6 Linear regression	101
5.2.7 Plot-level comparisons of mean RHG and %PPFD	102
5.2.8 Herbivory	102
5.3 Results	103
5.3.1 Mean height over time	103
5.3.2 Distribution of relative growth rates	104
5.3.3 Height distribution at study onset and after several years of exponential growth using empirical growth rates	108
5.3.4 Discrete analysis of growth rates and crown morphology	109
5.3.5 Linear regression	111
5.3.6 Plot-level comparisons of mean RHG and %PPFD	112
5.3.7 Herbivory	113
5.4 Discussion	114
5.4.1 Height fluctuations of saplings in the understory	114
5.4.2 Inter-regional differences in sapling growth and crown morphology	115
5.4.3 The effect of canopy opening on sapling growth and crown morphology	115
5.4.4 Light as a predictor of growth at the individual sapling level	118

5.4.5 Variation among permanent plots	120
5.4.6 Summary	121
5.4.7 Synoptic model of factors affecting sapling growth and mortality	122
CHAPTER 6. Management implications	169
6.1 Introduction: the use of advance regeneration in natural disturbance-based management	169
6.2 Empirical population estimates of growth and mortality for trembling aspen, balsam fir, black spruce, and white spruce, in low and high light environments	171
6.3 Growth and mortality compared in high and low light environments	172
6.4 Individual-level predictors of mortality risk	172
6.5 The need for long-term data	173
6.6 Specific recommendations	174
REFERENCES.....	176
APPENDICES.....	189

ABSTRACT

Mortality, height growth, and crown morphology of established natural regeneration of trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.)), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) BSP) are characterized for locations across the Canadian boreal forest over a 2.5-year period. Long-term monitoring plots of advance regeneration in high and low light environments associated with the absence or presence of canopy cover were established in spring 2000 to ensure a western, central, and eastern representation of each species. Survival, height growth, and crown morphology were assessed each year and a relative measure of light availability was recorded at the apex of each sapling. Mortality rates have been established for each species, and apart from a few exceptions are similar among study locations. Annual mortality is highest for aspen regeneration (37.48%), followed by balsam fir (4.41%), black spruce (2.06%), and white spruce (1.71%). Survival analysis techniques are used to provide unbiased estimates of survival time and individual mortality risk for aspen and fir - the only two species demonstrating appreciable mortality. Median survival times for saplings are generally greater than two years. Live crown ratio has a marked influence on mortality risk - more so than either light availability or size. Mean relative height growth (RHG), L:B ratio (leader shoot:lateral branch), and live crown ratio are significantly higher in the absence of canopy cover than under full canopy closure for some but not all species and study locations. The species traditionally considered most shade tolerant of those examined (balsam fir and white spruce) may differ in their growth response to increased light availability from less shade tolerant aspen and black spruce. The distribution of RHG under shaded conditions tends to be significantly positively skewed, which may have important implications for future forest growth: fast rates of height growth at an early sapling stage in the forest understory may confer advantages to subsequent recruitment into the canopy. The growth and mortality rates presented may improve the reliability of foresters' projections of future stand conditions and can be used to derive and test alternative management strategies.

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LIST OF FIGURES

Figure 1.1. Summary of trends in sapling growth and survivorship in relation to shade tolerance, based on evidence provided in the literature.....	22
Figure 3.1. Locations of permanent monitoring plots for natural regeneration of trembling aspen (TA), balsam fir (BF), white spruce (WS), and black spruce (BS) in boreal forests of Alberta, Manitoba, Ontario, and Québec.....	52
Figure 4.1. Finite annual mortality rates for advance regeneration growing under open canopy conditions (unshaded bars) and closed canopy conditions (shaded bars).	79
Figure 4.2. Finite mortality rates of trembling aspen (A) and balsam fir (B) natural regeneration for summer (S) and winter (W) adjusted to a common time base of one year.	80
Figure 4.3. Kaplan-Meier estimated survival curves for natural regeneration of trembling aspen. Separate functions are shown for each study location, for open (A) and closed (B) canopy conditions.	81
Figure 4.4. Kaplan-Meier estimated survival curves for natural regeneration of trembling aspen. Separate survival functions are shown for open canopy (broken line) and closed canopy (solid line) conditions for EMEND, AB, Lac La Biche, AB, Duck Mountains, MB, Manitoba Shield, MB, and Duparquet, QC.	82
Figure 4.5. Kaplan-Meier estimated survival curves for natural regeneration of balsam fir. Separate functions are shown for each study location, for open (A) and closed (B) canopy plots.	83
Figure 4.6. Kaplan-Meier estimated survival curves for advance regeneration of balsam fir. Separate survival functions are shown for open canopy (broken line) and closed canopy (solid line) conditions for EMEND, AB, Duck Mountains, MB, Duparquet, QC, Forêt Montmorency, QC, and Chicoutimi, QC.	84
Figure 4.7. A modification of Pedersen's (1998) schematic of Manion's (1981) tree mortality model (after Johnson [1989]) applied specifically to saplings.	85
Figure 5.1. Dynamic states of aspen suckers within the size range sampled (approximately 1-2 m at study onset), growing in the shaded understory. An individual stem may shift in either direction between a fully leafed out form (A) and a suppressed form (B, C) in which the main axis appears dead, with either no shoots (B), or one or more basal or side shoots (C).	125

Figure 5.2. Mean height of aspen suckers over time in A.) EMEND, AB, B.) Lac La Biche, AB, C.) Duck Mountains, MB, D.) Manitoba Shield, MB, and E.) Duparquet, QC. Broken lines chronicle aspen height in open canopy (clearcut) conditions, and solid lines show mean aspen height in closed canopy hardwood forests.....	126
Figure 5.3. Mean height of balsam fir saplings over time in A.) EMEND, AB, B.) Lac La Biche, AB, C.) Duck Mountains, MB, D.) Duparquet, QC, E.) Forêt Montmorency, QC, and F.) Chicoutimi, QC. Broken lines chronicle sapling height in open canopy (natural gap) conditions, and solid lines show mean sapling height in closed canopy mixed coniferous forests.....	127
Figure 5.4. Mean height of black spruce saplings over time in A.) Manitoba Shield, MB, B.) Iroquois Falls, ON, and C.) Ashuapmushuan Reserve, QC. Broken lines chronicle sapling height in open canopy (carefully harvested) conditions, and solid lines show mean sapling height in closed canopy black spruce forests.....	128
Figure 5.5. Mean height of white spruce saplings over time in A.) EMEND, AB, B.) Lac La Biche, AB, C.) Duck Mountains, MB, and E.) Duparquet, QC. Broken lines chronicle sapling height in open canopy (post-disturbance) conditions, and solid lines show mean sapling height in closed canopy mixedwood forests.....	129
Figure 5.6 A-E. Frequency histograms of aspen relative growth rate (RHG, cm/year) for open and closed canopy conditions at EMEND, AB (A), Lac La Biche, AB (B), Duck Mountains, MB (C), Manitoba Shield, MB (D), and Duparquet, QC (E).	130
Figure 5.7 A-F. Frequency histograms of balsam fir relative growth rate (RHG, cm/year) for open and closed canopy conditions at EMEND, AB (A), Lac La Biche, AB (B), Duck Mountains, MB (C), Duparquet, QC (D), Forêt Montmorency, QC (E), and Chicoutimi, QC (F).	133
Figure 5.8 A-C. Frequency histograms of black spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at Manitoba Shield, MB (A), Iroquois Falls, ON (B), and Ashuapmushuan Reserve, QC (C).	136
Figure 5.9 A-D. Frequency histograms of white spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at EMEND, AB (A), Lac La Biche, AB (B), Duck Mountains, MB (C), and Duparquet, QC (D).	138
Figure 5.10 A-E. Frequency histograms of trembling aspen height at study onset ($t=0$) and after several years of projected exponential growth for open and closed canopy conditions in EMEND, AB (A), Lac La Biche, AB (B), Duck Mountains, MB (C), Manitoba Shield, MB (D), and Duparquet, QC (E).	140

Figure 5.11 A-F. Frequency histograms of balsam fir height at study onset (t=0) and after several years of projected exponential growth for open and closed canopy conditions in EMEND, AB. (A), Lac La Biche, AB (B), Duck Mountains, MB (C), Duparquet, QC (D), Forêt Montmorency, QC (E), and Chicoutimi, QC (F).	145
Figure 5.12 A-C. Frequency histograms of black spruce height at study onset (t=0) and after 15 years of projected exponential growth for open and closed canopy conditions at Manitoba Shield, MB (A), Iroquois Falls, ON (B), and Ashuapmushuan Reserve, QC (C).	151
Figure 5.13 A-D. Frequency histograms of white spruce height at study onset (t=0) and after several years of projected exponential growth for open and closed canopy conditions in EMEND, AB, (A), Lac La Biche, AB (B), Duck Mountains, MB (C), and Duparquet, QC (D).	154
Figure 5.14. Scatterplot of mean RHG by mean %PPFD for all permanent plots of trembling aspen. Individual points represent permanent plots for each canopy (light) treatment and region combination. Open circles represent high light, open canopy plots and shaded circles represent low light, closed canopy plots.	158
Figure 5.15 Scatterplot of mean RHG by mean %PPFD for all permanent plots of balsam fir. Individual points represent permanent plots for each canopy (light) treatment and region combination. Open circles represent high light, open canopy plots and shaded circles represent low light, closed canopy plots.	159
Figure 5.16. Scatterplot of mean RHG by mean %PPFD for all permanent plots of black spruce. Individual points represent permanent plots for each canopy (light) treatment and region combination. Open circles represent high light, open canopy plots and shaded circles represent low light, closed canopy plots.	160
Figure 5.17. Scatterplot of mean RHG by mean %PPFD for all permanent plots of white spruce. Individual points represent permanent plots for each canopy (light) treatment and region combination. Open circles represent high light, open canopy plots and shaded circles represent low light, closed canopy plots.	161
Figure 5.18. Summary model of the factors affecting sapling height growth, crown morphology and survival based on results from this study, literature pertaining to boreal or North American species, and field observations.	162

LIST OF TABLES

Table 2.1. Formulations of height, radius, and biomass growth rates used in the recent literature for examining sapling growth.....	44
Table 3.1. Environment Canada climate normals (1971-2000) and more recent summary climate information from meteorological stations nearest to each of the study locations.....	53
Table 3.2. Number of saplings of each species that were monitored in each study location, broken down by canopy treatment and permanent plot within each canopy treatment.....	54
Table 3.3. Mean %PPFD at sapling apices for each species/study location/canopy combination.....	56
Table 4.1. Number of trembling aspen saplings alive at each spring and fall census, beginning spring 2000.....	86
Table 4.2. Number of balsam fir saplings alive at each spring and fall census, beginning in spring 2000.....	87
Table 4.3. Number of black spruce saplings alive at each spring and fall census, beginning in spring 2000.....	89
Table 4.4. Number of white spruce saplings alive at each spring and fall census, beginning in spring 2000.....	90
Table 4.5. Finite mortality rates for each species, study location, and canopy regime. Mortality rates are the proportion of saplings that die per year.....	91
Table 4.6. Cox PH regression models for trembling aspen regeneration growing under either open (post-harvest) or closed canopy conditions, for each study location.....	93
Table 4.7. Cox PH regression models for balsam fir advance regeneration growing under either open (natural gap) or closed canopy conditions, for each study location.....	94
Table 5.1. Summary statistics for %PPFD, RHG, RDG, initial live crown ratio, initial L:B ratio, initial height and initial basal diameter of trembling aspen for each canopy regime and region.....	163
Table 5.2. Summary statistics for %PPFD, RHG, initial live crown ratio, initial L:B ratio, initial height and initial basal diameter of balsam fir for each canopy regime and region.....	164

Table 5.3. Summary statistics for %PPFD, RHG, initial live crown ratio, initial L:B ratio, initial height and initial basal diameter of black spruce for each canopy regime and region.....	165
Table 5.4. Summary statistics for %PPFD, RHG, initial live crown ratio, initial L:B ratio, initial height and initial basal diameter of white spruce for each canopy regime and region.....	166
Table 5.5. Coefficients of determination and significance levels for simple linear regressions of RHG, RDG, live crown ratio, and L:B ratio against %PPFD for natural regeneration of white spruce, black spruce, balsam fir, and trembling aspen.....	167
Table 5.6. Percentage of live saplings of trembling aspen and balsam fir browsed each year. Values are means across the 2.5 years comprising the study period.....	168

LIST OF APPENDICES

Appendix 1. Selected photographs of long-term monitoring plots of natural advance regeneration of trembling aspen, balsam fir, white spruce, and black spruce in open canopy and closed canopy conditions.	189
Appendix 2. Site descriptions including canopy and soil characteristics, for each permanent plot and study location.	195
Appendix 3. Sample size (n) and standard deviation (SD) for mean relative height growth (RHG) and %PPFD for each permanent plot, for all four species.	201

CHAPTER 1

THE FUNCTION OF ADVANCE REGENERATION IN BOREAL FOREST STAND DYNAMICS

1.1 Introduction

Established sapling banks in mature forests are a critical source for forest renewal following natural disturbance events such as natural decline, windfall, or insect outbreaks, which cause canopy break-up but leave the understory intact (Morin and Laprise 1997, Kneeshaw et al. 1998). This advance regeneration is characteristic of boreal forests of North America where shade tolerant coniferous species such as balsam fir (*Abies balsamea* (L.)) and white spruce (*Picea glauca* (Moench) Voss) are able to persist and grow slowly for long periods of time in the shaded understory (Morin and Laprise 1997). Advance regeneration can be defined as the sexual and vegetative tree regeneration present in a mature forest that is potentially able to replace the mature canopy following disturbance (Greene et al. 1999). The ability of advance regeneration of shade tolerant species to respond to sudden release following canopy breakup may confer an advantage over shade intolerant species (Wright et al. 2000). Recent simulations of forest dynamics have demonstrated that interspecific differences in growth and mortality resulting from variation in species-specific shade tolerance can have profound effects on forest structure and composition (Kobe et al. 1995, Kobe 1997, Kobe and Coates 1997).

North American fire cycles have been getting progressively longer throughout the boreal forest over the past century as a result of increasing temperatures and changes in land use (Bergeron and Archambault 1993, Flannigan et al. 1998, Weir and Johnson 1998, Weir et al. 2000, Bergeron et al. 2001). During the Little Ice Age climate may have been under the influence of an atmospheric circulation that increased the southerly flow of cold and dry arctic air masses. With the end of the Little Ice Age and the migration of the polar front towards higher latitudes, the southern boreal forest may have experienced a greater penetration of warm and humid air masses, and decreased frequency of drought (Bergeron and Archambault 1993). Some regions of the boreal forest may experience stand-initiating events less frequently now than in the past. Individual or group tree mortality is the dominant disturbance in infrequently burned boreal forests, and gap

dynamics govern canopy structure and composition (Kenkel et al. 1997b, Kneeshaw and Bergeron 1998, Cumming et al. 2000, McCarthy 2001).

The purpose of this review is to summarize the literature describing the ecology of advance regeneration and its role in gap dynamics with an emphasis on the boreal forest, as an overall introduction to this study. A general description of the North American boreal forest, a brief overview of fire and additional forms of recurring disturbance, and a short introduction to succession theory are provided to put into context this discussion of advance regeneration. Drawing from the recent body of ecological literature, the focus is to review the function of advance regeneration in gap dynamics, to summarize observed vegetation patterns following canopy gap formation, and to discuss the importance of differential growth and mortality of advance regeneration - resulting largely from interspecific differences in shade tolerance - in determining forest structure and composition in the absence of frequently recurring fire.

1.2 Succession in the North American boreal forest

1.2.1 Defining characteristics of the North American boreal forest

The North American boreal forest has a transcontinental distribution, spanning more than 10° latitude, from the east coast to the west coast (Payette 1992). The northern limit of the boreal forest is the tree line in the arctic, at the July 13°C isotherm, and at approximately the southern extent of the arctic front during the summer season (Oechel and Lawrence 1985). The southern limit of the boreal forest is less well defined, but it usually occurs on the July 18°C isotherm, which is the average location of the arctic front during the winter (Oechel and Lawrence 1985). In Alaska and western Canada the boreal forest developed during the early Holocene after glaciers retreated about 12 500 years before present (Oechel and Lawrence 1985, Payette 1992), while in eastern North America late deglaciation resulted in boreal forest that is much younger at 4000-8000 years old (Payette 1992). Climatic factors that are unique to the high latitudes at which boreal forests are found include a short growing season, wide seasonal temperature fluctuation, low solar elevation angles, cold soil temperature, permafrost, poorly drained

soils, a thick forest floor, low nutrient availability, and recurring forest fires (Oechel and Lawrence 1985, Zasada et al. 1992). The broadly-defined boreal forest is usually divided into three zones or community types, which correspond with major moisture and thermal gradients decreasing from south to north. Closed-crown forests are the dominant community type in the southern part of the boreal range with boreal-mixed forest ecotone at the very southern edge; a lichen woodland/open-crown forest occurs in the central portion of the boreal forest; and forest-tundra ecotone occurs in the northernmost reaches of the boreal forest range (Rowe and Scotter 1973, Oechel and Lawrence 1985, Payette 1992).

The distribution of boreal tree species across the continent is largely determined by local climate and soil conditions (Zasada et al. 1992). Relatively few species exist or dominate across the entire range of the mixedwood boreal. These include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), paper birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), black spruce (*Picea Mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), tamarack (*Larix laricina* (Du Roi) K. Koch) and balsam fir (*Abies balsamea* L.) (Greene et al. 1999). Other dominant tree species with more limited distributions include lodgepole pine (*Pinus contorta* Dougl. ex Loud. Var. *latifolia* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), which have western distributions from the Yukon through interior British Columbia and western Alberta, and eastern white cedar (*Thuja occidentalis* L.), red pine (*Pinus resinosa* Ait.) and eastern white pine (*Pinus strobus* L.) which occur in the southern mixedwood boreal forests of eastern Canada (Rowe and Scotter 1973). Several other hardwood and softwood species are important components in different regions of the boreal forest. There exists a decreasing moisture gradient across the boreal forest from eastern to western Canada, which influences both arboreal species composition, and fire frequency (Van Wagner 1983). Variation in abundance, distribution, and relative composition of tree species at smaller scales within the continental landscape is affected by many different factors, including disturbance regime and species-specific reproductive characteristics.

1.2.2 Fire disturbance

Large-scale wildfire is well established as a principal driving force of boreal forest vegetation dynamics. Fires in the boreal forest are primarily lightning-caused, high intensity crown fires that result in extensive mortality of canopy and understory plants and remove large amounts of the forest floor organic matter (Johnson 1992). Such fires recur every 50-500 years (Gauthier et al. 2000). The mean fire rotation period or fire-free interval of the boreal forest south of the forest-tundra is typically less than 150 years (Johnson 1992, Payette 1992). The frequent occurrence of fire in the boreal forest results from the interaction of the large conifer component with airstream and weather patterns that create appropriate spring and summer temperature and precipitation patterns for fuel drying, and lightning for ignition (Johnson 1992). Conifers are ideal fuel because of characteristics such as their many small needles and branches, long canopy lengths, and low foliage moisture (Johnson 1992). At the landscape level these fire disturbances result in patches of forest of differing age, areal extent, and floristic composition (Payette 1992, Turner and Romme 1994).

Since the end of the Little Ice Age, approximately 150 years ago, fire cycles in the North American boreal forest have increased in length as a result of ensuing climate changes and changes in land use (Bergeron and Archambault 1993, Flannigan et al. 1998, Weir and Johnson 1998, Weir et al. 2000, Bergeron et al. 2001). One explanation for this possible decrease in fire frequency with increasing temperature is that during the Little Ice Age climate may have been under the influence of atmospheric circulation that brought an increased frequency of cold and dry arctic air masses further south. With the end of the Little Ice Age and the migration of the polar front towards higher latitudes, the southern boreal forest may have experienced a greater penetration of warm and humid air masses, and decreased frequency of drought (Bergeron and Archambault 1993). As increasing fire-free intervals and resulting old growth forests become more common, individual or group tree mortality resulting from other forms of disturbance will dominate and gap dynamics rather than catastrophic fire disturbance will determine the structure of the forest canopy (Kenkel et al. 1997b, Kneeshaw and Bergeron 1998, Cumming et al. 2000, McCarthy 2001).

1.2.3 Additional forms of disturbance

Gap disturbance was defined by Kuuluvainen (1994) as a change in forest stand structure following the death of single trees or small groups of trees. More generally, a disturbance is "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett 1985). McCarthy (2001) characterized gap dynamics as small- or micro-scale disturbance of the forest canopy in which the gaps formed by single or small group mortality create growing space that is subsequently occupied by released advance regeneration, or seedling recruitment from seedbanks, budbanks, or newly dispersed propagules. In the absence of frequent fires, gap dynamics may structure the canopy composition (Kneeshaw and Bergeron 1998).

Canopy trees may die standing, snap off, or uproot (McCarthy 2001). Canopy gap formation in hardwood forests is often a sudden event, such as windthrow. Gaps in coniferous stands are often created slowly over a number of years, for example, by spruce budworm outbreaks (*Choristoneura fumiferana*), which defoliate trees leaving standing boles (Kneeshaw and Bergeron 1998), or by root rot infections that kill mature trees slowly, eventually resulting in windfall gaps (Whitney 1989, 1995). Gap formation in conifer-dominated forests is usually the end result of several interacting factors (Kuuluvainen 1994). The relative importance of factors contributing to gap formation varies with tree age, species, stand structure, time of year, and geographic and topographic location (Kuuluvainen 1994).

Prominent causes of gap-formation in North American boreal forests include pathogen damage leading to windthrow and stem breakage (Whitney 1989, 1995), snow loading and ice damage leading to top and stem breakage (Gill 1974), and spruce budworm-caused mortality in eastern boreal forests (Morin et al. 1993, Morin 1994, Morin and Laprise 1997, Kneeshaw and Bergeron 1998). Spruce budworm outbreaks are a dominant form of disturbance in eastern boreal forests dominated by balsam fir (Bergeron and Leduc 1998). These outbreaks cause large-scale gaps in the canopy without destroying the lower advance regeneration layer, thereby influencing the canopy structure of older boreal forests (Kneeshaw and Bergeron 1998). Host size and

abundance, and the relative proportion of coniferous to hardwood (non-host) trees, all affect spruce budworm-caused mortality (Bergeron et al. 1995). Outbreaks of other insect pests such as the larch sawfly (*Pristiphora erichsonii*) and hemlock looper (*Lambdina fiscellaria*) in coniferous boreal forests, and the tent caterpillar (*Malacosoma disstria*) in deciduous boreal forests, are other common forms of disturbance (Bergeron et al. 1998). Mammal herbivory (Bryant and Chapin 1986, McInnes et al. 1992) and destruction by fungal pathogens (Whitney 1989) may also influence stand structure.

1.2.4 Succession theory

Following large-scale natural disturbance, forest stands gradually re-establish beginning with re-colonization of pioneer species. Subsequently, numerous factors interact to influence forest composition and structure over time. The concept of plant succession was first formed in the late nineteenth century by Cowles, and was further developed by F. E. Clements in 1916 (Shaffi and Yarranton 1973, Johnson 1979). Clements' concepts constitute what is now known as "classical succession", which dominated successional theory for over 40 years in the first half of the 20th century (Cook 1996). Clements suggested that vegetation changes that occur over time are unidirectional and predictable, usually leading to a fixed or stable regional or climatic "climax" community (McCook 1994, Cook 1996). This successional theory was based on the mechanisms of competition, and "reaction" - in which plants influence and modify their environment so as to favour invasion by new, later-successional species. In this model vegetation communities exhibit "relay floristics" in which pre-climax communities make way for subsequent waves of species, implying obligate facilitation (Noble and Slatyer 1980, McCook 1994, Cook 1996).

Succession in the classical sense of the term represents "a development towards an equilibrium between organisms and the environment, an equilibrium that is reached at the climax" (Shaffi and Yarranton 1973). More recently, succession has been defined as "changes in species composition and abundance during or following disturbance of a site", "the change in natural systems and the understanding of the causes and direction of such change", and "the outcome of loss and retention of species" at a particular location

(McCook 1994). Arboreal succession in particular can be regarded as the “replacement of canopy trees by the understory of the same or different species” (Johnson 1992). The term succession has also been used by several authors to describe characteristics of an ecosystem other than vegetation composition, such as species diversity, productivity and biomass, that also change through time (Cattelino et al. 1979).

In 1926 H. A. Gleason, a contemporary of Clements, proposed an alternative mechanism for succession to Clements' facilitation model. Gleason suggested that succession is an individual-based rather than community-controlled process, determined by complex initial species assemblages and stochasticity (Abrams et al. 1985, McCook 1994, Cook 1996). However, both Gleason and Clements regarded disturbance as uncommon and not an integral component of the successional process (Cook 1996). This notion conflicts with the frequent and variable disturbance regimes experienced by the boreal forests of North America. Egler's pivotal succession theory proposed in 1954, which is incorporated into modern successional theory, focused on the importance of initial floristic composition after a disturbance (Wilson et al. 1992). It was suggested that the propagules of the entire successional sequence at a particular site are present soon after disturbance, and that it is simply the unfolding of these species over time that results in compositional changes in the canopy (McCook 1994, Cook 1996, Wilson et al. 1992). Egler also suggested that there may exist variation in the relative abundance of species present immediately after disturbance as a result of chance events such as the availability of propagules, and that the resulting stochastic initial floristic composition determines what the successional trajectory of a post-disturbance site will be (Wilson et al. 1992). The concept of initial floristic composition contrasts sharply with Clements' notion of relay floristics (Abrams et al. 1985).

In subsequent years, many important ideas contributed to modern successional theory, such as Noble and Slatyer's (1980) vital attributes model. A vital attribute was described as "an attribute of a species which is vital in determining its role in vegetation replacement sequences" (Nobel and Slatyer 1980). The authors summarized what they considered to be the most important groups of vital attributes of species. These included the method of arrival or persistence of species at a site during and after a disturbance, the ability to establish and grow to maturity in the developing community, and the time taken

for a species to reach critical life stages. Frelich and Reich (1995) summarized five directional models of succession that have emerged from the literature. These include a "cyclic" succession model, in which fire resets the cycle; "convergent" succession, which is the classic Clementsian model of succession where vegetation in two or more states both converge to the same state; "divergent" succession in which one community diverges into two or more states over time as a result of the magnification of minor initial differences; "parallel" succession - which the authors note to be common in the boreal forest - where communities in different states both undergo disturbance and return to their original states; and "individualistic" succession or 'multiple pathways', where in a given area, at different times, different successional pathways may occur as a result of the interaction of stochastic variables (such as the timing of seed years of the dominant species, drought, and disturbance regimes).

1.2.5 Canopy replacement following gap formation

Vegetation patterns that are controlled to a large degree by fire regime are further influenced by disturbances that occur on a much smaller scale; forests that burn only infrequently are dominated by gap dynamics. Vegetation dynamics within canopy gaps may exert a strong influence on stand canopy composition, particularly in older forests, which are prone to long fire cycles (Kneeshaw and Bergeron 1998). Canopy gaps may promote the coexistence of species by fostering the growth of young hardwood trees in old conifer-dominated stands, or alternatively gaps may favour replacement of an individual of a species by another individual of the same species (Lertzman 1995).

In the western boreal forest, Cumming et al. (2000) found that the occurrence of gaps increased with stand age. Gaps were found to begin forming in trembling aspen stands 40 years after stand initiation, as a result of synchronous mortality of small aspen clones. It was suggested that the white spruce advance regeneration in the understory may procure some height growth in these gaps, but don't replace the aspen canopy. Therefore, gap formation favoured the replacement of dead aspen by other aspen trees. Similarly, Morin (1994) found that balsam fir stands are perpetuated through the positive response of advance regeneration following spruce budworm outbreaks. In contrast, Kneeshaw and

Bergeron (1998) studied gap dynamics in the southeastern boreal forests of Québec and found that gap formation in young stands promoted gradual replacement of hardwoods with later successional conifer species. Small gaps in young aspen stands led to species replacement by more shade tolerant conifers, which maintain established sapling banks of advance regeneration in the understory. Conversely, it was found that gap formation in older coniferous stands promoted the maintenance of a hardwood component in the canopy. Evidence suggests that small gap formations may promote diversity in the canopy; larger-scale gap formation may perpetuate the dominant canopy species, in particular for young hardwood stands, but also for balsam fir forests susceptible to spruce budworm outbreak.

Spruce budworm dynamics

Kneeshaw and Bergeron (1998) found that comparably large spruce budworm gaps in old growth forests resulted in the maintenance of shade intolerant species in the canopy (also shown by Bergeron and Dansereau [1993]), and an increase in white cedar. This contrasts with the cyclical model of continued balsam fir maintenance suggested by previous studies (Zoladeski and Maycock 1990, Morin et al. 1993, Morin 1994, Frelich and Reich 1995, Morin and Laprise 1997). There are several potential explanations for these apparently conflicting observations of canopy dynamics following spruce budworm outbreak. Firstly, a mixed deciduous stage may only last until the advance regeneration of conifers replace the dead conifer component of the canopy (Bergeron and Dansereau 1993). Therefore, spruce budworm outbreaks may mediate species coexistence of hardwoods and conifers in old growth stands immediately after the outbreak, but also form a self-regulating, interdependent system with balsam fir. Secondly, the frequency and size of outbreaks may exert a strong influence on the relative recruitment of hardwoods and advance regeneration following outbreak. Outbreak size is partially influenced by the relative proportion of conifers to non-host hardwood species in the canopy (Bergeron et al. 1995). Thus, the relative abundance of conifers and hardwoods may also affect the canopy composition following spruce budworm outbreak. For instance, Batzer and Popp (1985) found that conifer stands with a moderate mix of non-host species in the overstory prior to spruce budworm outbreak had the most abundant

balsam fir regeneration. This occurred as a result of the deciduous component of the canopy limiting the severity of the outbreak, thereby allowing mature balsam fir trees to survive and produce seed. Finally, another potential explanation for differences observed in post-outbreak dynamics is longitudinal differences in outbreak behaviour. In central boreal forests that are prone to spruce budworm defoliation, outbreaks last longer and proceed more slowly than in the east (Zoladeski and Maycock 1990). This may influence the relative abundance of shade intolerant species and advance regeneration competing for canopy space following gap formation. In summary, there exists the possibility of spruce budworm outbreaks acting both as a cycling mechanism for balsam fir and as a mechanism which mediates the coexistence of shade intolerant early successional hardwoods with later successional coniferous species.

1.3 Growth and mortality of advance regeneration

1.3.1 The ecological process of mortality

Tree mortality is a common and complex ecological process critical to both population and community dynamics in forest ecosystems (Franklin et al. 1987). Death of mature canopy trees provides many resources for other trees and organisms in the ecosystem, including increased light availability (Franklin et al. 1987). Recent literature suggests that mortality of juvenile trees in the understory is also a critical process affecting forest dynamics (Lorimer 1981, Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Kobe and Coates 1997).

Factors affecting tree mortality can be categorized as abiotic or biotic, extrinsic or intrinsic, and autogenic or allogenic; however, these classifications ignore the complex interactions among different agents of mortality (Franklin et al. 1987). Important abiotic factors that may influence tree mortality, for juveniles in particular, include natural environmental stresses such as flooding, drought, severe temperature, ice, and excess sunlight, catastrophic events such as fire and lightning, and chemical pollution, wind and climate change (Franklin et al. 1987, Waring 1987). Important biotic factors affecting tree mortality include competition, herbivory, mechanical damage, disease and

senescence (Franklin et al. 1987, Waring 1987). In recent literature, "catastrophic" or "growth-independent" mortality resulting from agents such as fire, windthrow, and/or severe epidemics is usually distinguished from "growth-dependent" mortality resulting from senescence, competition, and climate effects (eg. Kobe and Coates 1997, Bigler and Bugmann 2003).

Franklin et al. (1987) proposed that Manion's (1981) model of tree disease and resulting decline be extended as a general model for tree mortality: a downward "mortality spiral". In this conceptual model the many cumulative and sequential events that contribute to decline of a tree are likened to a downward spiral towards death, where different stress factors and damaging events facilitate the occurrence of subsequent events, and the chance of recovery becomes more limited with each event. An example of tree mortality resulting from a sequence of events given by Franklin et al. (1987) is the tendency for windthrow of trees containing significant pathogen damage such as butt rot (*Polyporus schweinitzii*). Pedersen (1998) evaluated this mortality model by examining the radial growth history of dead oak trees (*Quercus* spp.). Specifically, the author tested the idea that tree death is attributable to long-term stresses that predispose trees to injury by short-duration inciting stresses. In 76% of the 63 dead overstory trees studied mortality was indeed the long-term result of a combination of environmental stresses resulting in reduced growth prior to sudden, permanent declines in growth, supporting a sequential model of tree mortality. Although saplings have not endured "predisposing" stresses (long-term factors such as competition that increase susceptibility to subsequent stresses or events) for periods as long as have mature trees, they are generally more sensitive to environmental stresses (Franklin et al. 1987). Predisposing factors such as resource competition and climate, and short-term "inciting" stresses that impact sapling function and vigour such as disease, herbivory, or frost damage, may interact and contribute to a downward spiral for advance regeneration, in a similar manner to that demonstrated for mature trees (Pedersen 1998).

1.3.2 The relationship between sapling growth and mortality

In recent years forest ecologists have begun to examine the relationship between tree growth and mortality (Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Kobe and Coates 1997, Walters and Reich 2000, Wyckoff and Clark 2000, Lin et al. 2001, Bigler and Bugmann 2003). An inverse relationship between growth and mortality is generally recognized (low growth is correlated with mortality), and has been demonstrated and applied in predictive models of growth-dependent mortality for juvenile trees (Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Kobe and Coates 1997, Walters and Reich 2000, Lin et al. 2001). Several studies have shown that growth, but not size, is an important predictor of sapling mortality (Kobe et al. 1995, Kobe 1996, Lin et al. 2001). Growth rates integrate the effects of many factors affecting sapling performance, and therefore act as an index for mortality risk (Wyckoff and Clark 2000). Walters and Reich (2000) submit two explanations for the negative relationship between growth and mortality for juvenile trees: (1) growth rates might be correlated with other factors that increase juvenile tree survival, such as carbohydrate storage concentrations or structural and chemical defense mechanisms, or alternatively (2) high growth rates result in a faster release from size-dependent mortality.

1.3.3 Shade tolerance in juvenile trees

Suppression was defined by Franklin et al. (1987) as the limitation of a tree's growth by the presence of another, usually larger, tree. Interspecific variation in light-dependent growth and mortality (shade tolerance) of saplings is generally considered to be a key factor underlying forest succession (Pacala et al. 1994, Walters and Reich 1996, Lin et al. 2001). Recent literature suggests that interspecific differences in sapling shade tolerance form a continuum rather than distinct classes (Pacala et al. 1994, Wang et al. 1994, Kobe and Coates 1997, Lin et al. 2001). Across species, growth rates and survival of juvenile trees generally increase with increasing light availability (Pacala et al. 1994, Walters and Reich 2000). This may be because carbon balance in young trees is often light-limited (Pacala et al. 1994). Limited light availability reduces seedling growth most

significantly at extremely low light levels (Loach 1970, Walters and Reich 2000). Light availability in combination with species-specific shade tolerance affect sapling growth and survival in a forest understory. Light availability in the understory is influenced at the canopy level by canopy composition, stand density, sky conditions and solar angle (Messier et al. 1998). Understory species composition and abundance are also important factors influencing light availability in the sub-canopy (Messier et al. 1998).

Lorimer (1981) examined growth and mortality of larger understory saplings (>2.5 cm diameter at breast height) of seven species in site replicates in oak forests in southern New York state. Saplings were assigned to crown and size classes. To account for some of the differences in growing conditions among individual saplings, a simple competition measure was derived (diameter of sapling/mean diameter of overstory trees). Although there was a relationship between mortality and crown class (level of suppression), within a crown class the differences in mortality among species did not correspond to the expected order of shade tolerance (where more shade tolerant species were expected to exhibit lower mortality). It was suggested that factors in addition to tolerance were likely affecting mortality rates. Species-specific relationships between mortality and competition illustrated that interspecific differences are most pronounced in the smallest size classes of trees. As expected, the more shade tolerant species exhibited higher growth rates in the understory and lower growth rates in the overstory than the less shade tolerant species.

The relationship between sapling growth and mortality as a defining characteristic of shade tolerance

Pacala et al. (1994) and Kobe et al. (1995) examined sapling growth and mortality for 10 tree species with various traditional rankings of shade tolerance, in a transition oak-northern hardwood forest in northeastern United States. It was found that although there is a trade-off between species-specific growth at low and high light, the ranking of species from fast growing at high light to fast growing at low light did not correspond to traditional classifications of shade tolerance. There was also a strong inverse relationship between height growth at high light, and survivorship at low light (Figure 1.1). The order of species in this case did correspond to traditional rankings of shade tolerance. It was concluded that species-specific relationships between sapling growth at high light and

mortality at low light, rather than relationships between sapling growth at high and low light (as suggested by Lorimer [1981]), can be used to define shade tolerance.

A relationship between sapling growth and mortality, and traditional classifications of shade tolerance was further demonstrated by Lin et al. (2001). It was shown for seven tree species in southeastern Texas that the species-specific effect of radial growth rate on mortality became less important as traditional ranking of shade tolerance increased (Figure 1.1). In other words, the more shade tolerant a species, the less sensitive it was (in terms of mortality) to changing growth. This supports the idea that increased survivorship at low light, rather than increased growth (relative to shade-intolerant species) at low light, is a characteristic of shade-tolerance.

Wright et al. (2000) examined the effect of the duration of periods of natural suppression and release on sapling growth for 11 tree species of varying shade tolerance in British Columbia. Periods of suppression were defined as years in which growth was below some threshold value - below which mortality sharply increased - derived for each species. Threshold values for shade tolerant species occurred at much lower light levels than for shade intolerant species. Saplings from all species had undergone periods of suppression and release, and the frequency of these events was highly correlated with mean sapling age for a species. The response to growth history differed between shade tolerant and shade intolerant species: recent periods of suppression had a detrimental effect on current response to light for shade intolerant species. Results suggested that saplings of shade tolerant species retain their ability to respond positively to natural release despite a growth history involving periods of suppression, whereas less shade tolerant species exhibit growth decline during suppression and a delayed response to release. The effect of growth history on a species may be a means of characterizing its shade tolerance (Figure 1.1).

Although elevated sapling growth in low light is not generally considered to be a characteristic of shade tolerance (Pacala et al. 1994, Kobe et al. 1995, Lin et al. 2001), the relationship between shade tolerance and growth at extremely low light for *young seedlings* remains unclear. Walters and Reich (1996) showed that young seedlings of *shade tolerant* North American tree species have greater rates of growth than shade intolerant species in *extremely limited* light conditions (2% of canopy light). In contrast,

Kitajima (1994), for 13 tropical tree species, and Walters and Reich (2000), for 10 North American tree species, found that *shade intolerant* species generally exhibited higher relative growth rates than shade tolerant species in extremely low light conditions (less than or equal to 2% of canopy light). Walters and Reich (2000) suggested that these discrepancies were largely a result of two differences in methodology between the studies: Walters and Reich (1996) examined seedlings in an outdoor experiment over a two-year period, whereas Kitajima (1994) and Walters and Reich (2000) examined seedlings growing in greenhouse conditions, over two- and four-month periods, respectively. Therefore, the factors influencing growth and mortality (winter, herbivory, the relative importance of early factors such as seed size) differed between the two types of studies. Walters and Reich (1996) suggested that traits contributing to shade tolerance were likely related to biomass and energy conservation more than they were related to increased growth in extremely low light conditions. Similarly, Loach (1970) concluded that factors other than the efficiency of photosynthetic systems in low light were necessary for characterizing shade tolerance in tree seedlings.

Additional defining characteristics of sapling shade tolerance

Messier et al. (1999) suggested that the ability of shaded understory trees to curb their height growth and modify their crown to maximize light interception is a defining characteristic of shade tolerance (Figure 1.1). Both Williams et al. (1999) and Claveau et al. (2002) demonstrated that saplings of shade tolerant coniferous species exhibit more plastic crown morphology across variation in light conditions than saplings of shade intolerant coniferous species (Figure 1.1). Kobe (1997) suggested that interspecific differences in shade tolerance of juvenile trees may be explained by the degree of carbohydrate allocation to storage: saplings of shade tolerant species allocate more total nonstructural carbohydrates to storage than do intolerant species (Figure 1.1). De Lucia et al. (1998) examined the pattern of biomass allocation among saplings of varying shade tolerance in the northeastern United States. It was found that traits such as high specific leaf area (leaf area/leaf mass), and leaf area ratio (leaf area/sapling mass), which were expected to be important under shaded conditions, were not related to shade tolerance. Instead it was proposed that the examined species exhibited different growth strategies

relating to a trade-off in biomass allocation to traits favouring high growth rates and those conferring resistance to herbivores and pathogens.

1.3.4 Factors in addition to shade tolerance and light availability that influence variation in sapling growth and mortality

Light limitation in understory conditions governs sapling performance and might be expected to obscure effects on growth or mortality resulting from other limited resources. However, a study by Kobe (1996) in northern hardwood forests in the northeastern United States demonstrated that in fact limited resources other than light can affect sapling performance in a light-limited environment. It was suggested that both water and calcium availability were partially responsible for differences in sapling performance that were observed among study locations. Kobe et al. (1995) found interspecific differences in sapling survivorship among sites with differing pH. Pacala et al. (1994) found that soil moisture had no significant effect on interspecific differences in sapling growth. It was suggested that either water was not a limiting factor, or that the amount of variation in water availability was insufficient for the detection of water limitation. Other factors such as insect and pathogen damage, and plant-herbivore interactions, may also differentially affect the realized growth and mortality of natural regeneration of different tree species.

Within a species, saplings in higher resource environments would be expected to exhibit higher growth rates (Kobe and Coates 1997). For example, a positive growth response to natural increases in light availability has been widely demonstrated for saplings (Lieffers and Stadt 1994, Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Beaudet and Messier 1998, Drobyshev and Nihlgård 2000, Wright et al. 2000, Claveau et al. 2002). Walters and Reich (2000) found that both light availability and nitrogen supply affected growth rates and survival of young seedlings. However, for established saplings, Kobe (1996) found that nitrogen availability did not affect growth. Nitrogen may play a more important role in the establishment of very young seedlings than it does for the growth and survival of well-established saplings with more extensive root systems. Kobe and Coates (1997) found that intraspecific mortality of several species in northwestern British Columbia varied among sites that likely differed in soil moisture.

Canopy gap characteristics

Gap size is well documented as a major factor determining post-disturbance tree succession (see review by McCarthy 2001). Shade tolerant species that exist as advance regeneration in the shaded understory are generally more successful in exploiting increased light environments of small gaps; whereas intolerant species may better exploit larger canopy gaps (McCarthy 2001), with the exception of balsam fir (shade tolerant) growing under extensive spruce budworm-caused gaps.

Post-disturbance conditions differ substantially from those experienced by saplings prior to disturbance. Drobyshev and Nihlgård (2000) examined growth of saplings of Norway spruce (*Picea abies* (L.) Karst.) along a gradient of gap sizes; growth was found to be positively related with gap size. Saplings were also found to exhibit greater growth with increased water availability. It was suggested that variation in both environmental conditions, and in the ability of saplings to respond to environmental changes were the factors responsible for observed variation in sapling growth. Important environmental changes accompanying gap formation include higher light, lower air humidity, and higher water availability in the upper soil horizons (Drobyshev and Nihlgård 2000). It was suggested that gap size was more important than annual climatic variation for influencing sapling height growth.

Kneeshaw and Bergeron (1996) found that the abundance of advance regeneration of six boreal tree species in the southwestern boreal forests of Québec was positively correlated with the presence of spruce budworm-caused gaps. However, shrub competition, which was higher in larger gaps, was negatively correlated with the abundance of advance regeneration. It was submitted that there exists a trade-off between increased resource availability and increased competition from shrubs with increasing gap size. Similarly Drobyshev (1999) demonstrated for *Sphagnum-Myrtillus* forests that spruce sapling abundance was higher in smaller gaps. Active recruitment of other species limited spruce relative abundance. Abundance of advance regeneration may respond differently than individual sapling growth to current levels of overstory (gap size) and understory competition: sapling growth may be positively correlated to gap size, whereas abundance of shade-tolerant advance regeneration appears to be negatively correlated to gap size. Kneeshaw and Bergeron (1996) found that abiotic site variables including soil

texture, drainage, deposit type, stoniness, depth of organic matter layer, slope, and topography were poorly correlated with sapling densities of most species studied.

1.4 Summary

In the absence of frequently recurring fire, vegetation dynamics within canopy gaps may exert a strong influence on canopy composition, particularly within older forests where canopy gaps are larger and occur more frequently (Kneeshaw and Bergeron 1998). In hardwood stands, small gaps have been shown to lead to species replacement by more shade tolerant conifers, which maintain established sapling banks of advance regeneration in the understory (Kneeshaw and Bergeron 1998), and also to canopy replacement by different individuals of the same species (Cummings et al. 2000). Gap formation in older coniferous stands may also either promote the coexistence of species in the canopy or foster canopy replacement by different individuals of the same species. Spruce budworm outbreaks may act both as a cycling mechanism for balsam fir and as a mechanism which mediates the coexistence of shade intolerant early successional hardwoods with later successional coniferous species.

Factors affecting the performance of advance regeneration may interact and contribute to a "downward spiral" towards death. Different stress factors may facilitate the occurrence of subsequent damaging events, limiting the chance of sapling recovery with each event in a similar manner to that demonstrated for mature trees (Pedersen 1998). Recent simulations of forest dynamics have demonstrated that interspecific differences in sapling growth and mortality resulting from variation in species-specific shade tolerance can have profound effects on forest structure and composition (Kobe et al. 1995, Kobe and Coates 1997). A review of the recent literature on sapling growth and mortality has provided a summary of sapling characteristics that can be used to define species-specific shade tolerance. Recent studies have shown that species-specific relationships between sapling growth at high light and mortality at low light can be used to define shade tolerance (Pacala et al. 1994, Kobe et al. 1995). Lin et al. (2001) demonstrated that saplings of more shade tolerant species were less sensitive (with respect to survival) than saplings of shade intolerant species to changes in growth under

different light conditions. Other sapling characteristics that may reflect shade tolerance include the ability of shaded understory trees to curb their height growth and modify their crown to maximize light interception (Messier et al. 1999, Williams et al. 1999, Claveau et al. 2002), the degree of carbohydrate allocation to storage (Kobe 1997), and the lack of effect of recent periods of suppression and release on current growth (Wright et al. 2001).

In addition to light availability and shade tolerance, environmental factors such as soil water availability and pH have been suggested as potential factors affecting sapling performance (Kobe et al. 1995, Kobe 1996). Micro-environmental changes following canopy gap formation also affect sapling growth (Drobyshev and Nihlgård 2000). Gap size may be positively correlated with sapling growth (Drobyshev and Nihlgård 2000) if associated understory competition is limited. The abundance of advance regeneration may be positively associated with the presence of canopy gaps, but negatively correlated to gap size if understory competition is strong (Kneeshaw and Bergeron 1996). As forests more commonly escape fire for long periods, small-scale disturbances and resulting gap dynamics involving advance regeneration become increasingly important in determining forest structure and composition (Kneeshaw and Bergeron 1996). An understanding of the response of advance regeneration to environmental changes associated with canopy gap formation is important for interpreting stand dynamics, and for refining silvicultural practices in which advance growth is preserved as immediate growing stock to renew forests.

1.5 Justification for study and overall objectives

A better understanding of sapling growth and mortality is necessary to predict forest growth in systems dominated by gap disturbances. Moreover, characterizing changes in boreal forest canopy structure that result from various disturbance processes will help in assessing the sensitivity of boreal ecosystems to the structural changes that may arise with environmental stress and global climate change (Franklin et al. 1987, Holling 1992). The response of established natural regeneration to environmental changes associated with canopy gap formation is of interest for interpreting stand dynamics: differential growth and survival of tree saplings both within and among

species may have substantial effects on forest composition during secondary succession (Pacala et al. 1994, Kobe et al. 1995, Kobe 1996). Furthermore, the response of advance regeneration to changes in canopy closure is important for refining silvicultural practices in which advance growth is preserved as immediate growing stock to renew forests (Ruel et al. 1995, Örlander and Karlsson 2000, Ruel et al. 2000, Kneeshaw et al. 2002). To explore strategies of managing advance regeneration in boreal forests we need to understand the ecology of advance regeneration growing in the shaded understory (Messier et al. 1999), including its response to changes in canopy closure.

Advance regeneration in sustainable forest management

Descriptive knowledge of differential survival and growth of tree species under closed canopy conditions and in canopy gaps (shade tolerance) has for many years formed an important component of silvicultural systems in forest types around the world (McCarthy 2001). With goals of emulating natural disturbance regimes foremost in mind, management approaches that mimic gap dynamics through the use of uneven-aged silviculture are being newly explored in gap-disturbed forests in North America (Coates and Burton 1997, McCarthy 2001). The characterization of growth and mortality in both shaded and unshaded environments can be used to help predict sapling response to uneven- and even-aged silvicultural approaches that protect advance regeneration.

Overall objectives

The broad objective of this study is to better understand the critical processes of growth and mortality of advance regeneration of several important boreal tree species, in different light conditions and regions of the Canadian boreal forest. To characterize the mortality of natural regeneration that has survived the initial years of extremely high mortality, this study examines saplings at the crucial post-establishment phase of development (advance regeneration). Existing studies of sapling mortality have been based on retrospective analyses (eg. Kobe et al. 1995); however, long-term monitoring of regeneration is necessary to supplement such studies and address assumptions made therein, and to more fully understand this important phase of stand development. This study was initiated to provide such long-term data and has already monitored mortality

over a 2.5-year period. Through a collaborative effort among several different research groups across the country, this study will increase our understanding of longitudinal variations and trends in mortality of advance regeneration. This knowledge will contribute to more unified theories of boreal stand development, and facilitate management implementation of this research across the country.

Objectives include summarizing interspecific and inter-regional differences in sapling growth and mortality, and determining the effects of canopy openness on sapling growth and mortality. To address these objectives, monitoring plots of advance regeneration of four important boreal tree species were established in different regions of the Canadian boreal forest, in low and high light conditions associated with the presence or absence of canopy cover. Light availability within each of these light environments is assessed, since light availability at the individual level, which may vary within a defined level of canopy closure, is a critical factor governing growth and mortality processes in the understory (Lieffers et al. 1999). The ability of individual-level light availability, size and crown morphology to predict individual mortality will be determined to help characterize mortality of advance regeneration. The effect of individual-level light availability on growth and crown morphology will also be determined.

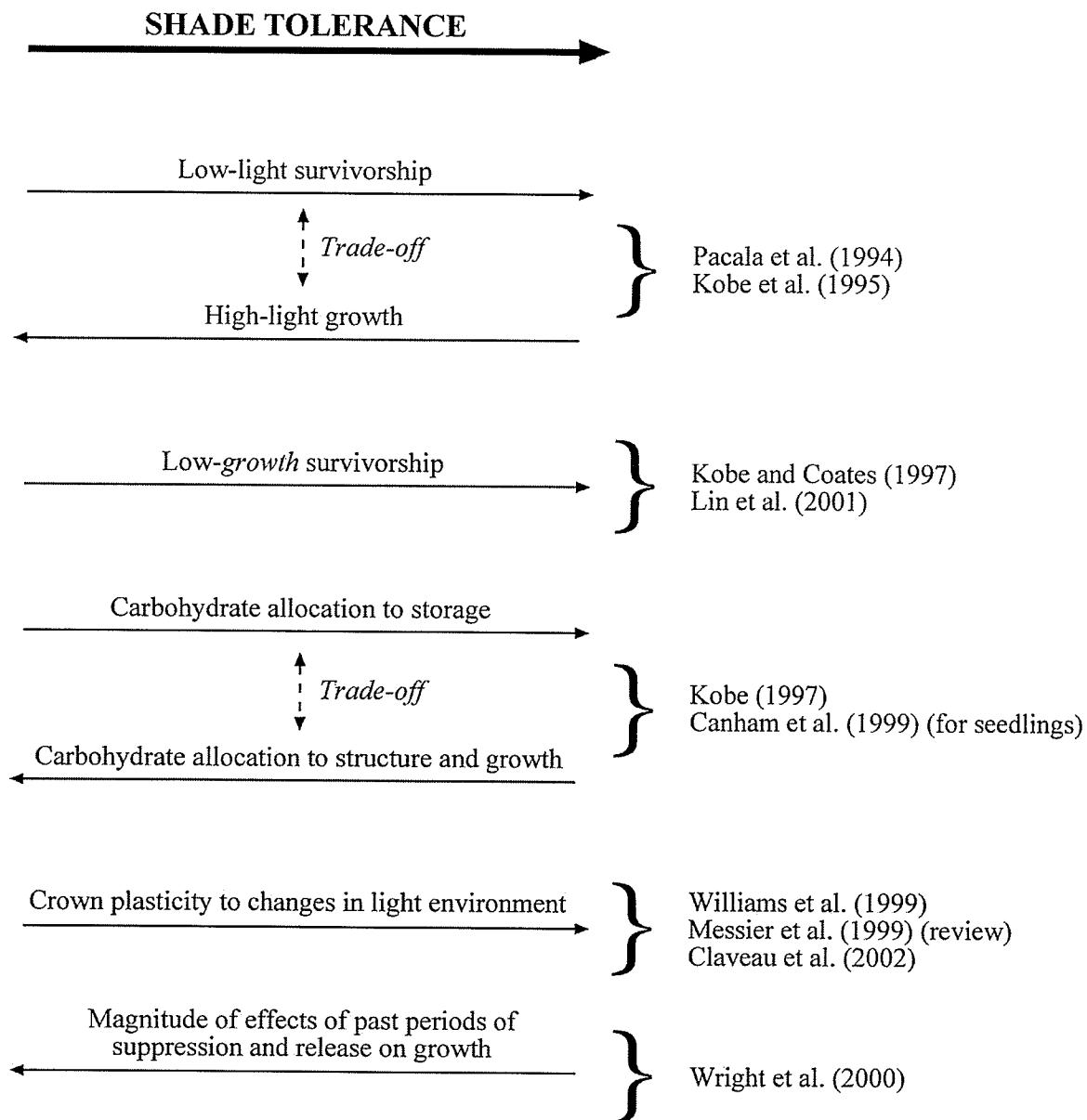


Figure 1.1. Summary of trends in sapling growth and survivorship in relation to shade tolerance based on evidence provided in the literature. Arrows indicate direction of increase. Differential carbohydrate allocation to storage may partially explain the observed trade-off between low-light survivorship and high-light growth (Kobe 1997).

CHAPTER 2

ANALYTICAL APPROACHES TO CHARACTERIZE GROWTH AND MORTALITY OF JUVENILE TREES

2.1 Introduction

The long-term success of a sapling in attaining canopy stature is dependent upon numerous factors affecting its growth and risk of mortality (Messier et al. 1999). Sapling growth and mortality can be examined using an individual-based approach, which has been shown to increase our understanding of population and community processes (Zens and Peart 2003).

Plant growth analysis is a classic analytical approach based on the derivation of a standardized measure of growth of an individual, the relative growth rate (Richards 1969, Sesták et al. 1971, Hunt 1978, 1982, Wilson 1981, Charles-Edwards et al. 1986). Although this measure has been widely used in botanical and agricultural literature, some debate exists as to its suitability as a measure of tree growth (Brand et al. 1987). Its suitability as a growth measure for tree saplings will be discussed.

Unlike growth rates, mortality rates cannot be measured directly from individual plants. However, analytical methods exist for examining the risk of mortality at the individual level. One means of examining sapling mortality is to consider a (0,1) outcome of "dead" or "alive" for each individual. An alternate response variable for examining individual mortality is "time until death", which contains more information than does a simple binary code. Survival analysis involves statistical analyses for which the response variable of interest is time until event occurrence (Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996, He and Alfaro 2000). As will be shown, this approach is particularly useful for ecological studies, though relatively novel to the field of plant ecology.

The intent of this review is to describe two central analytical concepts that can be utilized for characterizing individual sapling growth and mortality: 'classical' methods of plant growth analysis and novel application of survival analysis. An introduction to each topic will be provided and pertinent applications in recent ecological literature will be reviewed. In addition, the opening discussion of growth analysis will include an account

of the historical derivation of relative growth rate, and the presentation of survival analysis will include detailed methodological explanations for important non-parametric models.

2.2 Plant growth analysis: an historical sketch and its application to juvenile trees

2.2.1 Introduction

Plant growth analysis is based on a standardized measure of growth of an individual, the relative growth rate (RGR), or of a stand, the crop growth rate (CGR) (Wilson 1981). RGR is the increase in plant material per individual over time (Richards 1969, Hunt 1978, 1982, Charles-Edwards et al. 1986). CGR is the increase in plant material per unit time multiplied by the number of individuals per unit ground area (Wilson 1981). These standardized growth rates are sometimes expressed as the product of leaf area and net assimilation rate (the increase in plant material per unit leaf area per unit time) (Wilson 1981). Leaf area is generally standardized per unit of plant dry weight for individuals (the leaf area ratio) or per unit of ground area for stands (the leaf area index) (Sesták et al. 1971, Wilson 1981). Relative growth rates can be derived using any plant characteristic whose changing magnitude is measured (Sesták et al. 1971). Common measures of plant growth include total dry weight, separate dry weights of different plant parts, shoot or branch size (height, diameter), and numbers of various plant parts such as leaves and stems per plant or sample (Sesták et al. 1971).

Common growth variables for tree saplings include total height, basal diameter, crown length, mean crown diameter, length of the leader branch, length of the longest lateral branch in the uppermost whorl, and the number of branches at the uppermost node (Williams et al. 1999, Claveau et al. 2002). Relative growth rates derived from measures of height or branch length are critical measures of sapling performance because it is through this extension growth that saplings are able to exploit available space and higher light microsites and possibly overtop surrounding vegetation to pre-empt access to light (Beaudet and Messier 1998; Falster and Westoby 2003). The competitive advantage

associated with height growth is dependent on height relative to surrounding plants rather than absolute height (Falster and Westoby 2003).

In addition to RGR, alternate standardized morphological measures can be computed and examined in conjunction with RGR for a more complete description of whole-plant performance. These include live crown ratio (crown length/total height), crown profile (crown length/mean crown diameter), leader to lateral branch ratio (L:B ratio), and height to diameter ratio (Beaudet and Messier 1998, Williams et al. 1999, Claveau et al. 2002). The L:B ratio is often used to examine growth of shade tolerant coniferous species because it reflects plastic change in crown form from a conical shape to a more flat-topped shape that may accompany changes in sapling photosynthetic efficiency (Williams et al. 1999).

Hunt (1978, 1982) summarized two overall approaches to plant growth analysis: (1) the "classical" approach, where plant growth is followed over time with relatively infrequent measurements but with large replication of measurements and plant size is averaged over a period intervening two successive measurements; and (2) the "functional" or "curve-fitting" approach, where measurements are more frequent and instantaneous values of growth are derived from curves fitted to the data. Both of these approaches are considered empirical (Thornley 1976, Hunt 1978). A third approach to the modelling of plant growth analysis is a "mechanistic" approach, where growth is modelled based on dividing a plant system into components, and examining their individual behaviour and interactions to understand the workings of the whole system (Thornley 1976). The focus of this discussion is classical plant growth analysis, as many studies of sapling growth have utilized a classical approach.

The historical and mathematical derivation of RGR will be explained, its appropriateness for the study of individual sapling growth considered, and the use of growth analysis in recent ecological studies of juvenile trees summarized. Much of the historical discussion will be illustrated using plant dry weight as the growth variable since plant dry weight has traditionally been considered and adopted as a suitable measure of plant growth; thus, plant dry weight commonly appears in classic literature on the subject of plant growth analysis.

2.2.2 The evolution of plant growth analysis

In 1919, Blackman wrote that in “many phenomena of nature we find processes in which the rate of change of some quantity is proportional to the quantity itself”. He proceeded to compare individual plant growth to increases in compound interest where the amount of interest accrued is proportional to the amount of capital. Blackman suggested that the simple equation which best describes this type of continuous growth for annual plants is the exponential function:

$$W_2 = W_1 e^{r(t_2-t_1)} \quad [2.1]$$

where W_2 and W_1 are the dry weights at time t_2 and t_1 respectively, and r is the constant rate of increase of W over time. Blackman named this constant the ‘efficiency index’ of dry weight production, or the ‘economy constant’ of a plant. He noted that r would likely decrease once plant growth had progressed beyond early stages, such as at the initiation of reproductive organ development. West et al. (1920) emphasized that the proportion of growing plant material to total plant material is not constant over time and therefore the growth rate expressed per unit of plant material cannot remain constant.

A plant cannot realistically grow indefinitely at an exponential rate within the constraints of environmentally and internally imposed limitations. Briggs et al. (1920) and West et al. (1920) pointed out that alternative simple models such as the logistic equation had been suggested for a more realistic description of plant growth. The logistic or autocatalytic equation introduces a dynamic rate of increase that decreases with increasing plant weight. The logistic equation can be written as:

$$W = \frac{A}{1+be^{-kt}} \quad [2.2]$$

where W is the dry weight at time t , A is the maximum dry weight of the plant, and b and k are constants (Richards 1959, 1969).

As interest in functional empirical and mechanistic approaches to plant growth analysis continued to grow throughout the twentieth century, several mathematical

models deemed appropriate for plant growth analysis emerged from the literature. Models that have been suggested for describing plant growth within the constraints of internal controls and environmental limitations include the time power function, the above logistic equation, the mono-molecular function, and the Gompertz growth equation (Richards 1959, 1969); and the Michaelis-Menton equation, which models resource-dependent growth (Thornley 1976). Hunt (1978) suggested that the most widely useful expression for a functional approach to plant growth analysis is that put forth by Richards in 1959. Richards' (1959) flexible model for plant growth analysis expands upon a growth function originally proposed by von Bertalanffy in 1941 and is a generalization of the logistic equation (Hunt 1978).

2.2.3 Relative growth rate

West et al. (1920) introduced the term ‘relative growth rate’ (RGR) to describe the percentage dry weight increase of a plant. The percentage dry weight increase is the rate of increase standardized by total plant weight. West et al. (1920) provided the equation for RGR for the specific case of plants undergoing exponential growth. Solving the exponential equation (Equation 2.1) for the rate of increase r (RGR) we obtain:

$$RGR = \frac{\ln(W_2) - \ln(W_1)}{t_2 - t_1} \quad [2.3]$$

This increase is the average RGR over a given time interval from t_1 to t_2 for a plant exhibiting exponential growth (Briggs et al. 1920, West et al. 1920, Fisher 1921, Richards 1969). If a plant demonstrates true exponential growth then RGR will be constant as Blackman (1919) suggested. Therefore, a constant RGR characterizes exponential growth just as a constant absolute (non-standardized) growth rate characterizes linear growth (Richards 1969). The RGR for the special case of a plant showing logistic or autocatalytic growth is a linear function of W :

$$RGR = k \left(\frac{A-W}{A} \right) \quad [2.4]$$

where k is a constant, and again W is the changing dry weight, and A is the maximum dry weight of the plant. Unlike the constant RGR of exponential growth, the RGR for the logistic function is dynamic and declines linearly with increasing W (Richards 1969).

Fisher (1921) made an important clarification of the idea of RGR by showing that regardless of the underlying growth curve exhibited by a plant the standardized growth rate at any instant is necessarily:

$$RGR = \frac{1}{W} \frac{dW}{dt} . \quad [2.5]$$

Richards (1969) and Hunt (1978) elucidate how this instantaneous measure of RGR is derived, and how the corresponding formula for an average measure of RGR can be derived for a plant exhibiting any underlying functional form of growth. A growth curve is a plot of the size of some plant characteristic (W) against time or age (Richards 1969). This curve could resemble a linear, exponential, logistic, or an altogether different type of function. Regardless of the form of the growth function, the instantaneous rate of change of plant size (W) over time (t) is the derivative of W with respect to t , dW/dt . In other words the rate of change is the slope of the tangent to the curve at time t (Richards 1969). This is a measure of the instantaneous absolute growth rate (not standardized by total plant size) of the plant at time t . The standardization of growth by total size allows for comparison among species and among individuals of different size and age. By dividing the instantaneous absolute growth rate by total plant size the instantaneous RGR is obtained (Equation 2.5). Richards (1969) demonstrates that if $\ln(W)$ is plotted against time using a functional approach, then the instantaneous slope of this curve is equal to the instantaneous RGR obtained by dividing the absolute instantaneous growth rate by total plant size:

$$\text{Instantaneous slope of } \ln(W) \text{ vs. } t = \frac{d\ln(W)}{dt} = \frac{1}{W} \frac{dW}{dt} = RGR . \quad [2.6]$$

Therefore, the instantaneous slope of the curve of $\ln(W)$ (the natural log of plant size) plotted against time is the instantaneous RGR regardless of the form of the underlying growth curve (Fisher 1921, Richards 1969). It follows that the average RGR over a given time interval is the average slope between two values of t for the curve $\ln(W)$ plotted against time, which can also be calculated by integrating the instantaneous RGR (Sesták et al. 1971). Thus, mean RGR over a time interval is calculated according to Equation 2.3.

In summary, any growth curve can be semi-log transformed by plotting the natural log of plant size against time to generate a curve with an average (or instantaneous) slope equal to the average (or instantaneous) RGR (Richards 1969). Some confusion here arises because this general formula for mean relative growth rate (general in the sense that the formula holds true regardless of the underlying form of the growth curve) is the same as the mean relative growth rate historically discussed for the special case of a plant exhibiting exponential growth (Equation 2.3) (Fisher 1921, Richards 1969).

2.2.4 An alternative standardized growth rate for woody plants

RGR is expressed as the unit plant increase per unit plant material per unit time. Since woody plants continuously accrue non-productive tissue, larger or older trees may have lower RGR because the annual increment of a tree's growth becomes a diminishing proportion of its total size (Brand et al 1987, Waring 1987). Brand et al. (1987) proposed that growth analyses of trees should be based on annual incremental growth rather than total size. This incremental growth rate (IGR; referred to as the "relative production rate" by Brand et al. [1987]) is derived by substituting into Equation 2.3 (average growth) or Equation 2.6 (instantaneous growth) a measure of incremental tree growth for a given year. For instance, the instantaneous IGR is:

$$IGR = \frac{d \ln(\Delta W)}{dt} = \frac{1}{\Delta W} \frac{d \Delta W}{dt} \quad [2.7]$$

where ΔW is the incremental growth for a given year. The formula for average IGR is obtained by integrating the formula for instantaneous IGR. Thus, mean IGR is calculated using the formulation:

$$IGR = \frac{\ln(\Delta W_2) - \ln(\Delta W_1)}{t_2 - t_1} \quad [2.8]$$

where ΔW_2 and ΔW_1 are incremental growth values for time t_2 and t_1 respectively. Rather than computing growth as a proportion of total plant size, IGR standardizes the instantaneous rate of change of incremental growth over time ($d\Delta W/dt$) by incremental growth (ΔW). A single measure of IGR compares the incremental growth of an individual from one year to the next, thereby measuring the growth trend over time. For example, if a sapling grew 12 cm in height in one year, and 10 cm in the next, it would show a negative IGR for that period. A second sapling that grew 1 cm in one year, and 1.2 cm in the next would show positive IGR, but with the same absolute value for IGR as the first sapling.

Brand et al.'s (1987) argument for using annual increment rather than total size as the basis for growth analysis of trees is clear for calculations of RGR which standardize growth by total weight or diameter (plant dimensions which are largely comprised of non-photosynthetic material). However, the influence of non-productive tissue on computations of RGR using height requires more consideration. Williams et al. (1999) found that saplings of Douglas-fir (*Pseudotsuga menziesii* var. *glaucia* (Beissn.) Franco) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var. *latifolia* Engelm) <2 m exhibited higher relative height growth rates than saplings >2 m in low light environments receiving less than 30% of above-canopy photosynthetic photon flux density (400-700nm waveband). The authors suggested that higher maintenance costs for larger saplings resulted in less carbon availability for height growth in shaded environments.

Bigler and Bugmann (2003) incorporated measures of both average growth and change in growth increments over time in their predictions of growth-dependent tree mortality and found that both types of measures were important in predicting mortality. It was suggested that in addition to average growth measures, increases or decreases in

growth over time are important for assessing tree response to environmental conditions. IGR may be useful as a standardized measure of tree growth where individuals have accumulated much woody material (for growth estimates using radius or biomass) and also for examining increases or decreases in tree growth (growth trends) over time.

2.2.5 Applications of growth analysis to saplings

Size definition of a sapling

RGR has commonly been used for examining growth of tree seedlings (Loach 1970, Walters et al. 1993, Kitajima 1994, Cornelissen et al. 1996, Swanborough and Westoby 1996, Reich et al. 1998, George and Bazzaz 1999, Beckage and Clark 2003). Fewer studies have utilized RGR as a measure of sapling growth, partially because less research has been conducted on trees at sapling stages. Good and Good (1972) defined eastern hardwood saplings as trees greater than 30 cm in height and less than approximately 10 cm in diameter at breast height (DBH). Similarly, Kobe et al. (1995) and Kobe (1996) defined hardwood saplings as trees that are greater than 25 cm in height, which do not have any foliage reaching the canopy. Drobyshev (1999) used 20 cm as a lower limit to define Norway spruce (*Picea abies* (L.) Karst.) saplings. By using minimum size criteria to define saplings, very young seedlings that may exhibit different growth and mortality responses are excluded. In temperate and boreal regions of the northern hemisphere a minimum height of 20-30 cm is commonly used to define saplings (Good and Good 1972, Kobe et al. 1995, Kobe 1996, Drobyshev and Nihlgård 2000, Claveau et al. 2002, Kneeshaw et al. 2002). However, there is also some variation in the value of this height threshold. Other minimum height values that have been used to define saplings include: 1 m (Kneeshaw and Bergeron, 1996, 1998), 50 cm (Wright et al. 2000), 15 cm (Pacala et al. 1994), 10 cm for coniferous species (Williams et al. 1999), and 50 cm for hardwood species (Beaudet and Messier 1998). Upper size criteria include maximum height of 12 m (Wright et al. 2000), 14 m (Drobyshev 1999) or DBH of 5 cm (Kneeshaw and Bergeron, 1996, 1998).

Recent applications of growth analysis to saplings

Williams et al. (1999) utilized mean RGR (Equation 2.3) to calculate sapling height growth for Douglas-fir and lodgepole pine, as did Zamora et al. (2001) for Scots pine saplings (*Pinus sylvestris* L.) in a Mediterranean environment, and Hartvigsen et al. (1995) for cottonwood saplings (*Populus deltoides* Marsh.) (Table 2.1). DeLucia et al. (1998) used mean RGR for determining increase in plant dry mass for saplings of several eastern North American hardwood species. Alternatively, studies of sapling growth have derived standardized measures of growth by dividing the annual growth increment (absolute growth rate) by size, a slightly different formulation from mean RGR (Pacala et al. 1994, DeLucia et al. 1998). These formulations are similar to that for *instantaneous* RGR (Equations 2.5, 2.6), where absolute instantaneous growth rate is standardized by total size. The difference between these formulations and instantaneous RGR is that the absolute growth rates in these studies are annual growth increments, not instantaneous values.

Despite the obvious correlation between total height and height growth, absolute growth (growth not standardized by total size, ie. $\Delta\text{size}/\Delta\text{time}$) has been utilized in several studies of sapling growth (Good and Good 1972, Lorimer 1981, Coley 1988, Beaudet and Messier 1998, Drobyshev and Nihlgård 2000, Lin et al. 2001, Claveau et al. 2002). Örlander and Karlsson (2000) examined absolute height growth of Norway spruce (*Picea abies* L.) seedlings and saplings but first grouped all individuals: individuals <20 cm, between 20 and 50 cm, and <100 cm. Absolute radial growth of saplings has been used in studies incorporating sapling growth within more complex models of sapling mortality (Kobe et al. 1995, Kobe 1996, Kobe and Coates 1997). In general, no single measure of growth has been utilized throughout recent studies of tree saplings; several formulations including RGR and alternate standardized and non-standardized computations have been used to address various objectives (Table 2.1).

2.3 Survival analysis: introductory methodology and applications in plant ecology

2.3.1 Background: conventional mortality rates

The simplest way to estimate mortality for a population is to monitor deaths in a sample population over a defined census interval (Sheil et al. 1995, Sheil and May 1996, Krebs 1999). Such an approach assumes constant mortality over time. "Finite" or average mortality rates are derived by dividing the number of individuals that have died over the time period by the starting number of individuals in a sample. Similarly, finite survival rates are derived by dividing the number of individuals alive at the end of a time interval by the number alive at the beginning of the interval, or by computing 1-(finite mortality rate) (Krebs 1999). These finite (observed) rates are easily standardized to any desired time base (Krebs 1999).

Survival or mortality can also be described using instantaneous rates. A simple functional form used in ecology to depict a constant change in population size over time is the geometric model, or in its integrated form, the exponential decline model (Sheil et al. 1995, Krebs 1999):

$$N_t = N_0 e^{rt} \quad [2.9]$$

where N_t is the number of individuals at time t , N_0 is the number of individuals at the start of the census period, and r is the instantaneous mortality rate (always negative). If the equation is rearranged by taking the natural logs of both sides to solve for r , and t is set to 1 unit, then the instantaneous mortality rate r is derived as follows:

$$r = \ln(N_t/N_0). \quad [2.10]$$

Therefore, instantaneous mortality rate r , is the natural log of the finite survival rate N_t/N_0 (Sheil et al. 1995, Krebs 1999). In addition to assuming constant mortality over time, instantaneous mortality rates are based on an assumption that death occurrence (in a short time interval) is proportional to the number of individuals alive at that time.

Instantaneous rates and finite rates are nearly the same when rates are very small, but they diverge from one another as mortality rates increase (Krebs 1972, Sheil et al. 1995). Instantaneous mortality rates are useful mathematically because they are additive (Krebs 1972); however, finite rates rather than instantaneous mortality rates should generally be reported for ease of interpretation (Krebs 1999) and for consistency among studies (Sheil et al. 1995).

2.3.2 Introduction to survival analysis

In ecological applications, mortality has traditionally been examined at the population level by estimating mortality rate. Zens and Peart (2003) point out that such population-level measures ignore variation in mortality risk (probability of mortality) that occurs within most populations. A conventional mortality rate derived from a population sample exhibiting variation in mortality risk among individuals inherently underestimates the mortality rate of the population (Zens and Peart 2003). This is because the proportion of high risk to low risk individuals in a sample decreases as individuals die, resulting in a sample distribution that is no longer reflective of the population (Sheil and May 1996, Zens and Peart 2003). Individual-based approaches have been shown to increase our understanding of important ecological processes at the population and community levels, and should be used for examining mortality (Zens and Peart 2003).

One way to examine individual mortality is to consider a (0,1) outcome of “dead” or “alive”. Contingency tables and logistic regression could be used to determine the effects of any factor variables of interest on such a binary response variable. For instance, Bigler and Bugmann (2003) used logistic regression to predict tree mortality from a range of variables. An alternate response variable for examining individual mortality is “time until death”, which contains more information than does a simple binary code. Ecological processes in addition to that of mortality can also be described in terms of “time until event occurrence”; time until a flower is visited by an insect pollinator (Muenchow 1986), duration of stand growth since fire (Johnson and Gutsell 1994), and time to attack of trees by insect herbivores (He and Alfaro 2000) have all been described using survival analysis.

Survival analysis (or failure time analysis) involves statistical analyses for which the individual response variable of interest is time until an event occurs (Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996, He and Alfaro 2000). This variable is generally referred to as survival time or failure time and denoted as T. Survival analysis is well suited not only to data that form a time series, but for data that contain censored information. Censorship occurs when the exact survival time of an individual is unknown as a result of either the study period ending before all individuals fail or from loss of an individual during the study period (Muenchow 1986, Pyke and Thompson 1986, Parmar and Machin 1995, Kleinbaum 1996, Krebs 1999, He and Alfaro 2000).

Survival analysis makes use of the partial information provided by censored data. This approach is useful for ecological studies where marked individuals may be lost, or where the study period is too brief for all individuals to experience an event (Muenchow 1986). When censorship occurs, simple calculations of proportion of individuals experiencing an event by time t (mortality rate) may overestimate the rate of occurrence because the exact survival time of individuals with censored observations is unknown (He and Alfaro 2000).

The following discussion of survival analysis provides an introduction to central concepts, an overview of some seminal non-parametric models commonly used for describing “time until event” data, and a summary of the application of survival analysis in vegetation research.

2.3.3 Descriptions of survival time distribution

Probability distributions for the survival time variable (T) can be represented by several different functions, including the probability density function, and the more common survivorship and hazard functions (Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996, He and Alfaro 2000, Zens and Peart 2003). These functions are simply different forms of describing the distribution of survival times for a population, and are mathematically related. The probability density function is a rate, and contains the probability statement of event occurrence in the interval t to $t+\Delta t$, where Δt approaches zero:

$$f(t) = \lim_{\Delta t \rightarrow 0} \frac{\text{Probability (event occurrence in interval } t \text{ to } t + \Delta t)}{\Delta t} \quad [2.11]$$

(modified from Parmar and Machin 1995, He and Alfaro 2000). The survival function $S(t)$ is a probability statement that an individual's survival time (T) is longer than some specified time t :

$$S(t) = P(T > t). \quad [2.12]$$

The hazard function is an instantaneous conditional failure rate:

$$h(t) = \lim_{\Delta t \rightarrow 0} \frac{\text{Probability } (t < T < t + \Delta t \mid T \geq t)}{\Delta t} \quad [2.13]$$

which contains the conditional probability statement that the event (indicated by survival time T) will occur in the time interval between t and $t + \Delta t$, given that the survival time T is greater than or equal to t (modified from Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996, He and Alfaro 2000). These three density functions have the following relationships:

$$f(t) = \frac{d[1 - S(t)]}{dt} \quad [2.14]$$

and

$$h(t) = \frac{f(t)}{S(t)} = - \frac{d[\log S(t)]}{dt} \quad [2.15]$$

where the most commonly used survival and hazard functions are inversely related (modified from Parmar and Machin 1995, Kleinbaum 1996, He and Alfaro 2000).

2.3.4 The Kaplan-Meier estimate of survivorship

The non-parametric Kaplan-Meier (KM) or product-limit survivorship function estimates the population probability of survival past time t (Kaplan and Meier 1958, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996, Krebs 1999). Survivorship probabilities can be estimated for each time t by the Kaplan-Meier method:

$$\hat{S}(t) = \prod_{i=1}^k \left(1 - \frac{d_i}{n_i}\right) \quad [2.16]$$

where $\hat{S}(t)$ is the KM estimate of probability of survival past time t ; k is the number of time interval checks for possible deaths for a given time t ; d_i is the number of deaths recorded for time interval i ; and n_i is the number of individuals alive at the beginning of time interval i (modified from Kaplan and Meier 1958, Parmar and Machin 1995, Krebs 1999). These estimated survival rates differ from simple calculations of finite survival rate (number alive at end of study/number alive at beginning of study) because they are a product of survival probabilities for all previous times at which mortality was censused, and because the number at risk at the beginning of each time period is considered, allowing for the analysis of censored information. However, if no mortality or censoring occurs *before* time t (but mortality occurs *at* time t), the KM survivorship estimate at time t reduces to simple finite survival (proportion of survivors) (Kaplan and Meier 1958). "At risk" individuals are defined as those with a survival time greater than or equal to time t , which includes those found dead at that census since they are considered at risk just up to that point (Parmar and Machin 1995, Kleinbaum 1996).

The KM survivorship curve is a step function that changes values only at observation times when events (not censorship) were noted to occur, and is discontinuous at these points (Kaplan and Meier 1958). In some situations it might be desirable to examine the event of interest within larger defined time intervals than those in which the data were collected. In this case actuarial estimates of survival are used (Kaplan and Meier 1958, Parmar and Machin 1995). The total period of observation is first divided

into a series of user-defined time intervals. The actuarial assumption is made that censored survival times occur uniformly throughout a given time interval, and the number of censored observations (c_i) is divided by 2 (Kaplan and Meier 1958, Parmar and Machin 1995). Therefore, the number alive and at risk (n_i) would be equal to $n_i - (c_i/2)$ in Equation 2.16.

2.3.5 Estimating percentiles from a survivorship curve

The median survival time for a set of data is the time at which the estimated probability of survival is 50% (Muenchow 1986, Parmar and Machin 1995). This value, or any other percentile or survival time, can be read directly from a graph of survivorship.

2.3.6 Comparing the overall survival of two or more groups

Survival differences between two or more groups can be examined by comparing their survivorship curves. The overall difference between curves can be tested using one of several available statistical tests. A quantitative estimate of this difference can be derived by comparing the relative hazard (the observed number of deaths divided by the expected number of deaths under a null hypothesis of no difference between the groups) of the groups. The ratio of relative hazard for two groups is known as the hazard ratio, and is usually presented with 95% confidence intervals for the estimate (Parmar and Machin 1995). Hazard ratios greater than one demonstrate a greater hazard or risk of mortality for the group in the numerator, and values less than one indicate higher risk for the group in the denominator. A hazard ratio of one suggests no difference in hazard or survivorship between two groups.

The most common statistical procedure for testing the significance of survival differences between two or more groups is the Log-Rank test (Pyke and Thompson 1986, Hutchings et al. 1991, Parmar and Machin 1995, Kleinbaum 1996). However, there are several alternative tests available. To ensure that important survival differences between groups are recognized, consideration should be given to which statistical test is most appropriate for a given data set and objectives (Pyke and Thompson 1986, Muenchow

1986, Hutchings et al. 1991, Parmar and Machin 1995, Kleinbaum 1996). The Log-Rank test utilizes the same observed and expected counts determined in computing the hazard ratio and is based on a Chi-squared distribution. It should be used as a global measure to compare entire survivorship curves rather than specific points on two or more curves (Muenchow 1986, Parmar and Machin 1995).

2.3.7 Cox's Proportional Hazards model

The hazard function is an instantaneous rate of event occurrence (a function of time) and is inversely related to the survivorship function (Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996). Cox's Proportional Hazards (PH) nonparametric regression model estimates an individual's hazard based on both the baseline hazard (the population hazard prior to consideration of any predictor variables) for the population sample and also on its values for n factor variables (Cox 1972, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996). The general form for the Cox proportional hazards model is:

$$h(t, \mathbf{X}) = h_0(t) \exp \left[\sum_{i=1}^n B_i X_i \right] \quad [2.17]$$

where $h(t, \mathbf{X})$ is the Cox hazard, which is a function of both time and the n predictor variables being used to predict an individual's hazard (denoted by \mathbf{X}); $h_0(t)$ is the baseline hazard function, which is inversely related to $S(t)$, and is an instantaneous probability of event occurrence per unit time; and B_1, B_2, \dots, B_n are the coefficients for the n predictor variables X_1, X_2, \dots, X_n , respectively (modified from Cox 1972, Schoenfeld 1980, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996).

KM survivorship curves and associated hazard ratios provide the same survival information for any individual within a group of individuals used to derive a given KM curve. Cox PH provides an estimate of survival for each individual, distinguished from other individuals by its specific values for the set of predictor variables. A hazard ratio measuring the relative survival of any two individuals is the ratio of their Cox hazards.

The baseline hazard function in each individual's Cox hazard will cancel out upon division when computing the HR and consequently the baseline hazard function does not need to be specified to estimate HR (Cox 1972, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996). The HR becomes a function of only the predictor variables and their coefficients. It follows that $\exp(B_j)$ for a single predictor variable X is the predicted change in hazard for a unit increase in the variable, and is the hazard ratio for two individuals differing in their value for a single predictor variable by one unit. Similarly it can be shown that if more than one variable is entered into the model, the hazard ratio for a given variable remains $\exp(B_j)$ once B_j has been adjusted for the effects of other variables (Kleinbaum 1996).

For valid interpretation of variable effects in a Cox model, the underlying assumption of the model, that the hazard for one individual is proportional to the hazard for any other individual where the hazard ratio is independent of time, must be met (Cox 1972, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996). Methods for testing this assumption include several graphical approaches (Cox 1972, Schoenfeld 1982), which are summarized in Kleinbaum (1996), a goodness-of-fit test (Schoenfeld 1980), and the use of time-dependent variables, also described in Kleinbaum (1996). The most common and straight-forward of these approaches is to examine $-\ln(-\ln S(t))$ over time for individuals or groups of individuals with different values of predictor variables. If the log-log transformed survival curves are approximately parallel over time, then the assumption is met (Cox 1972, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996). In comparison with the goodness-of-fit test this method is somewhat subjective but allows the detection of localized departures from proportionality (Kleinbaum 1996). Furthermore, it is suggested that a conservative approach be used: unless deviations from parallelism are dramatic the proportional hazards assumption can be considered met (Kleinbaum 1996).

2.3.8 Applications of survival analysis in plant ecology

Survival analysis has been widely used in the health sciences and for reliability testing of industrial products for decades but only recently has it been applied to

ecological studies (Meunchow 1986, He and Alfaro 2000, Zens and Peart 2003). There are numerous applications in the current zoological literature (recent examples include Pollock et al. 1989a,b, Renner and Davis 2001, Fernandez and Huntington 2002, Ornelas et al. 2002; see review by Zens and Peart 2003), but fewer applications to plant ecology (Meunchow 1986, Pyke and Thompson 1986, Hutchings et al. 1991, Johnson and Gutsell 1994, He and Alfaro 2000, Wycoff and Clark 2000, Lin et al. 2001, Beckage and Clark, 2003). Muenchow (1986) and Hutchings et al. (1986) introduced survival analysis into botanical literature in the same volume of the journal *Ecology*. Both papers discussed the potential for ecological applications of survival analysis. Hutchings et al. (1986) summarized and explained available tests for comparing survivorship curves in the context of plant population ecology and seedling predation experiments. To demonstrate an ecological application of survival analysis, Muenchow (1986) used KM survivorship functions and Cox regression models to compare the frequency of pollination events between male and female flowers of the dioecious plant *Clematis lingusticifolia* Nutt. A Cox-Mantel test for differences between KM curves suggested that male flowers were visited more frequently than female flowers. Cox's PH model was used to determine the effect of predictor variables on the frequency of pollination events. Gender and flower density were found to be significant predictors of frequency of pollinator visits.

Further applications of survival analysis in vegetation research occur in several recent studies of tree growth and mortality. He and Alfaro (2000) used survival analysis to describe attack frequency of white pine weevil (*Pissodes strobi*) on young white spruce trees in British Columbia. Non-parametric KM estimates of survival were determined, and a Log-Rank test demonstrated that there a significant difference in survivorship (time to weevil attack) between trees that were pre-defined as either resistant or susceptible based on variables summarizing attack intensity, severity and tree tolerance over an approximately ten year period. Parametric models of hazard and survivorship were also empirically developed, and regression analysis was used to determine which factors were most important in predicting attack frequency. Wyckoff and Clark (2000) compared estimates of tree mortality derived from survival analysis with an alternate Bayesian approach. The two approaches yielded almost identical estimates of annual mortality for *Acer rubrum* L. and *Cornus florida* L.

Lin et al. (2001) used survival analysis to examine the relationship between shade tolerance, growth, and mortality for saplings (diameter at breast height 2-10 cm) of seven tree species in southeastern Texas. Parametric models were used to derive species-specific estimates of mortality, and size and growth were examined as predictor variables. Across species, diameter growth was more important than size in explaining sapling mortality. Survival analysis clearly showed that as shade tolerance increases, the effects of growth on mortality become less important, and that shade tolerance can thus be characterized by the relationship between sapling growth and mortality.

Most recently, Beckage and Clark (2003) used survival analysis to examine the effect of heterogeneity in understory cover, mineral nutrients, and moisture, and their interactions with canopy gaps, on the survival time of first-year seedlings of three coexisting tree species in the southern Appalachians. Kaplan-Meier survival estimates and parametric predictive models were utilized. Seedlings of the most shade-intolerant species, *Liriodendron tulipifera* L. (yellow poplar) had significantly shorter survival times than either shade tolerant *Acer rubrum* L. (red maple), or intermediately tolerant *Quercus rubra* L. (red oak). Survival times for all species were significantly higher under canopy gaps than under full canopy cover; furthermore, understory treatments of vegetation removal and fertilization also had significant effects on survival time/mortality risk. Both Beckage and Clark's (2003) and Lin et al.'s (2001) studies implemented techniques from survival analysis to answer ecological questions about growth and mortality of juvenile trees, integrating several of the ideas presented in this review.

2.4 Summary

The objective of this review is to discuss two important individual-based approaches, growth analysis and survival analysis, that are utilized in the current study for describing sapling growth and mortality. The principal growth response of interest is height growth, which is standardized among saplings of different initial size using RGR. A detailed historical and mathematical account of RGR has been provided prior to an argument supporting the use of RGR for this study of advance regeneration. There is some debate over the appropriateness of this measure for estimating tree growth, where

accumulated woody tissue may result in a negative relationship between RGR and size when a sufficiently wide range of tree sizes are considered. However, little discussion exists in the literature concerning the suitability of this growth measure for established saplings, which are comprised of proportionally less woody tissue than mature trees. It is unlikely that among a relatively narrow range of sapling sizes such as those examined in our study a negative trend between RGR and total size would exist. Furthermore, the influence of accumulated woody material in computations of relative height growth may be more complicated than for growth rates using diameter, volume, or biomass. A survey of recent literature of sapling growth indicates that RGR and alternative standardized and non-standardized rates of whole-plant growth have been utilized.

Conventional estimates of population mortality rates ignore variation in mortality risk among individuals and may underestimate or overestimate mortality. Survival analysis is an individual-based approach that reduces such bias in estimated mortality (Zens and Peart 2003). Furthermore, survival analysis optimally extracts important information from mortality data that form a time series and/or are censored. The data for the current 2.5-year study form a time series, and are largely censored. Clearly, survival analysis provides advantages over other more traditional methods for the current examination of sapling mortality. The most commonly used non-parametric models for describing mortality have been described in detail. These non-parametric models are popular largely because they minimize assumptions regarding the underlying functional form of data. Furthermore, KM estimates of survivorship and Cox estimates of hazard are robust in the sense that they very closely approximate results that would be attained using the correct parametric model for a given data set (Kleinbaum 1996). Current ecological applications of survival analysis demonstrate its potential for use in a wide array of ecological studies. Plant ecologists have recently begun to adopt these methods from other disciplines that have been utilizing survival analysis for decades.

Table 2.1. Example formulations of height, radius, and biomass growth measures used in the recent literature for examining sapling growth.

Measure of sapling size rate of increase	Study
Relative growth rate = $\frac{\ln(\text{Height}_2) - \ln(\text{Height}_1)}{t_2 - t_1}$	Hartvigsen et al. (1995) Williams et al. (1999) Zamora et al. (2001)
Relative growth rate = $\frac{\ln(\text{Biomass}_2) - \ln(\text{Biomass}_1)}{t_2 - t_1}$	DeLucia et al. (1998)
Standardized annual growth = $\frac{\text{Annual height increment}}{\text{Total height}}$	DeLucia et al. (1998)
Standardized annual growth = $\frac{\text{Annual ring width}}{\text{Stem radius}}$	Pacala et al. (1994)
Absolute growth rate = Annual height increment	Good and Good (1972) Coley (1988) Beaudet and Messier (1998) Drobyshev and Nihlgård (2000) Örlander and Karlsson (2000) Claveau et al. (2002)
Absolute growth rate = Annual ring width	Lorimer (1981) Kobe et al. (1995) Kobe (1996) Kobe and Coates (1997) Lin et al. (2001)

CHAPTER 3

DATA COLLECTION

3.1 Study Area

Paired (low and high light regimes associated with the presence or absence of canopy cover), replicated plots of natural regeneration of trembling aspen (*Populus tremuloides* Michx.), balsam fir (*Abies balsamea* (L.) Mill.), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (L.) Mill.) were established in late 1999 or early 2000 in study locations across the Canadian boreal forest. These locations include northwestern Alberta at the Ecosystem Management by Emulating Natural Disturbance (EMEND) study area, eastern Alberta between Calling Lake and Lac La Biche, west-central Manitoba in the Duck Mountains, southeastern Manitoba on the Canadian Shield ('Manitoba Shield'), northeastern Ontario near Iroquois Falls, western Québec near Lac Duparquet and the town of Duparquet, central Québec in the Forêt Montmorency north of Québec city, the Ashuapmushuan Reserve near Chibougamau, and north of Chicoutimi, Québec. Plots were selected to ensure a western, central, and eastern distribution of each species (Figure 3.1). All study locations are within the closed-crown boreal forest. For closed canopy conditions, white spruce regeneration was monitored in mixed hardwood stands of trembling aspen, balsam poplar (*Populus balsamifera* L.), and paper birch (*Betula papyrifera* Marsh.), with some white spruce and balsam fir; black spruce regeneration was monitored in lowland black spruce stands on organic soil; balsam fir regeneration was located within mixed coniferous stands of primarily white spruce and balsam fir, with a small hardwood component; and trembling aspen regeneration was monitored in mixed hardwood stands of predominately aspen and balsam poplar, with some white spruce and fir. Range of mean monthly temperature, and mean annual precipitation, are provided for each location; number of frost-free days and number of growing-degree days are provided for most locations (Table 3.1).

3.2 Field Methods

3.2.1 Plot establishment

Sites of abundant natural regeneration were chosen in adjacent high and low light environments. Only saplings meeting a defined size criteria were chosen in order to avoid censusing mortality associated with early establishment in the first 3-5 years after germination/sprouting, which has been recently investigated (Greene and Johnson 1998, Simard et al. 1998). Size (height) criteria were used since it is impossible to non-destructively age small saplings. The most prominent type of regeneration (sexual or asexual) was selected for each species. Coniferous saplings (sexually regenerated stems) between 0.2 and 1 m, and vegetative aspen root sprouts (suckers) between 0.3 and 2 m in height (since fast-growing aspen suckers can attain heights greater than 1 m in 1-2 years) were selected for monitoring. For advance regeneration of balsam fir and black spruce it was not always possible to distinguish between sexually regenerated saplings and vegetative layers without using intrusive methods. An attempt was made to select the same type of regeneration for permanent plot replicates of a given species in each study location (eg. balsam fir sites in gaps and shaded understory within a given study location appeared similar in their predominant modes of regeneration).

To examine the effect of light environment on saplings, natural regeneration was selected in low light environments under full canopy closure, and in high light environments under natural canopy gaps (fir), in clearcuts (aspen), in carefully harvested sites (black spruce), or in disturbed areas such as roadsides and abandoned gravel extraction pits (white spruce). The type of high light environment for each species (natural gap, clearcut, careful harvest, disturbed area) was chosen to ensure that sufficient natural regeneration could be located in open canopy conditions for each study location. With the exception of balsam fir, the occurrence of *natural canopy gaps* and associated densities of saplings within gaps were too low to obtain adequate sample sizes of natural regeneration within the specified size range; therefore, open canopy conditions resulting from anthropogenic disturbance were utilized for remaining species. In order to compare growth and mortality among regions, sites replicates were located on common soil

deposit types (glacial till soils for trembling aspen, balsam fir and white spruce, and organic soils for black spruce), and in stands of similar composition for each species studied. Adjacent high and low light environment sites were located as close to one another as possible to minimize site variation other than that of light availability between the defined light environments. Example photographs of open and closed canopy plots of natural regeneration of each species are provided in Appendix 1.

Based on conservative estimates of sapling mortality rates of 1% per year, an initial sample size of approximately 500 saplings per species per region was selected, to ensure a sample size of at least 30 dead individuals for each region and species at the end of a 5-6 year study period. Half of these saplings were located in low light environments, and the other half in high light environments. Three or four (in some cases more) paired (low and high light environment) plots of approximately 60-90 saplings were replicated for each species within each region (Table 3.2).

3.2.2 Sapling measurements

Mortality and morphological measurements

For each individual sapling, mortality was surveyed in the spring and fall of every year, beginning at site establishment in the spring 2000 up to the fall of 2002 (some study locations began monitoring mortality in the fall of 1999). An individual was considered dead if it had lost all leaf tissue or the needles present were brown, and if gentle surface scraping of the outer bark of the main stem revealed no living green tissue underneath. Growth and morphological variables were measured at the end of each growing season (in some cases, in particular for aspen, height was measured also in the spring to monitor changes in height resulting from winter herbivory and dieback). Dimensions recorded include height, length of the leader branch and length of the longest first-order lateral branch subtending the leader (for coniferous species), depth of live crown, and basal diameter. Measurements were made to the nearest 0.5 cm, with the exception of basal diameter, which was measured to the nearest 0.1 or 0.01 cm. Height was measured as the length of the main stem from ground level to the highest live point on the tree, which was defined as the highest point at which a leaf was attached to the stem, or the highest live

bud. Saplings growing at an angle were straightened for height measurements and total stem 'length' rather than height was measured for individuals growing more or less prostrate to the ground; overall sapling condition was described.

For coniferous species, the length of the leader shoot (leader branch) from the previous year's node (end of previous year's growth) was measured. Similarly, the longest first-order lateral shoot (lateral branch) radiating from the previous year's node was measured. In some cases, on damaged or badly suppressed trees, there was no leader or lateral branch growth from the most recent node during the growing season. In this case leader and/or lateral branch lengths were recorded as zero. The depth of live crown was measured as the distance from the lowest to highest live point on a sapling. The basal diameter was measured at ground level, as close to the root collar as possible, with Vernier calipers. In order to examine growth and morphological response across saplings of various size and age, standardized response variables of relative height and diameter growth, leader to lateral branch ratio (L:B ratio), and live crown ratio were derived from these measurements for data analysis. For coniferous species, qualitative data describing sapling form (conical, irregular, umbrella-shaped), crown form (symmetric, asymmetric) and direction of crown growth (if asymmetrical) were also collected.

Light measurements

Individual sapling-level measures of light availability were collected for all study locations at some point during the study period. The relative amount of photosynthetic photon flux density (PPFD) in the 400 to 700 nm waveband ($\mu\text{mol/s/m}^2$) available at the apical bud and lowest live branch of each sapling was estimated. PPFD at the apex and lowest live portion of each sapling was determined using hand-held quantum radiation sensors (LI-190SA, Li-Cor Inc.) in conjunction with a light meter (LI-250 light meter, Li-Cor Inc.) or AcuPAR ceptometers (Decagon Devices Inc.). These measures were compared to above-canopy PPFD to estimate percent of above-canopy PPFD reaching each sapling. PPFD measurements were made on overcast days to estimate diffuse light availability (Messier and Puttonen 1995; Parent and Messier 1996). For some study locations where overcast days were limited, an alternative method was used: the average

of two light readings, one before and one after solar noon, was used to measure light availability at each sapling apex (see review by Lieffers et al. 1999).

For both techniques the radiation sensor was held stationary for 9-15 seconds at the apex of each sapling (methodology and equipment varied slightly among study locations), over which time the PPFD was averaged and provided by the light meter output device. For each measurement, the sensor reading and the time at the beginning and end of each PPFD reading were recorded manually on worksheets, or for readings taken with AccuPAR ceptometers, manually downloaded at the completion of light measurements for a given site. To obtain measures of %PPFD (a measure of the PPFD reaching a given sapling relative to maximum above-canopy light availability), above-canopy PPFD (baseline PPFD) was measured with a quantum sensor and data logger (LI-1400, Li-Cor Inc.; Campbell Scientific CR21 Micrologger) in the closest adjacent clearing receiving full light. Data loggers were programmed to monitor and average PPFD over a 30-second or one-minute interval. A digital watch was correlated with the clock of the data logger to ensure that the timed readings from the hand-held sensors (measuring PPFD for each sapling) would correlate with the PPFD readings collected by the data logger. The following equation was used derive %PPFD estimates:

$$\% \text{PPFD} = \frac{\text{Sapling PPFD}}{\text{Baseline PPFD}} \cdot 100\% \quad [3.1]$$

where sapling PPFD is the 9-15 second averaged reading from either the apex, or lowest live branches of the tree, and baseline PPFD is the corresponding reading from the data logger. The data logger value (averaged over a 30-second or one-minute interval) in which greater than half of the time elapsed for the sapling reading (averaged over a 9-15 second interval) fell, was chosen as the corresponding reading for full light conditions. For consistency across study locations, light measurements taken at the apex of each sapling but not at the lower branches were used in analyses. Mean %PPFD for species/study location/canopy combination are presented in Table 3.3.

Additional sapling-level measures

Monitored mortality, and measures of growth, morphology and light availability were in some cases (for some years, in some study locations) supplemented with additional information regarding overall sapling vigour. In addition to light, factors varying at the individual level that were considered most influential include herbivory by mammals, insect herbivory, pathogen damage, mechanical damage, competition (for both light and other resources), microtopography, and substrate. Data describing mammalian herbivory of each sapling was either indicated when present or ranked ordinally from 0-3, where 0 corresponds to no browse, 1 corresponds to mild browse of lateral branches, 2 corresponds to leader loss, and 3 corresponds to severe herbivory. Insect and pathogen damage were recorded as percent of leaf loss to the nearest 5%. Mechanical wounds were described qualitatively, and by length and width of trunk wound or number of broken branches. Microtopography immediately surrounding each sapling was recorded as flat, slope, mound, or depression, and surface substrate was recorded as organic, mineral, or coarse woody debris. Competition by surrounding vegetation was estimated as percent cover of overtopping trees and shrubs, and surrounding herbaceous plants and small seedlings and saplings. Exact methods for these vegetation estimates varied among study locations where this information was collected. For sites in Duck Mountains, MB, 1 m² circular quadrats were used to completely enumerate to species level all competing vegetation less than 2 m in height surrounding each sapling. Percent canopy and upper sub-canopy cover were visually estimated. Because of the large sample sizes requiring monitoring each year in each study location, the collection of these additional data describing sapling vigour and immediate surroundings was constrained by time. These data were not used beyond exploratory analyses.

3.3.3 Site-level measurements

To assess growing conditions at each plot, important site-level variables were measured for use in exploratory analyses and interpretation of results. The type of data collected and methodology used for site description varied among study locations. Stand measurements collected include elevation, slope, aspect, average canopy height, canopy

basal area, a brief soil description (a description of horizons, texture, drainage class, % coarse fragments), and a description of the understory vegetation present.

Average canopy height (m) was estimated by measuring, or visually estimating, the height for at least three trees greater than 5 m in height in the centre of the plot; in some study locations all tree heights in a site were estimated to derive average canopy height. Measurements made using a clinometer were derived by subtracting the reading at the bottom of the tree from the reading at the top (readings in percent), and multiplying this by the distance from the tree at which measurements were made. Basal area (m^2/ha) was computed using a prism sweep, or using the following calculation to obtain the basal area for all trees in a plot:

$$\text{Basal area} = (\pi/40000) [(\Sigma \text{dbh}^2)/\text{Area of plot}] \quad [3.2]$$

where $\pi/40000$ corrects diameter at breast height (dbh) measures (cm) to radius (m), and the area of the plot is in hectares (10000m^2). Therefore, basal area is in units of m^2/ha . One or more small soil pits were dug (until the B horizon was reached) at the centre of each plot and a brief description of soil horizons was made using the Canadian System of Soil Classification. Percent coarse fragment (using wire mesh sieves of 2mm) was the only substrate description consistently made for most study locations, to provide a basic estimate of drainage for each permanent plot. Vegetation cover for plots was described using cover class values, or using a series of 1m^2 quadrats to estimate % cover by species. Cover class values or % cover values of vegetation less than 2 m in height were estimated either to species level, or with species pooled and a list of species present. Collection of plot-level measures varied among study locations; nonetheless, measures provide some insight into growing conditions of each permanent plot and are useful for interpretation of results, and may be of use in future studies. Site descriptions of each permanent plot including canopy and soil characteristics are presented in Appendix 2.

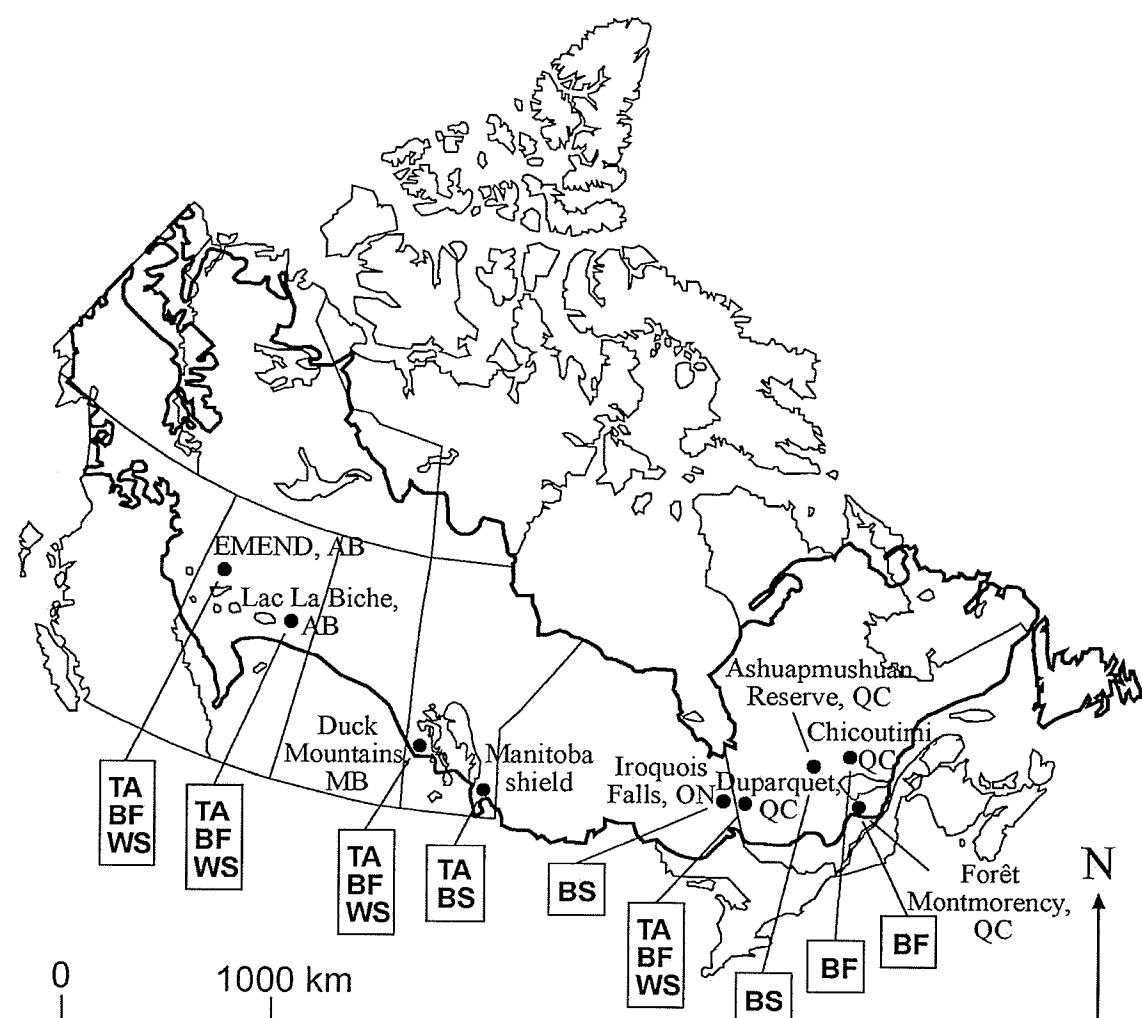


Figure 3.1. Locations of permanent monitoring sites for natural regeneration of trembling aspen (TA), balsam fir (BF), white spruce (WS), and black spruce (BS) in boreal forests of Alberta, Manitoba, Ontario, and Québec. Plots were established in the spring of 2000 except for Ontario and Chicoutimi sites, which were established in the fall of 1999. The broadly defined North American boreal forest is delineated by a bold line.

Table 3.1. Environment Canada climate normals (1971-2000) and more recent summary climate information from meteorological stations nearest to each of the study locations.

Study location	Location of weather station	Source of climate data	Census period	Range of mean monthly temperature (°C)		Mean annual precipitation (mm)	Mean number of frost-free days	Mean number of growing degree days >5°C
				January or February	July or August			
EMEND, AB	EMEND, AB	EMEND	2000-2001	-12.2	15.5	387.0 (from 2000)		
Lac La Biche, AB	Lac La Biche and Calling Lake, AB	Environment Canada	1997-2002; 1971-2000*	-18.0 (1997-2000, Calling Lake, AB)	16.6 (1997-2000, Calling Lake, AB)	397.2 (1997-2000, Calling Lake, AB)	145.8 (1971-2000, Calling Lake, AB)	1235.4 (1971-2000, Calling Lake, AB)
Duck Mountains, MB	Swan River and Boggy Creek, MB	Environment Canada	1997-2002; 1971-2000	-19.9 (1996-2001, Swan River, MB)	17.8 (1996-2001, Swan River, MB)	539.3 (1997-2000, Boggy Creek, MB)	161.0 (1971-2000, Swan River, MB)	1575.4 (1971-2000, Swan River, MB)
Manitoba Shield, MB	Pinawa, MB	Environment Canada	1997-2002; 1971-2000	-15.6 (1997-2002)	19.9 (1997-2002)	581.6 (1997-2001)	170.6 (1971-2000)	1690.6 (1971-2000)
Duparquet, QC	Rouyn-Noranda, Val-d'Or, QC	Environment Canada	1997-2002; 1971-2000	-17.2 (1971-2000, Val-d'Or, QC)	17.2 (1971-2000, Val-d'Or, QC)	914.8 (1971-2000, Val-d'Or, QC)	158.1 (1971-2000, Val-d'Or, QC)	1387.0 (1971-2000, Val-d'Or)
Iroquois Falls, ON	Timmins, ON	Environment Canada	1997-2002; 1971-2000	-17.5 (1971-2000)	17.4 (1971-2000)	831.3 (1971-2000)	154.8 (1971-2000)	1409.9 (1971-2000)
Forêt Montmorency, QC	Forêt Montmorency, QC	Forêt Montmorency, QC	1999-2001	-15.4	14.4	1376.8		
Ashuapmushuan Reserve, QC	Ashuapmushuan Reserve, QC	Ministry of Natural Resources, QC	1997-2002	-16.7	16.4	924.5 (2001-2002)		
Chicoutimi, QC	Chicoutimi, QC	On location	1998-2002	-18.5	15.9	1856.2		

* 1971-2000 climate normals available online at: www.climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html

Table 3.2. Number of saplings of each species that were monitored in each study location, broken down by canopy treatment and permanent plot. Ontario sites of black spruce regeneration and Chicoutimi sites of balsam fir regeneration were established in the fall of 1999. All other sites were established in the spring of 2000.

Study Location	Canopy treatment	SPECIES					
		ASPEN		BALSAM FIR		WHITE SPRUCE	
		Permanent plot name	Number of saplings	Permanent plot name	Number of saplings	Permanent plot name	Number of saplings
EMEND, AB	open	EMEND13	63	EMEND15	63	EMEND19	62
		EMEND14	62	EMEND16	63	EMEND20	62
		EMEND22	62	EMEND17	62	EMEND21	63
		EMEND23	63	EMEND18	62	EMEND24	63
	closed	Total	250	Total	250	Total	250
		EMEND13	63	EMEND15	63	EMEND19	62
		EMEND14	62	EMEND16	63	EMEND20	62
		EMEND22	62	EMEND17	62	EMEND21	63
Lac La Biche, AB	open	EMEND23	63	EMEND18	62	EMEND24	63
		LLB7	62	LLB1	62	LLB3	62
		LLB8	62	LLB2	63	LLB4	62
		LLB9	63	LLB5	62	LLB11	63
	closed	LLB10	62	LLB6	63	LLB12	63
		Total	249	Total	250	Total	250
		LLB7	62	LLB1	62	LLB3	62
		LLB8	62	LLB2	63	LLB4	62
Duck Mountains, MB	open	LLB9	63	LLB5	62	LLB11	63
		LLB10	38	LLB6	63	LLB12	63
		Total	225	Total	250	Total	250
		Hwy 366	90	Laurie Lake	90	Gravel pit	90
	closed	Hwy 83S	90	ast Blue Lal	90	Wetlands	88
		Hwy 83N	89	Childs Lake	90	Interp trail	86
		Total	269	Total	270	Total	264
		Hwy 366	87	Laurie Lake	90	Childs	91
Manitoba shield, MB	open	Hwy 83S	87	ast Blue Lal	90	HWY 366N	90
		Hwy 83N	90	Childs Lake	90	366 boundar	89
		Total	264	Total	270	Total	270
		2	108			1	95
	closed	3	91			2	110
		Total	199			3	90
		2	82			1	90
		3	93			2	95
Iroquois Falls, ON	open	Total	175			3	90
						Total	275
						Total	290
	closed					19-N	76
						11	76
						19-S	70
						16	70
						Total	292

Continued on next page.

Table 3.2 continued.

Study Location	Canopy treatment	SPECIES					
		ASPEN		BALSAM FIR		WHITE SPRUCE	
		Permanent plot name	Number of saplings	Permanent plot name	Number of saplings	Permanent plot name	Number of saplings
Duparquet, QC	open	1	103	4	161	4	129
		2	80	5	76	26	179
		4	94	150	71	28	40
		8	90	17	84		
		9	90	23	30		
				24	42		
				25	126		
	closed			30	36		
		Total	457	Total	626	Total	348
		3	76	6	81	11	65
Forêt Montmorency, QC	open	18	78	11	60	22	32
		19	59	12	92	27	184
		22	102	15f	87		
		31	47	16	92		
				29	81		
		Total	362	Total	493	Total	281
	closed						
		1	62				
		2	62				
		3	62				
Ashuapmushuan Reserve, QC	open	4	62				
				Total	248		
	closed						
		1	62				
		2	62				
		3	62				
Chicoutimi, QC	open	4	62				
				Total	248		
	closed						
	Overall	2700	Overall	3416	Overall	2163	Overall

Table 3.3. Mean %PPFD for each species/study location/canopy combination. Values are derived from saplings alive at the end of the study period. Mean %PPFD is significantly higher under open canopy than closed canopy conditions for all cases except for aspen and white spruce in Duparquet QC. t-tests were not performed for Manitoba Shield (aspen) and Chicoutimi (fir).

		ASPEN				BALSAM FIR				BLACK SPRUCE				WHITE SPRUCE							
		# ind		n=#ind		n=#plots		n=#ind		n=#plots		n=#ind		n=#plots		n=#ind		n=#plots			
		# ind	# plots	Mean %PPFD	sd	P	# ind	# plots	Mean %PPFD	sd	P	# ind	# plots	Mean %PPFD	sd	P	# plots	Mean %PPFD	sd	P	
EMEND, AB	open	238	4	68.81	8.52	0.0001	228	4	23.93	12.57	0.0372						250	4	41.95	17.01	0.0021
	closed	156	4	34.03	10.92		236	4	10.61	4.99							250	4	14.45	7.89	
Lac La Biche, AB	open	220	4	71.91	19.86	0.0027	250	4	14.32	8.77	0.0305						250	4	48.96	18.94	0.0062
	closed	202	4	26.76	9.62		248	4	8.88	4.75							245	4	21.13	12.66	
Duck Mountains, MB	open	208	3	69.66	30.13	0.0071	260	3	19.29	7.97	0.0044						264	3	67.19	15.90	0.0028
	closed	216	3	15.44	5.64		269	3	12.63	5.04							266	3	10.22	6.56	
Manitoba shield, MB	open	71	2	32.21	9.72	-										295	3	37.64	10.53	0.0012	
	closed	20	1	2.82	2.18											274	3	9.79	4.74		
Iroquois Falls, ON	open															288	4	46.5	19.32	0.0016	
	closed															275	4	10.84	4.58		
Duparquet, QC	open	102	5	71.95	21.49	-											195	2	87.80	18.22	0.0592
	closed	90	5	43.96	22.57												204	2	4.65	2.38	
Forêt Montmorency, QC	open																240	4	40.67	20.34	<0.0001
	closed																230	4	18.44	10.56	
Ashuapmushuan Reserve, QC	open																246	4	82.55	17.22	<0.0001
	closed																237	4	12.29	4.16	
Chicoutimi, QC	open																65	1	30.77	9.30	-
	closed																159	3	8.82	3.23	

CHAPTER 4

SAPLING MORTALITY IN CONTRASTING LIGHT ENVIRONMENTS FOR FOUR PREDOMINANT TREE SPECIES ACROSS THE CANADIAN BOREAL FOREST

4.1 Introduction

Survival analysis includes statistical analyses in which the response variable of interest is time until event occurrence (Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996, He and Alfaro 2000). This analytical approach is well suited to the present study of sapling mortality because it provides an individual-level assessment of mortality risk. Furthermore, the data form a time series, and are largely censored making them well suited to survival analysis. The majority of the saplings monitored for this study have censused survival times: their exact time until death is unknown as a result of the study period ending before death. Therefore, for each sapling, our data describe either time until death or time until censorship. For a sufficiently large sample size, conventional estimates of population mortality rates may yet provide useful estimates of mortality at the population rather than individual level. Moreover, conventional mortality rates for our data will lend themselves to straightforward comparison with relevant previous studies of the examined species.

The main objective of this chapter is to characterize the mortality of established natural regeneration of predominant boreal tree species including white spruce (*Picea glauca* (Moench) Voss), black spruce (*Picea mariana* (Mill.) BSP), balsam fir (*Abies balsamea* (L.)), and trembling aspen (*Populus tremuloides* Michx.) in different light environments associated with the presence or absence of canopy cover, across the Canadian boreal forest over an approximately 2.5-year period. The specific goals are to: (1) ascertain estimates of population mortality rates; (2) explicate any interspecific differences in sapling mortality; (3) summarize and explain any differential mortality across geographic regions; (4) determine the season of mortality; (5) compare species-specific population-level mortality rates and population-level survival times in open and closed canopy environments; and (6) determine the predictive ability of light, size, and crown morphology in explaining individual-level variation in mortality risk.

4.2 Analytical methods

4.2.1 Finite mortality rates

Estimation of mortality rates

If a sufficiently large sample from a population is monitored over a long period, fundamental rates such as mortality are often assumed to be characteristic for the population, despite heterogeneity within a population (Sheil and May 1996). In this study the populations are saplings (0.2-2m in height) of a given species growing under either full or partial/absent canopy closure. Species-specific finite annual mortality rates were established for open and closed canopy conditions for each region (study location) using Equation 4.1. Mortality rates were determined for each permanent plot, and also for data pooled from all plots within a given canopy regime. Trembling aspen and balsam fir were the only two species to exhibit appreciable mortality over the course of the study; seasonal mortality rates were determined for the growing season (June-September) and winter months (October-May) for these species. Data from the full study period were used for the derivation of each mortality rate; all rates were adjusted to a common time base of one year, using the following calculation:

$$\text{Adjusted finite mortality rate} = 1 - \exp \left[\left(\ln \left(\frac{\# \text{ alive at } t = x}{\# \text{ alive at } t = 0} \right) \right) \left(\frac{1 \text{ year}}{x \text{ years}} \right) \right] \quad [4.1]$$

where x is the time interval considered, ($\# \text{ alive at } t = x / \# \text{ alive at } t = 0$) is the finite survival rate for the time interval, and the natural log of the finite survival rate is the instantaneous mortality rate. Finite mortality rates can be rendered additive by converting them back to instantaneous mortality rates.

Comparison of mortality rates

Several discrete analyses were performed to compare mortality rates among species, among study locations, between light treatments, and between seasons. A two-way factorial design (Analysis of Variance) comparing mortality rates among species and

canopy regimes suggested a significant interaction between species and canopy treatment (open versus closed canopy conditions). Therefore, species comparisons were made separately for each canopy treatment. One-way Analysis of Variance (ANOVA) was used to test for significant differences in overall mortality rates among species: two analyses, one for open canopy conditions and one for closed canopy conditions were performed. The variation examined was that of species-specific mortality rates calculated for each study location, within which permanent plots were pooled to give an overall mortality rate for each light treatment. Plot-level mortality rates were not used for this ANOVA because of the natural hierarchy in the dataset: each study location is geographically very distant from others and has its own permanent plots. Therefore, examining all plots across all study locations for ANOVA of species-specific mortality would overlook this hierarchy and fail to distinguish between inter-replicate variation and inter-regional variation. Therefore, for the purposes of this chapter, plot replicates were pooled for each study location/canopy treatment combination to provide overall mortality rates for each study location and light treatment. Scheffé, Bonferroni and least significance difference multiple-comparison tests were used to establish where significant differences in mortality rates exist among the four examined species (Data Desk 6.1 for the MacIntosh, Data Description Inc.).

ANOVA was also used to examine differences in species-specific mortality rates among study locations. The variance examined was that of site-level mortality rates for each study location. Multiple-comparison tests were used to determine where differences in species-specific rates existed among study locations. Both Scheffé and Bonferroni tests led to the same results, which were more conservative than results using the least significant difference approach. Specific levels of significance for each significant comparison using Scheffé tests are reported.

For each species, two-tailed t-tests (assuming equal variance) comparing mean mortality rate between high and low light treatments were performed for each study location. For each of trembling aspen and balsam fir, the only two species to demonstrate appreciable mortality over the study period, a two-factor model was used to examine differences in mortality between open and closed canopy sites, and summer and winter mortality, for each study location. There were no significant interactions between canopy

treatment and season for any of the study locations, permitting plain interpretation of results. These two-way analyses were performed using plot-level mortality rates within each light treatment for each study location. Separate mortality rates were calculated for the growing season (June-September), and winter months (October-May), and standardized to one year. ANOVA, multiple-comparison tests, and T-tests were performed using Data Desk 6.1 for the MacIntosh (Data Description Inc.).

4.2.2 Survival analysis

Kaplan-Meier survivorship estimates for a group of saplings

The survival function $S(t)$ is the probability that an individual in a population survives past time t (Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996; Beckage and Clark 2003). The response variable is survival time (T), a continuous random variable representing in this study time from study onset at which sapling death occurs. The Kaplan-Meier (KM) or product-limit survivorship function is a nonparametric model that estimates for a population the probability of survival past a given time t (Kaplan and Meier 1958, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996, Krebs 1999). KM survival probabilities for each time t are determined according to the following equation:

$$\hat{S}(t) = \prod_{i=1}^k \left(1 - \frac{d_i}{n_i}\right) \quad [4.2]$$

where $\hat{S}(t)$ (from this point onward in this chapter referred to as $S(t)$) is the KM estimate of probability of survival past time t ; k is the number of time interval checks for possible deaths for a given time t ; d_i is the number of deaths recorded for time interval i ; and n_i is the number of individuals alive at the beginning of time interval i (modified from Kaplan and Meier 1958, Parmar and Machin 1995, Krebs 1999). These estimated survival rates differ from simple calculations of finite survival rate (number alive at end of study/number alive at beginning of study) because they are a product of survival probabilities for all previous times at which mortality was censused; and because the

number of saplings at risk (saplings that are alive as far as we know just up to the time of census) at the beginning of each time interval is considered, allowing for the analysis of censored information. If no mortality or censoring occurs until time t , the KM survivorship estimate reduces to simple finite survival (proportion of survivors) (Kaplan and Meier 1958). The resulting KM curve is a step function that changes values only at observation times when deaths (not censorship) were noted to occur, and is discontinuous at these points (Kaplan and Meier 1958).

KM survivorship curves were determined for aspen and fir - the only two species demonstrating appreciable mortality over the study period. Separate curves were derived for each study location and for open and closed canopy conditions. A Log-Rank test was used for within-species comparisons of KM curves across study locations, and to compare survival under low and high light within each study location. In addition, median survival times (time at which 50% cumulative mortality occurs) were estimated from KM curves.

Cox's Proportional Hazards

The hazard function is an instantaneous rate of event occurrence and is inversely related to the survivorship function (Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996). Cox's Proportional Hazards (PH) nonparametric regression model estimates a sapling's hazard based on both the baseline hazard (the population hazard prior to consideration of any individual-level predictor variables) for the sample and also on the sapling's specific values for n factor variables (Cox 1972, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996). Cox's Proportional Hazards (PH) nonparametric model was used to predict the hazard ratio for saplings receiving different relative light at their apex (%PPFD), and with different initial size (height, diameter) and crown morphology (live crown ratio). The general form for the Cox proportional hazards model is:

$$h(t, \mathbf{X}) = h_0(t) \exp \left[\sum_{i=1}^n B_i X_i \right] \quad [4.3]$$

where $h(t, \mathbf{X})$ is the Cox hazard, which is a function of both time and the n predictor variables being used to predict an individual's hazard (denoted by \mathbf{X}); $h_0(t)$ is the baseline hazard function, which is inversely related to $S(t)$, and is an instantaneous probability of death per unit time; and B_1, B_2, \dots, B_n are the coefficients for the n predictor variables X_1, X_2, \dots, X_n respectively (modified from Cox 1972, Schoenfeld 1980, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996).

KM survivorship curves provide the same survival information for any individual within a group of individuals used to derive a given KM curve; in this case the groups were saplings growing in either "open canopy" or "closed canopy" conditions. Cox hazard provides an estimate of mortality risk for each sapling, distinguished from other saplings by its specific values for the set of predictor variables. Cox hazard models were used to determine the hazard ratio (HR) for any two saplings. The HR is a measure of the relative mortality risk of two individuals and is derived by dividing the (Cox) hazard for one individual by the hazard for a different individual, where the two individuals being compared are distinguished by their values for the set of predictor variables (Kleinbaum 1996). The baseline hazard functions for each individual Cox hazard will cancel out upon division when computing the HR, consequently the baseline hazard function does not need to be specified to estimate HR (Cox 1972, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996).

$\text{Exp}(B_j)$ for a single predictor variable X is the predicted change in hazard for a unit increase in the variable, and is the hazard ratio for two individuals differing in their value for a single predictor variable by one unit. Therefore, $\text{Exp}(B_j)$ summarizes the effect of a predictor variable on mortality risk. Similarly it can be shown that if more than one variable is entered into the model, the hazard ratio for a given variable remains $\text{exp}(B_j)$ once B_j has been adjusted for the effects of other variables (Kleinbaum 1996).

The specific variables entered in a forward selection procedure into the model for each species/study location/light treatment combination include %PPFD, initial height, diameter, and live crown ratio. Growth was not used as a predictor variable because some individuals died before the end of the first study season before annual growth rates could be estimated. Percent PPFD was examined separately from morphological variables, resulting in two Cox models for each treatment combination: one predicting hazard from

light availability and one predicting hazard from morphological variables. L:B measures were missing (as a result of either a leader or lateral branch of zero) for a large proportion of the balsam fir saplings that died, therefore, L:B ratio was not used as a predictor variable. An ordinal measure of herbivory was also investigated as a predictor of mortality risk for some study locations, however, this derived variable did not predict hazard.

For valid interpretation of variable effects in a Cox model the underlying assumption of the model, which states that the hazard for one individual is proportional to the hazard for any other individual where the hazard ratio is independent of time, must be met (Cox 1972, Muenchow 1986, Parmar and Machin 1995, Kleinbaum 1996). A graphical approach, examining $-\ln(-\ln S(t))$ over time for individuals with different values of predictor variables was utilized. These graphs were generated many times over for different models and values of predictor variables. The log-log transformed survival curves were approximately parallel over time in all cases, meeting the proportional hazards assumption. All survival analysis was performed using SPSS 11.0 for Macintosh (SPSS Inc.).

4.3 Results

4.3.1 Survival tables

For each species and study location, the number of live saplings within each permanent plot at each census period was counted, and also tallied for each light environment (Tables 4.1-4.4). Natural regeneration of trembling aspen demonstrate appreciable mortality in both open (post-harvest) and closed canopy plots in all geographic regions (finite survival over the entire study period = $1688/2700 = 62.5\%$) (Table 4.1). In contrast, advance regeneration of coniferous species exhibit relatively little mortality over the 2.5-year study period (Tables 4.2-4.4). Of the coniferous species balsam fir saplings in both closed and open (gap) canopy sites demonstrate the highest overall mortality (finite survival = $3016/3155 = 95.6\%$) (Table 4.2). Nonetheless in every study location but Chicoutimi, QC, there were some balsam fir plots in which no

mortality occurred. In open canopy sites near Lac La Biche, AB, none of the monitored fir saplings died, and in closed canopy sites in Duck Mountains, MB, only one sapling died over the study period. Compared with balsam fir, considerably less mortality occurred for both spruce species. The overall finite survival for black spruce advance regeneration over 2.5 years is $1614/1648 = 97.9\%$ (Table 4.3), and for white spruce saplings is $2126/2163 = 98.3\%$ (Table 4.4). Some white spruce mortality occurred in sites in both Manitoba and Québec, but not in Alberta. In the Manitoba sites, mortality only occurred under closed canopy conditions and in Québec sites mortality occurred within both closed canopy and disturbed open canopy sites.

4.3.2 Finite mortality rates

Mortality rates compared across species

All finite mortality rates are in units of proportion dead/year. There is a significant difference in finite mortality rates among species for both open canopy ($P=0.030$) and closed canopy ($P=0.040$) conditions (Figure 4.1). Multiple-comparison tests show that trembling aspen mortality is significantly higher than that observed for any of the coniferous species, but only when using the least conservative multiple-comparison test (least significant difference). Variation in species-specific mortality rates is appreciable among study locations. Of the coniferous species, balsam fir exhibits the highest mortality rates, followed by black spruce and white spruce, however, differences are not statistically different.

Mortality rates compared across study locations (geographic regions)

Aspen mortality rates for the overall study period range from 2.16% in open canopy EMEND plots in Alberta, to 61.86% in closed plots in Manitoba Shield, MB, and are significantly different among study locations for open canopy ($P<0.0001$) and closed canopy ($P<0.0001$) treatments (Table 4.5). The highest aspen mortality rates occur in both open and closed canopy plots in Manitoba Shield (36.75% and 61.86% in open and closed canopy plots respectively), and in open canopy plots in Duparquet, QC (42.03%). Mortality rates in open canopy aspen plots in Manitoba Shield are significantly higher

than those for Duck Mountains, MB ($P=0.014$), EMEND, AB ($P<0.001$), and Lac La Biche, AB ($P=0.002$). Similarly, mortality rates in open canopy aspen plots in Duparquet are significantly higher than those for Duck Mountains ($P<0.001$), EMEND ($P<0.0001$), and Lac La Biche ($P<0.0001$). Mortality rates in closed canopy plots of aspen regeneration in Manitoba Shield are significantly higher than for all other study locations (EMEND $P=0.002$, Lac La Biche $P<0.0001$, Duck Mountains $P<0.001$, Duparquet $P=0.001$).

Balsam fir mortality rates range from 0% in open canopy plots in Lac La Biche, AB, to 6.73% in closed canopy plots in Chicoutimi, QC, and are significantly different among study locations for closed canopy conditions ($P=0.005$) (Table 4.5). Multiple-comparison tests show that this difference results from the higher overall mortality rates of balsam fir saplings in Chicoutimi as compared with Lac La Biche ($P=0.023$), Duck Mountains, MB ($P=0.029$), and Duparquet, QC ($P=0.060$). Black spruce mortality rates range from 0 to 2.63%, and are just significantly different at the 5% level for open canopy plots ($P=0.045$), however, conservative a posteriori tests show no significant differences among any study locations. Mortality rates for white spruce are the lowest of the coniferous species, ranging from 0 to 2.20% within a given canopy regime of a study location (Table 4.5). Mortality rates are significantly different among study locations for open canopy ($P=0.041$) and closed canopy ($P=0.036$) treatments. For closed canopy conditions the difference is between EMEND, AB and Duparquet ($P=0.040$). Mortality rates for spruce species are consistently low across all study locations.

Although there are significant differences among study locations, differences result from a few exceptions; there is consistency among most of the study locations. The few study locations that exhibit significantly different mortality rates have uncommon plot conditions compared to most study locations. The first of these exceptions are the low light treatment replicates of aspen regeneration in Manitoba Shield plots. Light availability under closed canopy conditions in these plots was much lower than that found in other study locations, as a result of an appreciable balsam fir component in the canopy; aspen regeneration growing in shaded understory conditions in other study locations was located under hardwood canopy. Balsam fir regeneration in Chicoutimi, QC also differs in mortality from plots of other study locations. The average height of

monitored saplings in closed canopy Chicoutimi plots is somewhat less than that found in other study locations, perhaps resulting in slightly higher overall mortality. Higher mortality rates in open canopy plots of aspen regeneration in Duparquet, QC as compared with other study locations is likely a reflection of differences in stem density and the level of self-thinning in plots of the different study locations.

Mortality rates compared between light environments, and between seasons

The only significant differences in seasonal mortality rates for aspen occur in Manitoba Shield, MB and Duparquet, QC (Figure 4.2 A). Mortality rates over the growing season are significantly higher than over the winter months for both study locations ($P=0.019$ and 0.039 for Manitoba Shield and Duparquet respectively). These two study locations exhibited the highest overall mortality rates; as cumulative aspen mortality increases over time a similar trend of higher mortality over the growing season may also become apparent in the Alberta and Duck Mountains, MB plots.

The only significant differences between mortality rates in open and closed canopy plots occurs in EMEND, AB plots ($P=0.001$), where aspen growing in closed canopy plots demonstrates higher mortality rates, and in Duparquet, QC plots ($P=0.002$) where aspen growing in open canopy post-harvest conditions exhibits higher mortality. There are no significant interactions between canopy treatment and season of mortality for any of the study locations.

Balsam fir mortality rates were significantly higher in summer than winter months only for Forêt Montmorency, QC ($P=0.005$) (Figure 4.2 B). Although mortality rates appear to be higher in closed canopy conditions than in canopy gaps for the easternmost Québec plots, the only significant difference in mortality rates between the two light environments occurs in the Duck Mountains plots in Manitoba, where rates are higher in plots with small canopy gaps ($P=0.028$). Again, there are no significant interactions between canopy treatment and season of mortality for any of the study locations.

4.3.3 Survival analysis

Trembling aspen

KM estimated survival functions for aspen regeneration are significantly different among regional study locations in both high light (Log-Rank statistic=590.0; P<0.0001) and low light environments (Log-Rank statistic=412.6; P<0.0001) (Figure 4.3). Relatively infrequent monitoring of mortality (twice annually) results in long plateaus and large steps in KM curves for aspen regeneration, which exhibited substantial mortality over the study period. After three growing seasons the probability of survival for aspen regeneration in open plots is lower for Duparquet, QC and Manitoba Shield, MB than for other regions. This mirrors the higher overall finite mortality rates determined for open conditions in these locations. The probability of survival decreases substantially at only 12 months for Duparquet, but after 24 months for Manitoba Shield. Although these two study locations exhibited similar high mortality in open conditions, the survival time for Duparquet plots was shorter. The Duparquet plots experienced high mortality over the first winter following plot establishment for open canopy sites, whereas Manitoba Shield plots exhibit high mortality over the third growing season. Apart from these two regions, survival curves are consistent among regions for aspen regeneration in post-harvest conditions. Under closed canopy conditions, the survival function decreases most dramatically in Manitoba Shield plots (again, a reflection of low light conditions resulting from a prominent balsam fir component in the canopy of these plots), but otherwise functions are similar across regions. Median survival time (time at which 50% of individuals have died) for most KM curves, with the exception of Manitoba Shield, and Duparquet locations, are slightly greater than two years.

There are significant differences between KM curves for high and low light environments for aspen regeneration in EMEND, AB (Log-Rank statistic=88.8; P<0.0001), Manitoba Shield, MB (Log-Rank statistic=101.4; P<0.0001), and Duparquet, QC (Log-Rank statistic=97.4; P<0.0001) (Figure 4.4). Probability curves illustrate longer survival times in high light environments for EMEND and Manitoba Shield, and in low light environments for Duparquet. Cox PH regression models for most study locations suggest that %PPFD availability at the leader of aspen saplings is a good predictor of

survival time for both open and closed canopy regimes (Table 4.6). Height and live crown ratio are consistently good predictors of survival time across regions and canopy regimes, with live crown ratio having the greatest influence on predicted survival. For each model, the likelihood ratio test of model performance and the Wald statistic are significant at the 0.05 level. Overall, the effect of live crown ratio on mortality risk is the most important of the factors examined; of the variables included in hazard models, unit change live crown ratio elicits the greatest change in mortality risk ($\exp(B)$).

Balsam fir

KM estimated survival functions for balsam fir advance regeneration are significantly different among regions for both open canopy conditions (Log-Rank statistic=11.8; $P<0.019$) and closed canopy conditions (Log-Rank statistic=27.4; $P<0.0001$) (Figure 4.5). Chicoutimi, QC plots were established earlier than other regions and mortality has been monitored for a longer interval (approximately 36 months). As a result, the overall decrease in cumulative survival is greatest for this study location under both open and closed canopy conditions. Nonetheless, if plots are compared at two years following establishment, the survival probability in closed canopy plots in Chicoutimi is still much lower than for other regions. This may be a result of the small initial size of some of the regeneration in these shaded plots. Median survival times are greater than two years for all study locations.

There are significant differences between KM curves of balsam fir regeneration in open and closed canopy conditions for Duck Mountains, MB (Log-Rank statistic=7.5; $P<0.0001$), Duparquet, QC (Log-Rank statistic=10.0; $P=0.002$), and Forêt Montmorency, QC (Log-Rank statistic=4.1; $P=0.044$) (Figure 4.6). Balsam fir survival time is longer under closed canopy regimes for Duck Mountains and Duparquet plots, whereas in the Forêt Montmorency plots survival time is longer under canopy gaps. Canopy gaps in the Forêt Montmorency region are large, the result of extensive spruce budworm outbreaks. In contrast, the canopy gaps in western Manitoba and Alberta are much smaller, the result of windfall and senescence of individuals or small groups of canopy trees. The longer survival time of fir under closed canopy conditions in the Duck Mountains and in Duparquet may be a reflection of different levels of competition, or other site-level

differences between plots in the two canopy regimes. Although open canopy conditions in Chicoutimi, QC, were also caused by spruce budworm outbreak, the canopy gap under which advance regeneration was monitored is smaller.

Within a given canopy regime, light is not consistently a good predictor of survival time for balsam fir (based on the small number of balsam fir saplings that died). This suggests that although light availability may influence balsam fir mortality at a “coarse” scale (e.g. comparing two dramatically different light environments), it does not predict variation in survival time within a given light regime (open or closed canopy conditions). However, live crown ratio is a good predictor of balsam fir survival time for both open and closed canopy conditions for three of the five study locations analysed, but not for Forêt Montmorency, QC and Chicoutimi, QC (Table 4.7). Cox regressions were not performed on Lac La Biche, AB or closed canopy Duck Mountains, MB plots because mortality in these plots is negligible. All models presented have significant likelihood ratio and Wald test statistics at the 0.05 significance level. Changes in mortality risk associated with unit change in live crown ratio ($\exp(B)$) are comparable to those for trembling aspen models.

4.4 Discussion

Estimates of species-specific population mortality rates for each light environment are generally consistent across regions (study locations) with a few exceptions that are explained by distinctive site-level growing conditions.

4.4.1 Interspecific differences in sapling mortality

Trembling aspen demonstrates higher mortality rates under low light conditions than the coniferous species examined; this is consistent with the postulate that species with higher growth rates in high-light environments exhibit low survivorship when suppressed (Pacala et al. 1994, Kobe et al. 1995, Lin et al. 2001). Interspecific differences in sapling mortality resulting largely from differences in shade tolerance have been shown to be critical in determining forest composition during secondary succession

(Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Kobe and Coates 1997). For instance, in northeastern USA, Kobe (1996) demonstrated using model simulations of forest dynamics that observed differences in species-specific sapling growth and mortality predicted the dominance of canopy tree species of plots differing in elevation and soil characteristics. In our study, differential mortality among aspen and the coniferous species in shaded environments are attributable mainly to differences in their relative shade-tolerance. However, within the more narrow range of shade-tolerance among coniferous species, interspecific differences may result from additional factors that vary among species such as herbivory.

In the present study, trembling aspen also exhibits the highest mortality of the species monitored in *high light* conditions; however, this is a result of extensive self-thinning in densely regenerated aspen cutovers. The relatively high mortality of balsam fir compared to that of spruce species in high light environments may be largely a result of differences in radiation levels among plots: balsam fir were located under natural canopy gaps, whereas spruce were located in exposed even-aged harvested stands (black spruce) or otherwise disturbed, high radiation locations (white spruce). Furthermore, as previously noted, herbivory is an important factor influencing the vigour of balsam fir saplings, but not of spruce regeneration. Variation in radiation levels within and among plots was addressed in other analyses using individual-level measures of %PPFD.

4.4.2 The season of mortality

Among study locations of trembling aspen regeneration there is variation in the relative number of saplings dying (magnitude of step) in summer (months 0-4, 12-16, 24-28) vs. winter (months 4-12, 16-24, 28-36) in Kaplan-Meier survivorship functions. Where differences in mortality between seasons are consistent each year and most dramatic (Figure 4.4 a and d closed canopy curves) it appears that more saplings die over winter than summer months. Similarly, Canham et al. (1999) examined mortality of two-year old hardwood seedlings in the northeastern United States over a one-year period and found mortality to be generally greater over the first winter than the first summer of the study. In our study this may be largely a result of longer time interval from fall to spring,

than spring to fall for biannual censuses of mortality. Finite mortality rates of seasonal mortality were adjusted to unit time of one year to compare seasonal mortality over an equal time period.

Finite mortality rates of aspen suggest increased summer mortality for most study locations, for both light environments; however, these differences were significant in only two of the study locations, Manitoba Shield, MB and Duparquet, QC, which also exhibited the highest aspen mortality rates. Therefore, as mortality increases over time for other study locations, a similar pattern of higher summer mortality may become evident. Results of Kobe's (1996) study suggest that saplings of deciduous species may generally respond to stress through mortality and coniferous species through reduced growth; it was postulated that this difference could result from differences in patterns of carbohydrate storage between coniferous and deciduous species. Deciduous species accumulate carbohydrate reserves throughout the growing season (demonstrated by Kobe's [1997] study), which permit refoliation the following year and also have a function in resistance to mortality agents. Seasonal carbon deficiencies may subsequently result in mortality. In contrast, coniferous species, which don't completely refoliate each spring (although they generate new foliage), maintain more constant levels of carbon reserves during the growing season, which function in resistance to mortality agents; carbon deficiencies in a coniferous sapling may subsequently result in reduced growth rather than mortality (Kobe 1996, 1997). Pattern of carbohydrate storage may explain in part the higher rates of aspen mortality observed in our study; furthermore, this may be pertinent to seasonal patterns in juvenile aspen mortality, which appear to exist.

As cumulative mortality in our monitored sample populations continues to increase over time, seasonal differences in sapling mortality may be further clarified. Alternatively, Franklin et al. (1987) point out that the actual time of tree death may in fact represent an arbitrary point on a continuum along which numerous stresses and events contribute to the eventual death of a tree. Therefore, although pressures exerted by mortality agents vary across seasons, the actual time of sapling death may be somewhat arbitrary. Nonetheless, if a sufficiently large sample of saplings is monitored over an adequate length of time, any observed seasonal differences in mortality may be reflective of those generally experienced by populations.

4.4.3 Differential mortality between high and low light environments, and among regions

Differences in trembling aspen mortality between open and closed canopy conditions are inconsistent across study locations: two of the five study locations examined are different from the others. These differences in finite mortality rates and survival time among study locations appear to be largely the result of differences in site-level conditions, specifically, differences in relative stages of self-thinning in the cutover sites, and of relative canopy composition in shaded sites.

The causes of mortality differ between open and closed canopy conditions. Mortality of aspen suckers in open canopy conditions is primarily a result of self-thinning of very dense young stands (Bella 1986, Lavertu et al. 1994, Greene et al. 1999, Prévost and Pothier 2003), but may also result from interspecific competition from tall shrubs such as beaked hazelnut (*Corylus cornuta* Marsh.) that re-sprout following harvest (Mallik et al. 1997). If self-thinning of aspen suckers in clearcuts decreases over time, mortality may be comparatively higher in closed canopy plots even though understory aspen suckers are generally less dense than under open canopy conditions (also noted by Shepperd et al. 2001, Prévost and Pothier 2003). Canopy and tall shrub layers attenuate light in closed stands, potentially resulting in high turnover of the aspen understory. Low soil temperature and stand-level factors such as age, also limit aspen regeneration density in the shaded understory (Perala 1990, Cumming et al. 2000), and tree and branch windfall contribute to mortality in closed canopy plots. Although mammal herbivory and pathogen/insect damage occur in both open and closed canopy plots (personal observation), the extent to which these factors affect mortality under open and closed canopy conditions may differ. These causal factors may differ not only between light environments but also among plots and study locations. Future measures of aspen stem density for open and closed canopy conditions would be of use for comparing mortality in open and closed canopy conditions, which differ in stem density and mechanisms governing mortality.

In general, there is no significant difference in finite mortality rates of balsam fir advance regeneration among study locations, or between closed canopy conditions and canopy gaps. However, mortality was altogether low, and if monitored for a longer

period, may differ between the two light environments examined, which with the exception of plots in eastern Québec, exhibited comparably subtle differences in radiation environment (see Table 3.3). Unlike population estimates of finite mortality rates, survival times of balsam fir saplings do differ significantly between open and closed canopy environments for three of the five study locations examined. However, these differences are inconsistent among study locations: survival time is greater in high light conditions only in Forêt Montmorency, QC, where high light conditions differ substantially in their radiation levels than adjacent closed canopy conditions. In Duck Mountains, MB, and Duparquet, QC, where differences between light environments are more subtle, survival times are significantly higher in closed canopy conditions. It appears that in light environments receiving high radiation such as spruce budworm gaps in Forêt Montmorency, survival time increases significantly compared to adjacent closed canopy conditions. Lower survival times under canopy gaps in Duck Mountains and Duparquet, and the lack of significant difference in survival time between open and closed canopy regimes in other regions, suggests that differences in mortality of advance fir regeneration between full canopy conditions and small canopy openings are not substantial after only 2.5 years of study. Such trends may change with subsequent mortality of balsam fir in these permanent monitoring plots. Alternatively, there may be a genuine lack of difference in fir mortality between closed canopy conditions and small canopy gaps. It was expected that mortality would generally be greater in closed canopy conditions (based the unhealthy appearance of some of the fir in the shaded understory). A lack of difference in fir mortality between shaded understory and small gap conditions suggests that shade-tolerant fir saplings survive just as well in heavily shaded conditions as in higher light environments associated with small canopy openings.

Insufficient mortality of black and white spruce saplings occurred to characterize spruce mortality in contrasting light environments. The only significant difference in spruce mortality between high and low light environments occurs in Iroquois Falls, ON, where black spruce mortality rates are significantly higher for plots under closed canopy conditions (3 deaths out of a sample of 290 saplings in open canopy conditions, and 17 deaths out of a sample of 292 saplings in closed canopy conditions). This suggests higher

mortality for black spruce advance regeneration when suppressed than in unlimited light environments.

Factors other than light may be important determinants of mortality for both coniferous advance regeneration, and vegetative suckers of trembling aspen. Canham et al. (1999) examined survival of two-year old hardwood seedlings under each of four canopy conditions: closed, small gap, large gap, and recent clearcut. They found that the biotic and abiotic factors that result in defoliation or loss of other tissues more strongly affect the survival of small seedlings than resource (light) availability associated with canopy closure. Although light availability and shade tolerance are dominant factors governing growth and mortality of advance regeneration, factors other than degree of canopy opening also influence growth and survival of larger juveniles. In our study important factors include mammal herbivory, insect and pathogen damage, frost damage, and perhaps competition for resources other than light such as water, nitrogen and other limiting nutrients in boreal environments. Herbivory was initially examined as a predictor in Cox hazard models. However, our ordinal measure of herbivory was not a good predictor of mortality risk for either aspen or fir for the study locations in which degree of herbivory was recorded (Duck Mountains, MB, EMEND, AB, and Lac La Biche, AB). More detailed herbivory information is needed to examine its effect on sapling mortality.

An important result of Kobe's (1996) study indicated that in addition to the most limiting resource (light) for a sapling population in the shaded understory, other factors such as water and nutrient availability can be simultaneously limiting. Kobe and Coates (1997) found that soil moisture had a negative effect on sapling survivorship for eight species in northwestern British Columbia. In the present study, resources other than light availability may also be limiting and influence sapling mortality. Further investigation into such factors is needed to more fully characterize mortality.

Beckage and Clark (2003) examined the effect of canopy closure on mortality of planted first-year seedlings of three deciduous species varying in shade-tolerance, in mixed-oak forests in the southern Appalachians. Utilizing survival analysis, the authors found that survival time for all three species over a three-year period was significantly higher under natural canopy gaps, which had significantly higher light levels than closed canopy plots. Differences in survival time between fully closed canopy and natural

canopy gaps are not as clear for balsam fir saplings in our study; however, the purpose of the present study was to examine mortality of established juvenile trees that were well-past initial years of high mortality. The effect of light environment and other factors associated with canopy gap formation appear to differ for young seedlings and established advance regeneration.

4.4.4 Light, size, and crown morphology as predictors of survival time

Trembling aspen survival time in both low and high light environments increases with light availability, height and especially with live crown ratio; the survival time of balsam fir is best predicted by live crown ratio. Lin et al. (2001) used parametric survival analysis techniques to assess the effects of size (diameter) and growth (absolute radial growth rate) on sapling mortality for seven tree species in southeastern Texas. Similar to our study, size was found to be a good predictor of mortality risk (where size is positively related to survival) only for one of the species studied while absolute radial growth rates (which are greater for larger saplings) were found to be consistently good predictors of mortality risk across species (where growth is positively related to survival).

The inability of %PPFD to predict balsam fir survival under shaded conditions or in canopy gaps suggests that factors other than light availability may be important determinants of mortality of shade-tolerant advance regeneration. However, because live crown ratio is generally considered to be reflective of light conditions, and since live crown ratio has a marked effect on mortality risk of balsam fir, light is undoubtedly an important factor. Our methodology for measuring light availability may not have captured the variation in radiation that might cause differential balsam fir mortality; it is possible that short bursts of intense direct radiation experienced throughout growing season, perhaps not directly correlated with the relative levels of diffuse radiation measured, affect mortality of shade-tolerant conifers. Furthermore, Cox PH regression models for balsam fir are based on relatively low levels of mortality for each region; a larger sample size of dead balsam fir saplings (which should be available in a few years) will help clarify the relationship between light availability and mortality in fir. Overall, our results corroborate previous evidence that height (for aspen only in our study) and in

particular live crown ratio (for both aspen and fir) are good indicators of mortality (Ruel et al. 1995). A larger sample size of dead coniferous saplings is needed to better understand the effects of various predictor variables on individual survival time.

4.4.5 Manion's conceptual model of the tree mortality process applied to saplings

Franklin et al. (1987) proposed that Manion's (1981) model of tree disease and resulting decline be extended as a general model for tree mortality: a downward "mortality spiral". In this conceptual model of tree mortality the many cumulative and sequential events that contribute to decline of a tree are likened to a downward spiral towards death, where different stress factors and damaging events precipitate subsequent stresses and the chance of recovery becomes more limited with each event. Pedersen (1998) evaluated this mortality model by examining the radial growth history of dead oak trees (*Quercus* spp.). The author tested the idea that tree death is attributable to long-term stresses, which "predispose" trees to injury by short-duration "inciting" stresses. It was found that tree mortality was indeed the long-term result of a combination of environmental stresses resulting in reduced growth prior to sudden, permanent declines in growth. Although the long-term effects of predisposing factors must differ, at least in their duration, for saplings than for mature trees, juvenile trees are generally more sensitive to environmental stresses (Franklin et al. 1987). Predisposing and inciting factors may interact to affect mortality of advance regeneration in a similar manner as has been demonstrated for mature trees (Figure 4.7).

The light environment associated with degree of canopy closure as examined in our study can be considered a predisposing factor, influencing the overall vigour (growth) of saplings. Light availability alone, without a specific inciting stress may result in sapling mortality, since live crown ratio is a consistently strong predictor of survival time (for trembling aspen and balsam fir); live crown ratio is largely a reflection of long-term light conditions. Pedersen (1998) found that approximately one quarter of the dead trees examined in his study showed no signs of an inciting stress. Further study may elucidate the relative proportion of sapling mortality resulting from predisposing factors alone and from a combination of predisposing factors and inciting stresses.

Important inciting stresses that may result in sudden growth decline of saplings include herbivory, insect or pathogen damage, frost damage, and mechanical damage from fallen trees and branches, ice buildup, and ungulate movement. Most of these factors were noted for our monitored saplings. Across study locations, to varying degrees, elk (*Cervus canadensis*), white-tailed deer (*Odocoileus virginianus*) and hare (*Lepus americanus*) were common herbivores of aspen and fir. "Shepherd's crook" (bent and blackened shoot) resulting from shoot blight (*Venturia macularis*) was often observed for aspen suckers, and there was much evidence of insect damage including defoliating larvae on aspen saplings, gall-forming insects, and aphids on both aspen and conifer saplings. Inciting factors such as insect and mammal herbivory might also be considered predisposing factors if repeated to such an extent that saplings remain in a continuous state of decreased vigour where they may be more susceptible to other inciting stresses. For instance, moderate insect defoliation of an otherwise healthy aspen sapling may not substantially reduce growth or result in mortality, however, in combination with factors such as low light availability, limitation of other resources (water and nutrients), mammal herbivory, and/or pathogen damage, insect defoliation may have an important impact. The effect of below-ground associations on growth and mortality of aspen suckers is an important factor that needs investigation (Cumming et al. 2000). Aspen adaptation to understory survival may be much different than that of species that propagate primarily through sexual reproduction.

4.4.6 Summary

This study provides much needed mortality rates for advance regeneration of white and black spruce, balsam fir, and trembling aspen across the boreal forest, occurring in naturally shaded understory and open canopy conditions; with a few exceptions, rates are similar among regions. Mortality is highest for aspen regeneration, followed by balsam fir, then black spruce, and white spruce. Although heterogeneity in mortality risk exists within populations, large numbers of saplings and repetition in study locations across the Canadian boreal forest suggest that the mortality rates presented are characteristic of each species (under the presence or absence of canopy cover) for the

sapling stage examined. These mortality rates provide useful and representative empirical estimates for use in growth and mortality functions in model simulations of forest stand dynamics.

Finite mortality rates differ between light environments only if the difference in radiation levels between environments is sufficiently large, and where appreciable mortality occurred to detect trends. Kaplan-Meier estimates of survivorship show similar, though more informative, trends in mortality between open and closed canopy conditions, and among study locations, to those demonstrated by finite mortality rates. Survival times provided unbiased estimates of sapling survivorship for trembling aspen and balsam fir for each study location and canopy treatment. The median survival time (time at which 50% of the individuals in the sample have died) for trembling aspen suckers of the size range examined is generally greater than two years, for both open canopy and closed canopy conditions. The median survival time for balsam fir saplings appears to be much longer. Live crown ratio is consistently a strong predictor of sapling mortality - more so than either %PPFD or sapling size. Threshold values of live crown ratio at which a defined level of mortality occurs (eg. 10%), can be derived from these Cox hazard models for in situ assessments of survival of advance regeneration in forest management applications.

Low light availability associated with full canopy cover might be considered a factor that increases sapling susceptibility to sudden inciting stresses (although not demonstrated in this study); alternatively, predisposing factors alone may account for sapling mortality. Further study may elucidate the relative proportion of sapling mortality resulting from predisposing factors alone and from a combination of predisposing factors and inciting stresses. To test Manion's model for saplings, specific inciting stresses such as herbivory and different forms of predisposing stresses should be quantified for live saplings, and subsequent time to mortality monitored. In order to characterize mortality of white and black spruce in different light environments and among regions, a longer study period is required to gather sufficient censored data. For a more complete characterization of sapling mortality, a more detailed examination of causal factors in addition to light availability is needed.

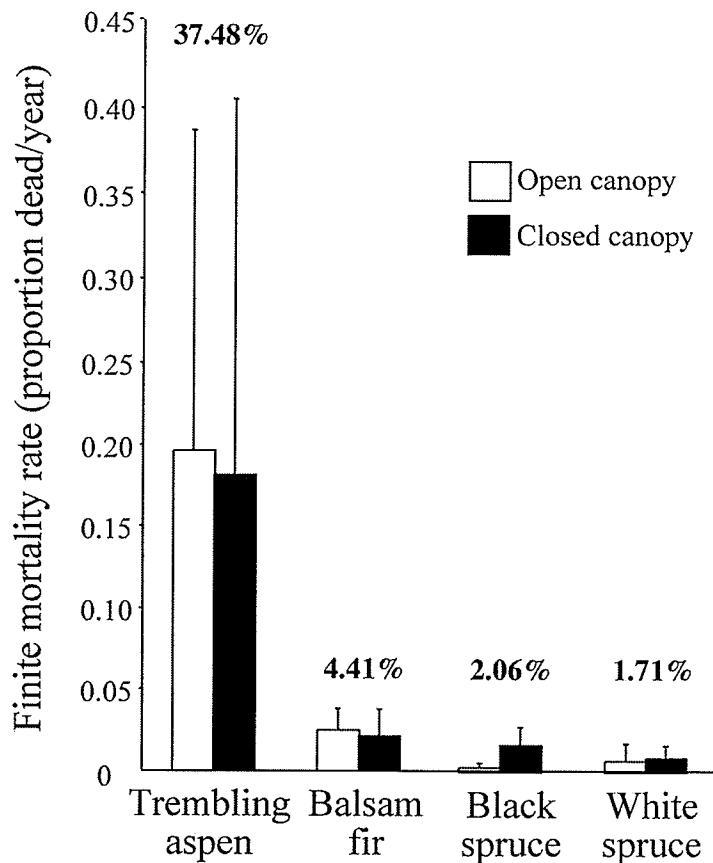


Figure 4.1. Finite annual mortality rates for advance regeneration growing under open canopy conditions (unshaded bars) and closed canopy conditions (shaded bars). Mortality rates were calculated using pooled data from all study locations for each species. Rates were determined for the entire study period, from spring 2000 until fall 2002, and standardized to one year. Percent mortality (finite mortality \times 100%) for each species (pooled across study locations and canopy conditions) are shown above standard deviation bars. For each species, a measure of standard deviation was calculated using separate finite mortality rates determined for each study location ($n=4$ for white spruce, $n=3$ for black spruce, $n=6$ for balsam fir, $n=5$ for aspen, where n is the number of study locations). Standard deviation bars therefore display inter-regional variation, which is substantial. Mortality is significantly different among species for both open canopy ($P=0.030$) and closed canopy ($P=0.040$) conditions.

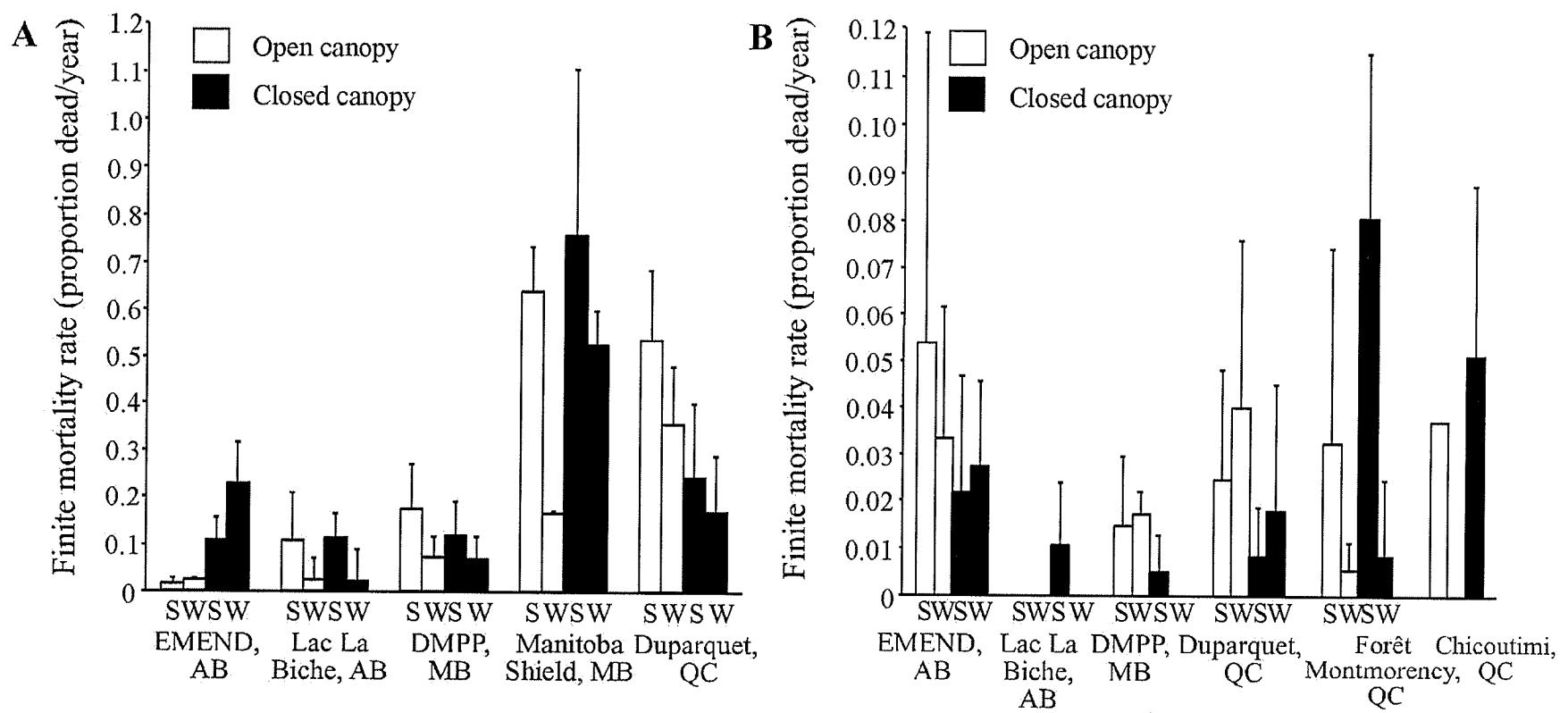


Figure 4.2. Finite mortality rates of trembling aspen (A) and balsam fir (B) natural regeneration for summer (S) and winter (W) adjusted to a common time base of one year. Unshaded bars represent mortality rates of natural regeneration growing in open canopy plots, and shaded bars summarize mortality rates under closed canopy conditions. Standard deviation measures were determined using mortality rates calculated for each permanent plot within a study location. Note difference in scale of y-axis between Figure 4.2A and B. A.) Aspen mortality differs significantly between summer and winter in Manitoba Shield, MB ($P=0.019$) and Duparquet, QC ($P=0.039$) plots. Significant differences in mortality between open and closed canopy plots occur for EMEND, AB ($P=0.001$) and Duparquet ($P=0.002$) plots. B.) Balsam fir mortality differs significantly between summer and winter only for Forêt Montmorency, QC plots ($P=0.005$). Significant differences in mortality between open and closed canopy plots occurs only for Duck Mountains, MB plots ($P=0.028$). Note: Chicoutimi, QC plots were monitored only in the fall to census annual mortality, and have only one permanent plot for open canopy conditions. There are no significant interactions between canopy condition and season of mortality for any of the study locations for either (A) or (B).

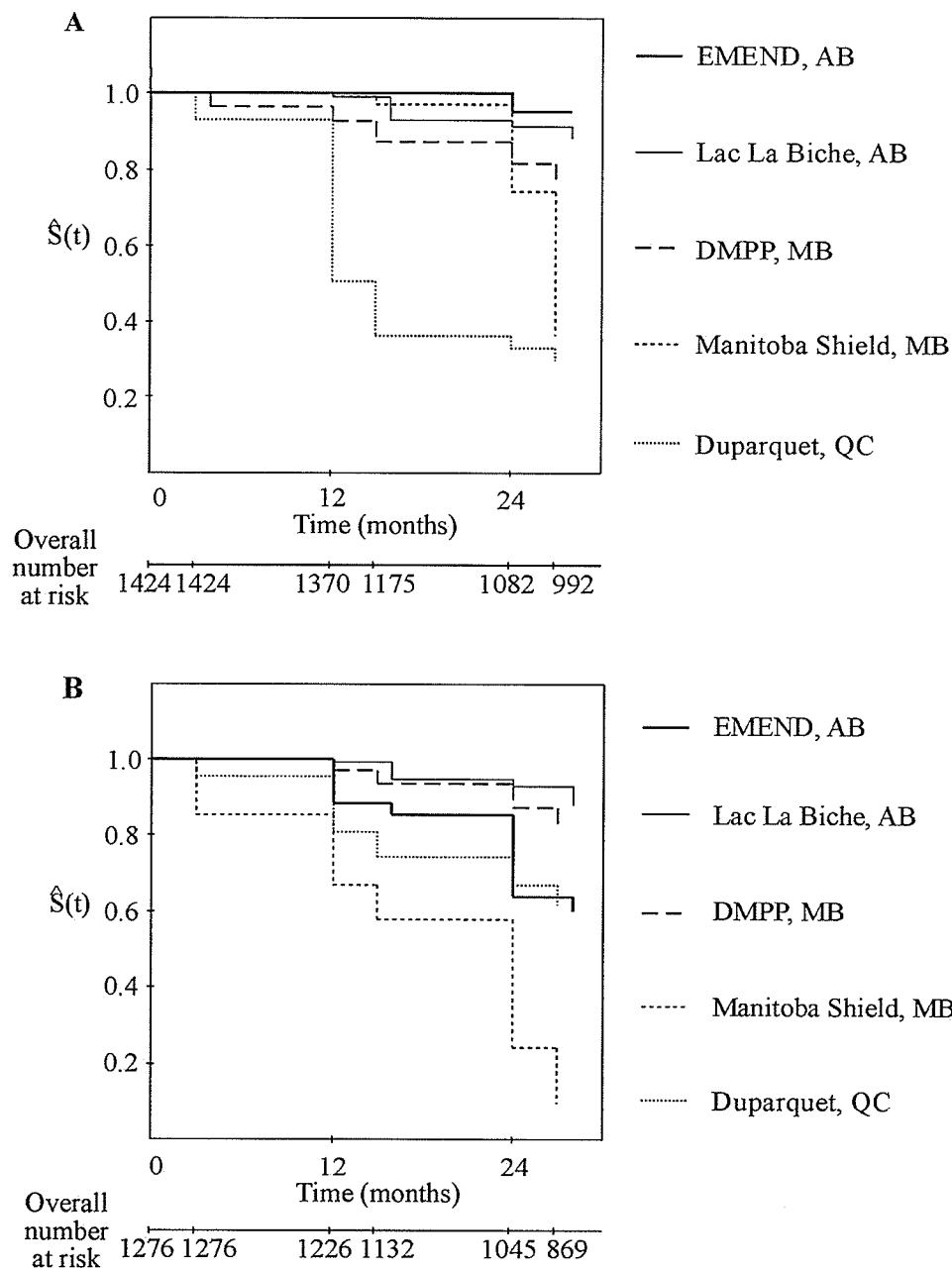


Figure 4.3. Kaplan-Meier survival curves for natural regeneration of trembling aspen. Separate functions are shown for each study location, for open (A) and closed (B) canopy conditions. $\hat{S}(t)$ is the estimated survival probability for a given time t . Monitoring began at the end of the first growing season ($t=3-4$ months) following plot establishment in the spring of 2000 ($t=0$). The overall number of saplings at risk for each light environment is shown for the most common census times among study locations. "At risk" individuals are defined as those with a survival time greater than or equal to time t , which includes saplings found dead at that census since they are considered at risk just up to that point. There is a significant difference among regional survivorship curves for open canopy conditions (Log-Rank statistic=590.0; $P<0.0001$), and for closed canopy conditions (Log-Rank statistic=412.6; $P<0.0001$). For all plots, the only censorship occurs at the end of the study period.

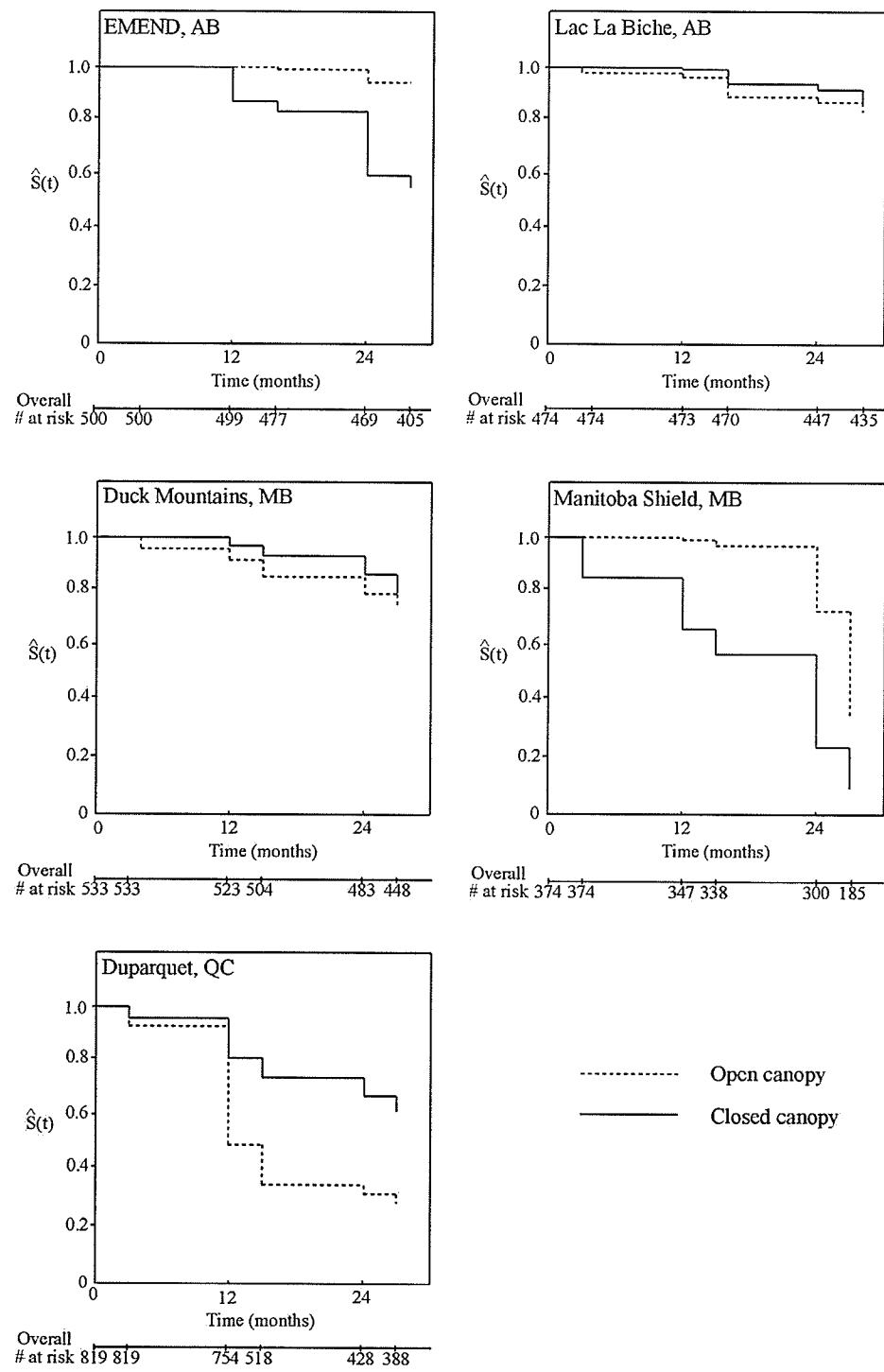


Figure 4.4. Kaplan-Meier survival curves for natural regeneration of trembling aspen. Separate survival functions are shown for open canopy (broken line) and closed canopy (solid line) conditions for EMEND, AB, Lac La Biche, AB, Duck Mountains, MB, Manitoba Shield, MB, and Duparquet, QC. Survival is significantly different between open and closed canopy for EMEND (Log-Rank statistic=88.8; $P<0.0001$), Manitoba Shield (Log-Rank statistic=101.4; $P<0.0001$), and Duparquet (Log-Rank statistic=97.4; $P<0.0001$), but not for Lac La Biche (Log-Rank statistic=0.01; $P=0.940$) or Duck Mountains (Log-Rank statistic=2.2; $P=0.014$).

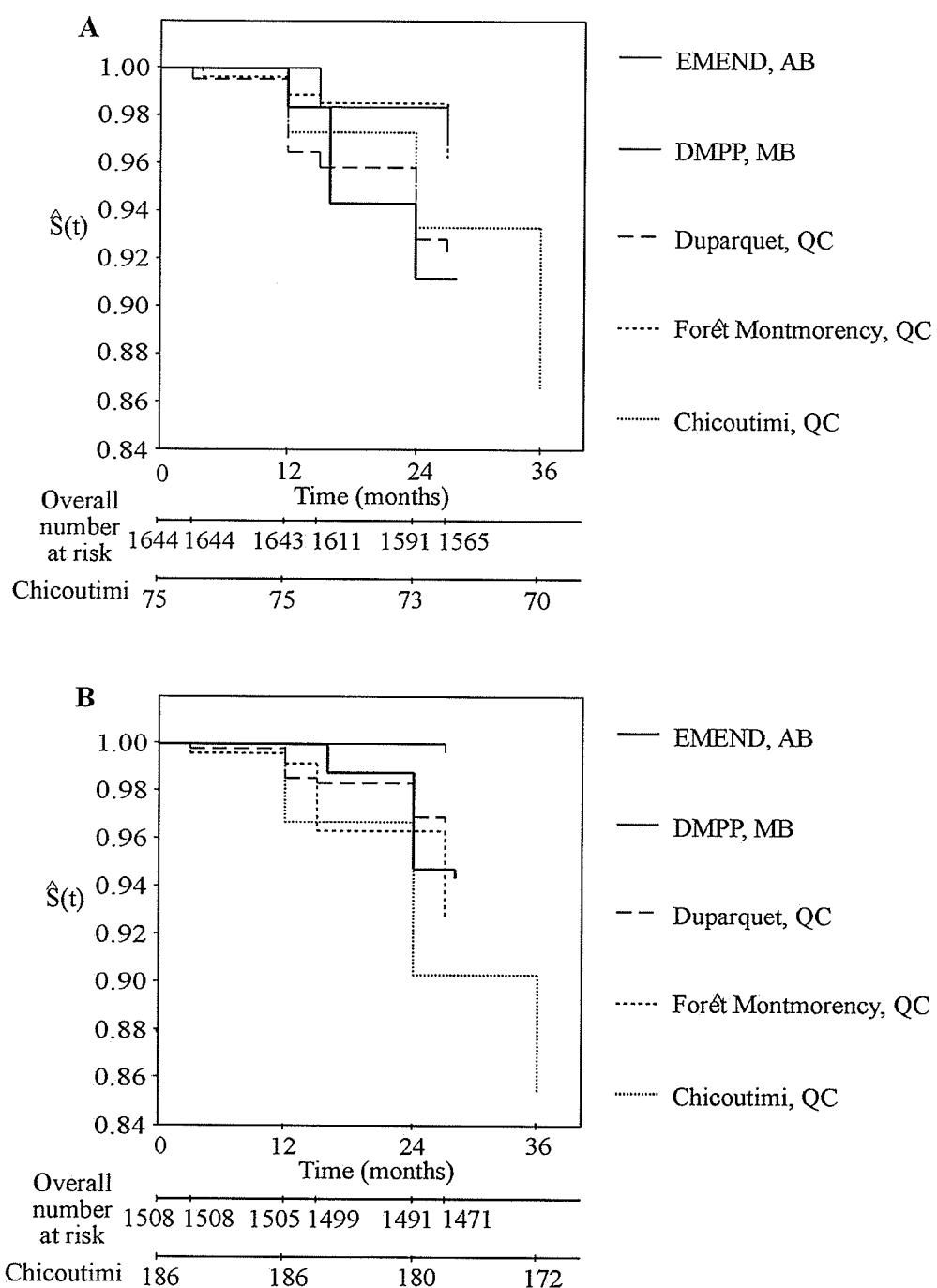


Figure 4.5. Kaplan-Meier survival curves for natural regeneration of balsam fir. Note difference in scale from Figure 4.3. Separate functions are shown for each study location, for open (A) and closed (B) canopy plots. $S(t)$ hat is the estimated survival probability for a given time t . Monitoring began at the end of the first growing season ($t=3-4$ months) following plot establishment in the spring of 2000 ($t=0$) for all but Chicoutimi, QC plots, where monitoring began in the fall of 1999. Lac La Biche, AB is not included in this analysis because of insufficient mortality. The overall number of saplings at risk for each light environment is shown for the most common census times among locations. There is a significant difference among curves for open canopy conditions (Log-Rank statistic=11.8; $P=0.019$), and closed canopy conditions (Log-Rank statistic=27.4; $P<0.0001$). For all plots, the only censorship occurs at the end of the study period.

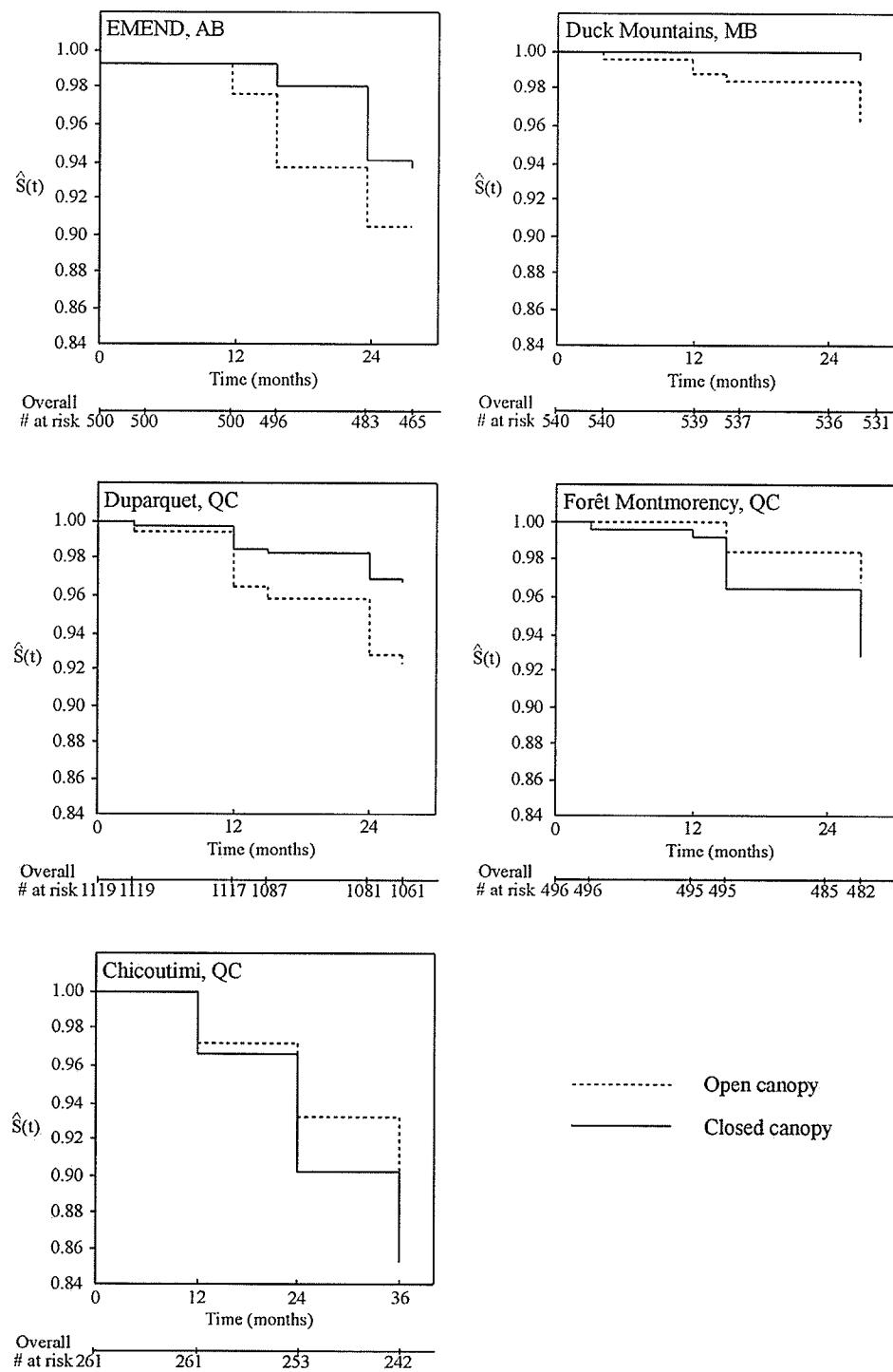


Figure 4.6. Kaplan-Meier survival curves for advance regeneration of balsam fir. Separate survival functions are shown for open canopy (broken line) and closed canopy (solid line) conditions for EMEND, AB, Duck Mountains, MB, Duparquet, QC, Forêt Montmorency, QC, and Chicoutimi, QC. Survival is significantly different between open and closed canopy for Duck Mountains (Log-Rank statistic=7.5; P=0.006), Duparquet (Log-Rank statistic=10.0; P=0.002), and Forêt Montmorency (Log-Rank statistic=4.1; P=0.044), but not for EMEND (Log-Rank statistic=2.0; P=0.157) or Chicoutimi (Log-Rank statistic=0.1; P=0.782).

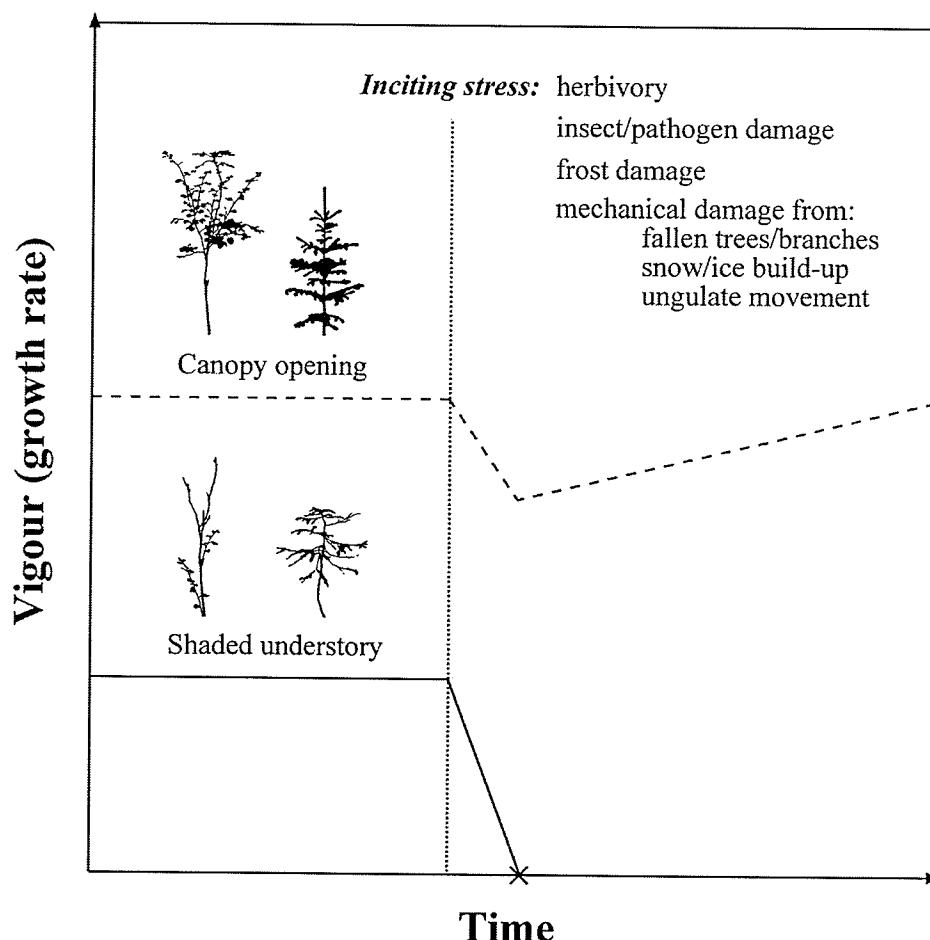


Figure 4.7. A modification of Pedersen's (1998) schematic of Manion's (1981) tree mortality model (after Johnson [1989]) as applied to saplings. The most important predisposing factor in our study is the light environment associated with the presence or absence of canopy cover. Variation in light environment within a defined level of canopy openness is also a predisposing factor. Inciting stresses listed above may differ in their effect on growth and mortality for saplings growing in different light environments. A sapling growing in a high light environment (broken line) may recover from a sudden inciting stress; in contrast, a sapling in a suppressed state in the shaded understory (solid line) may not recover from the same inciting stress (mortality indicated by an x). Variation in site conditions, and low overall mortality for coniferous species result in inconsistencies across study locations with respect to survival differences between open and closed canopy environments in our study. Light availability alone, without a specific inciting stress may result in sapling mortality, since live crown ratio is a consistently strong predictor of survival time and is largely a reflection of long-term light conditions. Further study may elucidate the relative proportion of sapling mortality resulting from predisposing factors alone and from a combination of predisposing factors and inciting stresses. Across species, different growth strategies may result in various responses to light environment.

Table 4.1. Number of trembling aspen saplings alive at each spring and fall census, beginning spring 2000.

Study Location	Canopy type	Plot	Number of live saplings					
			2000		2001		2002	
			Spring	Fall	Spring	Fall	Spring	Fall
EMEND, AB	open	EMEND13	63	63	63	62	59	58
		EMEND14	62	62	62	63	61	59
		EMEND22	62	62	62	62	61	61
		EMEND23	63	63	63	63	60	60
		Total	250	250	250	250	241	238
	closed	EMEND13	63	63	57	52	37	36
		EMEND14	62	61	61	61	54	51
		EMEND22	62	62	53	51	34	34
		EMEND23	63	63	56	55	39	35
		Total	250	249	227	219	164	156
Lac La Biche, AB	open	LLB7	62	62	61	59	59	58
		LLB8	62	62	62	62	61	58
		LLB9	63	63	63	61	60	60
		LLB10	62	62	60	50	47	44
		Total	249	249	246	232	227	220
	closed	LLB7	62	62	62	58	55	55
		LLB8	62	62	62	62	62	58
		LLB9	63	62	62	58	56	52
		LLB10	38	38	38	37	35	37
		Total	225	224	224	215	208	202
Duck Mountains, MB	open	Hwy 366	90	90	89	84	80	80
		Hwy 83S	90	85	80	75	65	59
		Hwy 83N	89	84	78	76	74	69
		Total	269	259	247	235	219	208
	closed	Hwy 366	87	87	87	81	75	71
		Hwy 83S	87	87	86	85	82	81
		Hwy 83N	90	90	84	82	72	64
		Total	264	264	257	248	229	216
Manitoba Shield, MB	open	2	108	108	107	106	81	43
		3	91	91	90	87	67	28
		Total	199	199	197	193	148	71
		2	82	73	68	59	24	19
	closed	3	93	75	73	48	13	1
		Total	175	148	141	107	37	20
		1	103	82	63	45	40	28
		2	80	77	52	41	41	40
Duparquet, QC	open	4	94	82	39	24	20	19
		8	90	85	33	24	23	20
		9	90	87	48	38	33	27
		Total	457	413	235	172	157	134
	closed	3	76	66	61	50	49	46
		18	78	71	45	40	37	35
		19	59	58	50	47	44	44
		22	102	99	88	83	76	73
		31	47	47	39	36	25	25
		Total	362	341	283	256	231	223
		Overall	2700	2596	2307	2127	1861	1688

Table 4.2. Number of balsam fir saplings alive at each spring and fall census, beginning in spring 2000.

Study Location	Canopy type	Plot	Number of live saplings					
			2000		2001		2002	
			Spring	Fall	Spring	Fall	Spring	Fall
EMEND, AB	open	EMEND15	63	63	63	63	63	63
		EMEND16	63	63	63	61	56	56
		EMEND17	62	62	60	59	59	59
		EMEND18	62	62	60	53	50	50
		Total	250	250	246	236	228	228
	closed	EMEND15	63	63	63	62	59	58
		EMEND16	63	63	63	63	63	63
		EMEND17	62	62	62	60	57	57
		EMEND18	62	62	62	62	58	58
		Total	250	250	250	247	237	236
Lac La Biche, AB	open	LLB1	62	62	62	62	62	62
		LLB2	63	63	63	63	63	63
		LLB5	62	62	62	62	62	62
		LLB6	63	63	63	63	63	63
		Total	250	250	250	250	250	250
	closed	LLB1	62	62	62	62	62	62
		LLB2	63	63	63	63	63	62
		LLB5	62	62	62	62	62	62
		LLB6	63	63	63	63	63	62
		Total	250	250	250	250	250	248
Duck Mountains, MB	open	Laurie L.	90	89	88	87	85	85
		East Blue L.	90	90	89	89	88	87
		Childs L.	90	90	90	90	88	88
		Total	270	269	267	266	261	260
	closed	Laurie L.	90	90	90	90	90	90
		East Blue L.	90	90	90	90	90	89
		Childs L.	90	90	90	90	90	90
		Total	270	270	270	270	270	269
Duparquet, QC	open	4	161	161	144	142	134	133
		5	76	76	74	72	72	71
		15o	71	71	70	70	70	67
		17	84	84	84	84	84	83
		23	30	30	30	29	29	30
		24	42	42	41	40	40	40
		25	126	126	122	122	118	118
		30	36	36	36	36	36	36
		Total	626	626	601	595	583	578
	closed	6	81	81	80	80	79	79
		11	60	59	59	59	59	59
		12	92	91	91	91	90	90
		15f	87	87	87	87	87	87
		16	92	92	90	90	90	90
		29	81	81	79	79	73	72
		Total	493	491	486	486	478	477

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Table 4.2. continued.

Study Location	Canopy type	Plot	Number of live saplings						
			2000		2001		2002		
			Spring	Fall	Spring	Fall	Spring	Fall	
Forêt Montmorency, QC	open	1	62	62	61	59	59	57	
		2	62	62	62	62	62	62	
		3	62	62	62	61	60	59	
		4	62	62	62	62	62	62	
		Total	248	248	247	244	243	240	
	closed	1	62	62	62	60	60	56	
		2	62	62	61	61	59	56	
		3	62	62	62	61	61	60	
		4	62	61	61	59	59	58	
		Total	248	247	246	241	239	230	
Chicoutimi, QC*	open	Lib24	73		70		65		
		Total	73		70		65		
	closed	Lib20	73		67		58		
		Lib23	99		97		93		
		Lib26	8		8		8		
		Total	180		172		159		
			Overall	3155	3151	3113	3085	3039	3016

*Mortality was monitored each fall for Chicoutimi plots beginning in the fall of 1999. Four saplings from Lib20, two from Lib24, and two from Lib26 died before fall 2000.

Table 4.3. Number of black spruce saplings alive at each spring and fall census, beginning in spring 2000.

Study Location	Canopy type	Plot	Number of live saplings						
			2000		2001		2002		
			Spring	Fall	Spring	Fall	Spring	Fall	
Manitoba Shield, MB	open	1	95	95	95	95	95	95	
		2	110	110	110	110	110	110	
		3	90	90	90	90	90	90	
		Total	295	295	295	295	295	295	
	closed	1	90	90	90	90	90	90	
		2	95	95	95	95	95	94	
		3	90	90	90	90	90	90	
		Total	275	275	275	275	275	274	
Iroquois Falls, ON*	open	21	80	80	80	80	80	80	
		13-1	70	70	70	70	69	68	
		13-2	70	70	70	69	69	69	
		24	70	70	70	70	70	70	
		Total	290	290	290	289	288	287	
	closed	19-N	76	75	73	73	72	72	
		11	76	76	75	71	71	69	
		19-S	70	70	70	70	70	68	
		16	70	68	67	67	66	66	
		Total	292	289	285	281	279	275	
Ashuapmushuan Reserve, QC	open	1	62	62	62	62	62	62	
		2	62	62	62	62	62	62	
		3	62	62	62	62	62	62	
		4	62	62	60	60	60	60	
		Total	248	248	246	246	246	246	
	closed	1	62	62	62	61	61	60	
		2	62	62	61	61	61	61	
		3	62	61	59	59	59	59	
		4	62	62	62	57	57	57	
		Total	248	247	244	238	238	237	
			Overall	1648	1644	1635	1624	1621	
							1614		

*Ontario plots were established in the fall of 1999. However, no mortality occurred in these plots before spring 2000.

Table 4.4. Number of white spruce saplings alive at each spring and fall census, beginning in spring 2000.

Study Location	Canopy type	Plot	Number of live saplings						
			2000		2001		2002		
			Spring	Fall	Spring	Fall	Spring	Fall	
EMEND, AB	open	EMEND19	62	62	62	62	62	62	
		EMEND20	62	62	62	62	62	62	
		EMEND21	63	63	63	63	63	63	
		EMEND24	63	63	63	63	63	63	
		Total	250	250	250	250	250	250	
	closed	EMEND19	62	62	62	62	62	62	
		EMEND20	62	62	62	62	62	62	
		EMEND21	63	63	63	63	63	63	
		EMEND24	63	63	63	63	63	63	
		Total	250	250	250	250	250	250	
Lac La Biche, AB	open	LLB3	62	62	62	62	62	62	
		LLB4	62	62	62	62	62	62	
		LLB11	63	63	63	63	63	63	
		LLB12	63	63	63	63	63	63	
		Total	250	250	250	250	250	250	
	closed	LLB3	62	62	61	61	60	60	
		LLB4	62	62	62	62	62	62	
		LLB11	63	63	62	62	61	60	
		LLB12	63	63	63	63	63	63	
		Total	250	250	248	248	246	245	
Duck Mountains, MB	open	Gravel pit	90	90	90	90	90	90	
		Wetlands	88	88	88	88	88	88	
		Interp trail	86	86	86	86	86	86	
		Total	264	264	264	264	264	264	
	closed	Childs	91	91	91	91	90	90	
		HWY 366N	90	90	90	90	90	90	
		366 boundary	89	88	88	87	87	86	
		Total	270	269	269	268	267	266	
Duparquet, QC	open	4	129	127	123	116	116	116	
		26	179	178	178	178	176	176	
		28	40	40	40	39	39	39	
		Total	348	345	341	333	331	331	
	closed	11	65	61	61	61	61	61	
		22	32	29	29	29	29	29	
		27	184	182	181	180	180	180	
		Total	281	272	271	270	270	270	
			Overall	2163	2150	2143	2133	2128	2126

Table 4.5. Finite mortality rates for each species, study location, and canopy regime. Mortality rates are the proportion of saplings that die per year. Raw data were pooled across permanent plots within each canopy regime of a study location to give an average mortality rate. Standard deviations for each study location/canopy regime were derived from mortality rates calculated for each permanent plot (replicate). Some variation in mortality rates exist among study locations for each species (see text for levels of significance and results of multiple-comparison tests). Probability values at $\alpha=0.05$ from t-tests of species-specific mortality rates between canopy treatments within each region are shown.

Species	Study location	Canopy regime	# permanent plots	Mortality rate	Standard deviation	P
Trembling aspen	EMEND, AB	open	4	0.0216	0.0118	0.019
		closed	4	0.1891	0.0727	
	Lac La Biche, AB	open	4	0.0535	0.0575	0.094
		closed	4	0.0531	0.0217	
	Duck Mountains, MB	open	3	0.1080	0.0601	0.641
		closed	3	0.0853	0.0547	
	Manitoba Shield, MB	open	2	0.3675	0.0508	0.370
		closed	2	0.6186	0.2749	
	Duparquet, QC	open	5	0.4203	0.0959	0.003
		closed	5	0.1937	0.0738	
Balsam fir	EMEND, AB	open	4	0.0401	0.0394	0.512
		closed	4	0.0253	0.0173	
	Lac La Biche, AB	open	4	0	0	0.182
		closed	4	0.0036	0.0041	
	Duck Mountains, MB	open	3	0.0166	0.0077	0.051
		closed	3	0.0016	0.0029	
	Duparquet, QC	open	8	0.0348	0.0264	0.455
		closed	6	0.0146	0.0182	
	Foret Montmorency, QC	open	4	0.0145	0.0179	0.159
		closed	4	0.0329	0.0143	
	Chicoutimi, QC	open	1	0.0489	0	-
		closed	3	0.0673	0.0471	

Continued on next page.

Table 4.5. continued.

Species	Study location	Canopy regime	# permanent	Mortality rate	Standard deviation	P
Black spruce	Manitoba Shield, MB	open closed	3 3	0 0.0016	0 0.0027	0.423
	Iroquois Falls, ON	open closed	4 4	0.0046 0.0263	0.0061 0.0121	0.035
	Ashuapmushuan Reserve, QC	open closed	4 4	0.0036 0.0200	0.0072 0.0126	0.073
White spruce	EMEND, AB	open closed	4 4	0 0	0 0	-
	Lac La Biche, AB	open closed	4 4	0 0.0089	0 0.0108	0.193
	Duck Mountains, MB	open closed	3 3	0 0.0066	0 0.0077	0.273
	Duparquet, QC	open closed	3 3	0.0220 0.0176	0.0213 0.0166	0.756

Table 4.6. Cox PH regression models for trembling aspen regeneration growing under either open (post-harvest) or closed canopy conditions, for each study location. The exponent of the variable coefficient B is a factor that predicts change in hazard for a unit increase in the predictor variable. Values < 1 indicate a decrease in hazard, or increase in predicted survival time, with increasing values of the predictor variable. The 95% confidence intervals for $\exp(B)$ are presented. Variables were entered into models using a forward likelihood ratio test at a 5% significance level. Only models with significant X^2 test statistics (a measure of change in -2Loglikelihood between successive models: each successive model has an additional predictor variable), and significant Wald test statistics (results displayed) are presented. *Percent PPFD was examined separately from morphological variables, resulting in two Cox models for each treatment combination: one predicting hazard from morphological variables (1) and one predicting hazard from light availability (2).

Region	Canopy regime	Model*	Variables in model	B	se	Wald statistic	df	P	95% CI for $\exp(B)$	
									Lower	Upper
EMEND, AB	open	1	Live crown ratio	-3.744	1.831	4.183	1	0.014	0.024	0.001 0.857
		1	Height	-0.033	0.006	29.252	1	<0.001	0.968	0.956 0.979
	closed	2	%PPFD leader	-0.054	0.012	21.526	1	<0.001	0.947	0.926 0.969
		2	%PPFD leader	-0.044	0.008	31.511	1	<0.001	0.957	0.942 0.972
Lac La Biche, AB	open	1	Live crown ratio	-5.448	1.249	19.043	1	<0.001	0.004	0.001 0.050
		2	%PPFD leader	-0.044	0.008	31.511	1	<0.001	0.957	0.942 0.972
	closed	1	Live crown ratio	-4.257	1.340	10.087	1	<0.001	0.014	0.001 0.196
		2	%PPFD leader	-0.052	0.025	4.274	1	0.039	0.950	0.905 0.997
Duck Mountains, MB	open	1	Height	-0.014	0.003	17.184	1	<0.001	0.987	0.980 0.993
		1	Live crown ratio	-4.564	0.888	26.406	1	<0.001	0.003	0.001 0.017
	closed	2	%PPFD leader	-0.043	0.006	47.306	1	<0.001	0.958	0.946 0.970
		2	%PPFD leader	-0.058	0.025	5.439	1	0.020	0.944	0.899 0.991
Manitoba Shield, MB	open	1	Height	-0.009	0.003	8.295	1	0.004	0.991	0.985 0.997
	closed	1	Height	-0.011	0.003	14.299	1	<0.001	0.989	0.983 0.995
Duparquet, QC	open	1	Height	-0.012	0.001	96.804	1	<0.001	0.988	0.985 0.999
	closed	1	Height	-0.011	0.002	43.415	1	<0.001	0.989	0.986 0.992

Table 4.7. Cox PH regression models for balsam fir advance regeneration growing under either open (natural gap) or closed canopy conditions, for each study location. The exponent of the variable coefficient B is a factor that predicts the change in hazard for a unit increase in the predictor variable. Values <1 correspond to a decrease in hazard, or increase in predicted survival time, with increasing values of the predictor variable. The 95% confidence intervals for $\exp(B)$ are presented. Variables were entered into models using a forward likelihood ratio test at a 5% significance level. Only models with significant X^2 test statistics (a measure of change in -2Loglikelihood between two successive models, where each successive model has an additional predictor variable), and significant Wald test statistics (results displayed) are presented. Study locations where none of the variables examined were important predictors of mortality risk are also shown. *Percent PPFD was examined separately from morphological variables, resulting in two potential Cox models for each treatment combination: one predicting hazard from morphological variables and one predicting hazard from light availability. Saplings growing under closed canopy in EMEND plots are the only ones for which the causal factor %PPFD is a good predictor of mortality

Region	Canopy regime	Variables in model	B	se	Wald statistic	df	P	$\exp(B)$	95% CI for $\exp(B)$	
									Lower	Upper
EMEND, AB	open	Live crown ratio	-4.324	1.541	7.876	1	0.005	0.013	0.001	0.271
	closed	Live crown ratio	-7.835	1.867	17.602	1	<0.001	0.0003	0.0001	0.015
		%PPFD leader*	-0.225	0.083	7.254	1	0.007	0.799	0.678	0.941
Duck Mountains, MB	open	Live crown ratio	-4.670	0.896	27.145	1	<0.001	0.009	0.002	0.054
Duperquet, QC	open	Live crown ratio	-1.291	0.395	10.654	1	0.001	0.275	0.127	0.597
	closed	Live crown ratio	-1.177	0.459	6.582	1	0.010	0.308	0.123	0.757
Forêt Montmorency, QC	open	-	-	-	-	-	-	-	-	-
	closed	-	-	-	-	-	-	-	-	-
Chicoutimi, QC	open	Diameter	-3.571	1.148	9.685	1	0.002	0.028	0.003	0.267
	closed	-	-	-	-	-	-	-	-	-

CHAPTER 5

SAPLING GROWTH AND CROWN MORPHOLOGY IN CONTRASTING LIGHT ENVIRONMENTS FOR FOUR PREDOMINANT TREE SPECIES ACROSS THE CANADIAN BOREAL FOREST

5.1 Introduction

Across forest types, studies of gap dynamics have recognized two categories of tree species: large gap specialists that require high levels of radiation, and small gap specialists that can survive for extended periods as saplings in low light (McCarthy 2001). Associated with these life history strategies are distinctive growth patterns. In the boreal forests of North America early successional species such as trembling aspen (*Populus tremuloides* Michx.) allocate photosynthate preferentially to height growth, whereas later successional species such as balsam fir (*Abies balsamea* (L.)), white spruce (*Picea glauca* (Moench) Voss), and black spruce (*Picea mariana* (Mill.) BSP) growing in the shaded understory may allocate resources more to lateral growth and/or foliage (McCarthy 2001). Furthermore, shade-tolerant coniferous species such as spruces, and in particular firs, exhibit plasticity of crown morphology in response to variable light conditions (Klinka et al. 1992; Williams et al. 1999; see review by Ruel et al. 2000); such conditions exist in forests dominated by gap-forming disturbances.

DeLucia et al. (1998) observed patterns of sapling biomass allocation corresponding to three different growth strategies in an eastern deciduous forest. These strategies were described as follows: (1) the maintenance of low specific leaf area (leaf area/leaf mass) and leaf area ratio (leaf area/sapling mass) as a defense mechanism against herbivores and pathogens; (2) the maintenance of high specific leaf area and leaf area ratio to achieve high growth rates in shade; and (3) the allocation of biomass to carbohydrate storage for opportunistic growth following gap formation. Various strategies for light competition might be considered a game theoretic problem, where the success of one strategy depends on which other strategies are present (Falster and Westoby 2003).

The response of established natural regeneration to environmental changes associated with canopy gap formation is of interest for interpreting stand dynamics; differential growth and survival of juvenile trees among species may have substantial effects on forest composition during secondary succession (Kobe et al. 1995, Kobe 1997, Kobe and Coates 1997). Furthermore, the response of advance regeneration to changes in canopy closure is important for refining silvicultural practices in which advance growth is preserved as immediate growing stock to renew forests (Ruel et al. 1995, Örlander and Karlsson 2000, Ruel et al. 2000; Kneeshaw et al. 2002).

Height and branch growth are critical measures of sapling performance because it is through this extension growth that saplings are able to exploit available space and higher light microsites, and potentially overtop surrounding vegetation to pre-empt access to light (Beaudet and Messier 1998, Falster and Westoby 2003). In conjunction with height growth, additional crown- or plant-level morphological measures can be examined for a more complete description of whole-plant performance in response to light availability. These measures include live crown ratio (crown length/total height), crown profile (crown length/mean crown diameter), leader to lateral branch ratio (L:B ratio), and height to diameter ratio (Beaudet and Messier 1998, Williams et al. 1999, Claveau et al. 2002). The L:B ratio is often used to examine growth of shade tolerant coniferous species because it reflects plastic change in crown form from a conical shape to a more flat-topped shape that may accompany changes in sapling photosynthetic efficiency (Williams et al. 1999).

Hunt (1978, 1982) summarized two overall approaches to plant growth analysis: (1) the 'classical' approach, where plant growth is followed over time with relatively infrequent measurements but with large replication of measurements and plant size is averaged over a period intervening two successive measurements; and (2) the 'functional' or 'curve-fitting' approach, where measurements are more frequent and instantaneous values of growth are derived from curves fitted to the data. A third approach to the modelling of plant growth analysis is a "mechanistic" approach, where growth is modelled based on dividing a plant system into components, and by examining their individual behaviour and interactions, understand the workings of the whole system (Thornley 1976). In the present study a classical approach is applied to investigate

sapling growth over a 2.5-year period, because our sample size is very large, but the growth measurements relatively infrequent.

The main objective of this chapter is to summarize differences in growth of established natural regeneration of important boreal tree species including white spruce, black spruce, balsam fir, and trembling aspen between contrasting light environments associated with the presence or absence of canopy cover, across the Canadian boreal forest. The specific goals are to: (1) summarize and explain height fluctuations (resulting from growth, herbivory, stem dieback and other causes) of saplings over a 2.5-year period; (2) compare distributions of height growth rates between contrasting light environments by assessing deviation of growth distributions from normality; (3) compare distributions of current height with projections of future height derived using empirical growth rates and a simple exponential model; (4) compare mean height and crown morphology between light environments; (5) determine the ability of %PPFD availability to predict growth and crown morphology within a defined category of canopy closure ("open" or "closed"); (6) compare mean growth rates and %PPFD availability among study locations and permanent plots; and (7) summarize the occurrence of mammal herbivory.

5.2 Analytical methods

5.2.1 Mean height over time

A considerable number of the saplings monitored exhibited a decrease in height from one year to the next during the course of the study. This occurred primarily in trembling aspen, and to a lesser degree in balsam fir, as a result of any combination of stem dieback, herbivory, and/or mechanical damage, which confound the effect of light on height growth. To summarize effective change in height over time for all monitored juveniles, a height-time curve was generated for each canopy treatment, study location, and species. Mean height and standard deviation for each canopy condition/study location/species combination was determined for each census time.

5.2.2 Derived response variables

In order to compare growth among saplings of different initial sizes, growth rates were standardized to unit size (relative growth rates). The average relative height growth rate (RHG) over the three growing seasons examined was determined for each sapling alive at the end of the study period according to Equation 5.1:

$$RHG = \frac{\ln(\text{height}_2) - \ln(\text{height}_1)}{\text{time}_2 - \text{time}_1} \quad [5.1]$$

where time_2 corresponds to end of the study period and time_1 corresponds to the beginning of the study. Measured annual heights for coniferous species were 'corrected' for growth analyses (in cases where no browse or dieback occurred) by adding the height increment (leader length) each year to the original height measurement. This approach was used for examining conifer height growth since inter-annual variation in height measurements was partially attributable to soft or variable ground conditions (coarse woody debris, feathermoss). Raw height measures were used for aspen. Although there was some variation in annual RHG from year to year, a main objective was comparing long-term growth in contrasting light environments; therefore, growth rates were averaged over the three growing seasons. For aspen, relative diameter growth (RDG) was calculated using the same formula but substituting basal diameter measurements in place of height measurements.

Two measures of crown morphology were examined. The ratio of the leader branch length to the length of the longest first-order lateral branch immediately subtending the leader (L:B ratio) was used to determine the degree of apical dominance over lateral growth (Kneeshaw et al. 1998, Williams et al. 1999, Ruel et al. 2000). This variable was examined for the coniferous species studied. In addition to L:B ratio, the ratio of depth of live crown to total height (live crown ratio) was examined for all four species. Values from the first year of the study were used.

5.2.3 Distribution of relative growth rates

Study locations were treated separately for all growth analyses, since starting conditions such as regeneration density and age, and external growing conditions such as stand age and density, and other environmental characteristics, differ among locations. Summary statistics were calculated and frequency histograms of average relative height growth (RHG) were generated for each species/study location/canopy condition combination to examine and compare growth distribution curves in low and high light environments.

Saplings exhibiting negative change in height over time were removed from analysis in an attempt to minimize the effect of herbivory, dieback, and mechanical damage from growth summaries. Saplings with growth rates of zero were included in analysis so as not to exclude suppressed individuals exhibiting a genuine lack of height growth (as opposed to those showing positive growth, but being browsed, or dying back over winter). This approach is relatively crude: undoubtedly some saplings that experienced herbivory and other forms of damage still show a positive (or zero) overall change in height over three growing seasons. Nonetheless, such an approach removes from analysis individuals exhibiting dramatic declines in height as a result of confounding factors such as herbivory or winter stem dieback. Individuals exhibiting unusually large increases in height as a result of re-sprouting from a previously inactive upper branch (common in aspen, see Figure 5.1) were removed from calculations of RHG summary statistics and generation of frequency histograms.

Departures from a normal distribution were assessed using beta measures of symmetry and kurtosis, which were modified for comparison to critical values (at a significance level of 0.05) provided in Zar (1999). To compare mean RHG in open and closed canopy conditions, t-tests (assuming unequal variance) were performed for each study location and species. Sample sizes for t-tests were the number of permanent plots in open and closed canopy conditions. The number of plot replicates is relatively low for a given canopy condition and study location (n ranges from 1 to 8) therefore, the power of each of the t-tests is low. Tests were not performed for aspen plots in Manitoba Shield, MB ($n=1$ in closed canopy conditions at the end of the study), or fir plots in Chicoutimi

QC (n=1 for open canopy conditions). Analyses were performed using Data Desk 6.1 for the MacIntosh (Data Description Inc.).

5.2.4 Height distribution at study onset and after several years of exponential growth using empirical growth rates

Given annual growth rates and initial heights, simple projections of future growth were derived for each sapling alive at the end of the study period and exhibiting positive change in height over time. Annual height at the end of a defined time period was estimated for each sapling using the basic model of exponential growth:

$$\text{Height}_t = \text{height}_0 e^{RHG(t)} \quad [5.2]$$

where height_t is the height at time t elapsed from study onset (time=0); height_0 is the initial height at study onset; and RHG is the estimated standardized height growth per year based on the three growing seasons of the study. Projections were truncated when the tallest trees in a given species/study location/light treatment group reached a maximum height of around 30 m; corresponding time elapsed ranged from 6-30 years depending on species, study location, and light environment. Frequency histograms of height at both study onset and at time t were examined for each species/study location/light treatment combination. Departures from a normal distribution were assessed using beta measures of symmetry and kurtosis, which were modified for comparison to critical values (at a significance level of 0.05) provided in Zar (1999). Analyses were performed using Data Desk 6.1 for the MacIntosh (Data Description Inc.).

5.2.5 Summary statistics and discrete analysis of growth rates and crown morphology

Summary statistics for each species were computed for RHG (and RDG for aspen), L:B ratio, live crown ratio, and %PPFD for each canopy regime within a study location. L:B and live crown ratios from the first year of the study were used. All individuals alive at the end of the study period were included, except those with missing values for the variable examined (eg. individuals with a missing leader branch, thus, no

value for L:B ratio). To compare sapling growth and morphological response variables, and light availability between open and closed canopy environments, t-tests were performed. Variables examined were %PPFD, RHG, RDG for aspen, live crown ratio, and L:B ratio for coniferous species. Sample sizes for t-tests were the number of permanent plots in open and closed canopy. All saplings alive at the end of the study period were included in these summary statistics and analyses. The number of plot replicates for open and closed canopy conditions is relatively low for each study location (n ranges from 1 to 8) therefore, the power of each of the t-tests is low. Statistical comparisons of initial height and diameter between light environments were not performed since size was used as the criteria for selecting saplings for plot establishment and was not the response variable of interest; however, summary statistics of these initial measures in both open and closed canopy environments are provided. Analyses were performed using Data Desk 6.1 for the MacIntosh (Data Description Inc.).

5.2.6 Linear regression

Simple linear regression models were examined for each species-study location-light treatment combination. Sapling response variables examined include RHG, RDG, L:B ratio, and live crown ratio, and the predictor variable of interest was relative light availability (%PPFD) at the level of the individual sapling. Again, only individuals that showed positive growth, and no evidence of browse or dieback were included in regression analysis. Live crown ratio and L:B ratio measurements were used from the study year when light measurements were made in a given study location. Some distributions of dependent variables, particularly RHG, differed significantly from normality for some species/study location/canopy treatment combinations. These data were natural log transformed, rendering them slightly more normal; regressions using transformed and non-transformed data were compared in such cases, and did not differ appreciably in their regression or significance. Thus, for consistency, results using non-transformed data are presented.

5.2.7. Plot-level comparisons of mean RHG and %PPFD

For each species, mean RHG values for each individual permanent plot were plotted against mean %PPFD measures for each permanent plot, across light environments and all study locations. The variation displayed in these scatterplots incorporates that of different canopy treatments, study locations, and permanent plots. Mean RHG and mean %PPFD have bimodal distributions when pooled across open and closed canopy treatments. Two groups of points in each species' scatterplot of mean plot RHG vs. mean plot %PPFD are evident: one in the upper right corner of the x-y plane corresponding to open canopy plots, and one in the lower left corresponding to closed canopy plots. Therefore, linear regression analysis was not performed using these data. Sample size and standard deviation for each mean RHG and %PPFD of a permanent plot were computed. In cases where notable variation among permanent plots was apparent within a given light environment and study location, one-way ANOVA was performed for initial heights in each of the replicates explain inconsistencies in growth and light availability among permanent plots.

5.2.8 Herbivory

Herbivory by mammals was commonly noted in most study locations for trembling aspen and to a lesser degree, balsam fir saplings, over the course of the study period. For each of these species the proportion of individuals browsed each year was determined for each light treatment and study location, and averaged to provide an overall estimate of the percentage browsed per year. Because herbivory was not monitored in all study locations each year, and the type of data collected was inconsistent among study locations, analyses were not performed to compare herbivory among light environments or study locations. Therefore, mean and standard deviations were computed only to provide a coarse description of herbivory.

5.3 Results

5.3.1 Mean height over time

Aspen suckers tend to exhibit a slight decrease in height from fall to spring each year, particularly under full canopy closure, for study locations that measured height in spring (Figure 5.2, A-C). This decrease may result from a combination of stem dieback over winter, browse, and also perhaps from conservative height measures in the spring before leafing out occurs. Dieback and browse were both extremely common and are likely the primary causes of slight overall decreases in mean height from fall to spring. There is a divergence over time between the height curves for aspen growing in low and high light environments, although this varies among study locations (Figure 5.2). The only study location that doesn't exhibit a divergence in aspen height curves between open and closed canopy conditions is Manitoba Shield, which had a comparably small number of saplings as a result of high mortality. The few living suckers in closed canopy conditions that remained at the end of the study period in this study location are a biased representation of suckers originally selected.

A difference in overall height change between light environments is also notable in two study locations for balsam fir (Figure 5.3), consistently among study locations for black spruce (Figure 5.4), and less consistently for white spruce (Figure 5.5). The marked separation of low and high light growth curves for black spruce reflects the dramatic difference in light conditions between the open (large carefully harvested areas) and closed canopy (black spruce forest) treatments.

Interestingly, there are some study locations in which growth curves for the two light treatments remain parallel with one another; nevertheless, the mean height for the high light environment is invariably higher than that in the low light environments. Although saplings were originally selected based on size criteria, the same size criteria was used in both open and closed canopy plots; therefore, the larger height of saplings in high light environments is reflective of the population from which they were sampled, not a result of sample bias. Differences in initial height among saplings may partially reflect age differences; however, the overall difference in heights between light environments is

suggestive of higher growth rates in higher light conditions. Permanent plots of each canopy treatment were paired such that conditions other than canopy closure were similar, and in most cases this meant that open and closed canopy plots were immediately adjacent to one another, and consisted of advance regeneration (for coniferous species) of similar age.

5.3.2 Distribution of relative growth rates

All RHG values presented (means and standard deviations) are in units of cm/year. For most study locations there are notable differences in the distribution of RHG of aspen suckers between low light and high light environments (Figure 5.6). This trend is also apparent for balsam fir (Figure 5.7), black spruce (Figure 5.8), and white spruce (Figure 5.9), although there are some exceptions. For instance, there is little difference in RHG distributions between closed canopy conditions and canopy gaps for balsam fir regeneration in EMEND, AB, and Duparquet, QC (Figure 5.7 A, D). All distributions except that of black spruce regeneration in high light conditions in the Ashuapmushuan Reserve, QC, are unimodal. RHG scales differ among study locations, since initial characteristics of the regeneration, and growing conditions, differ somewhat among regions, resulting in different expressed ranges of RHG.

Trembling aspen

Mean RHG of aspen suckers in open canopy conditions is not significantly higher than that under closed canopy conditions for any of the study locations (EMEND, AB, P=0.324; Lac La Biche, AB, P=0.257; Duck Mountains, MB, P=0.203; Duparquet, QC, P=0.121). A statistical test was not used to compare mean growth between open and closed canopy plots in Manitoba Shield, MB, because live saplings remained in only one closed canopy plot at the end of the study period (n=1 for closed canopy conditions).

RHG distributions differ in their symmetry between high and low light conditions for some study locations (Figure 5.6 A, C, D, E) but not for others (Figure 5.6 B). In all locations but Manitoba Shield, the upper 25th percentile is higher in open canopy conditions. Coefficients of skewness, which describe the deviation of the distribution

symmetry from that of a normal distribution, are in all cases but for EMEND, AB, more different from a normal distribution for closed canopy conditions than for open canopy, clearcut conditions. The negative skewness of RHG distribution for open canopy conditions in EMEND shows that most saplings are growing at the upper range of growth values exhibited, with very few growing at lower values of RHG as illustrated by the long "tail" trailing into lower values. For all other study locations, sapling response to higher light conditions is indicated by a more even spread of individuals among mid-range values of RHG in open canopy than closed canopy conditions. In contrast, poorer growth in lower light conditions is generally illustrated by the highly positively skewed distributions with long tails stretching into higher values, representing very few individuals growing at high values of RHG, and many growing at the lowest values of RHG. Growth distributions in open canopy conditions in EMEND, AB, and for both open and closed canopy conditions of Manitoba Shield, MB, are symmetric.

Across study locations, coefficients of kurtosis, which describe the degree of peakedness in the distributions' shape, are more mesokurtic (closer to normal distribution) for high light environments; however, the sign of the coefficient differs among study locations, and for Duparquet, QC, between light environments. Distributions for EMEND, AB, Manitoba Shield, MB, and high light plots in Duparquet have negative coefficients of kurtosis (platykurtosis), with shorter tails and a wider flatter "hump" than that of a normal distribution. This describes a clustering of values within the range of mean \pm standard deviation, particularly in closed canopy conditions where the coefficient deviates further from zero. On the other hand, Lac La Biche, AB, Duck Mountains, MB, and low light plots in Duparquet have positive coefficients of kurtosis (leptokurtosis), with longer tails and a more narrow central hump than a normal distribution; again, this is most dramatic in closed canopy conditions. These distributions describe a concentration of values around the mean and/or in the tails. All coefficients of kurtosis for closed canopy conditions are significant at $P=0.05$, except for Lac La Biche and Manitoba Shield; none of the frequency histograms for *open* canopy conditions differ significantly from mesokurtosis.

Balsam fir

Mean RHG is significantly higher in open canopy than closed canopy conditions only for one study location: Forêt Montmorency, QC ($P=0.002$) (Figure 5.7 E). There is no significant difference in mean RHG between open canopy and closed canopy conditions for EMEND, AB ($P=0.700$), Lac La Biche, AB ($P=0.094$), Duck Mountains, MB ($P=0.444$), or Duparquet, QC ($P=0.818$). RHG of balsam fir saplings may vary between open and closed canopy conditions only if the light environments are substantially different from one another. Statistical tests comparing mean growth between open and closed canopy conditions were not performed for Chicoutimi plots as there was only one plot replicate of open canopy conditions ($n=1$). Though mean plot growth rates were not significantly different between open and closed canopy conditions, more individuals exhibit RHG in upper range of values in open canopy conditions for most study locations as indicated by the upper 25th percentile, which is slightly higher for open canopy than closed canopy conditions (Figure 5.7).

The shape of RHG distributions for balsam fir saplings differ among study locations: differences in growth distributions between low and high light environments are inconsistent among study locations (Figure 5.7). Forêt Montmorency, QC, stands apart from other regions because of the much higher maximum values for RHG, and the marked difference in distributions between open and closed canopy conditions; although open and closed canopy histograms for Chicoutimi, QC are also distinct from one another. Both study locations differed from other locations by the nature of the canopy gaps under which balsam fir was monitored: open canopy conditions in these study locations resulted from large spruce budworm outbreaks. The difference in maximum RHG expressed under canopy gaps between Forêt Montmorency and Chicoutimi may be attributable to the size of the budworm gap (much more extensive in the Forêt Montmorency than the Chicoutimi location) and resulting light conditions (see below summary statistics of mean %PPFD at sapling apices for each study location and light treatment).

All balsam fir histograms, for both open and closed canopy conditions are significantly positively skewed; tails trailing into the upper ranges of RHG values illustrate that few saplings, under either closed canopy, or canopy gap conditions, exhibit

high growth rates in the range of values expressed. In addition, coefficients of kurtosis are significantly different from zero (leptokurtic) for all but closed canopy conditions in Lac La Biche, AB, open canopy conditions in Duck Mountains, MB, and closed canopy conditions in Forêt Montmorency, QC, and Chicoutimi, QC. In general, with the exception of balsam fir regeneration located under extensive spruce budworm-caused canopy caps, the differences in RHG distribution between low and high light environments is less pronounced for balsam fir than for aspen. This is likely a result of both differences in species response to light availability, and differences in light conditions between open and closed canopy conditions for these two species.

Black spruce

Mean RHG is significantly higher in open canopy than closed canopy conditions for all study locations (Manitoba Shield, MB, $P=0.0001$; Iroquois Falls, ON, $P<0.0001$; Ashuapmushuan Reserve, QC, $P=0.014$). All study locations of black spruce show a dramatic difference in distribution of growth rates between open and closed canopy conditions (Figure 5.8). The upper and lower 25th percentiles are higher in open canopy conditions. Histograms of growth rates in closed canopy conditions are significantly positively skewed; for Manitoba Shield, MB, and Iroquois Falls, ON, locations closed canopy histograms are also significantly leptokurtic. With the exception of open canopy (harvested) black spruce plots in Ashuapmushuan Reserve, QC - the only example of a bimodal distribution of growth rates within a defined light environment - growth distributions in open canopy conditions are not significantly different from normal; however the positive skewness of the growth distribution in open canopy Manitoba Shield, MB, plots is significant. As compared with trends for aspen and fir, differences in growth distribution between canopy conditions are marked for black spruce, where vast carefully harvested sites have markedly different light environments than the understory of closed black spruce stands. Black spruce growth distributions are similar to those for balsam fir (both are shade-tolerant coniferous species) occurring under extensive spruce budworm gaps, where light conditions differ dramatically from adjacent shaded understory conditions.

White spruce

Mean RHG is significantly higher for open canopy than closed canopy conditions for Lac La Biche, AB ($P=0.009$) and Duck Mountains, MB ($P=0.049$), but not for EMEND, AB ($P=0.405$) or Duparquet, QC ($P=0.379$). Frequency histograms of white spruce height growth are similar among study locations: the lower and upper 25th percentiles are higher in open than closed canopy conditions, and growth distributions in closed canopy conditions are significantly positively skewed. In all cases but one (Figure 5.9 A), closed canopy histograms are also significantly leptokurtic. Distributions for open canopy conditions in EMEND and Duparquet are also significantly positively skewed, and leptokurtic; however, distributions for open canopy conditions are generally more normal than those for closed canopy conditions. The upper 25th percentile is higher for open canopy conditions for all study locations.

5.3.3 Height distribution at study onset and after several years of exponential growth using empirical growth rates

For all four species there is marked difference in symmetry and kurtosis of height distributions for both open and closed canopy conditions before and after several years of predicted exponential growth (Figures 5.10-5.13). In general, positive skewness and kurtosis of height distributions both increase over time. All height distributions but one (Figure 5.10 D, which has a comparably low sample size) have symmetry and kurtosis significantly different from that of a normal distribution after several years of exponential growth. Over time, if the few individuals exhibiting the highest growth rates in our study continue to outgrow the majority of saplings (assuming a basic model of exponential growth) future height distribution will be significantly positively skewed and leptokurtic. The majority of individuals will exhibit heights lower than the mean, and heights will be more clustered around the mean and/or tails more so than a normal distribution, as a result of a few individuals being considerably taller than the majority (positive skewness).

In many cases, the degree of skewness and kurtosis is more pronounced in one light environment than the other, within a study location. In open canopy conditions for this study, light is not a limiting factor for white spruce or black spruce, which are located

in sparsely populated post-harvest stands (black spruce), or disturbed roadsides and abandoned gravel extraction pits (white spruce). For open canopy conditions, light is perhaps more limiting for balsam fir growing in canopy gaps (less so when gaps are extensive in size), and for aspen suckers growing in post-clearcut stands exhibiting extremely dense vegetative regeneration.

Although many factors will restrict future growth and survival of the fastest growing saplings, exponential projections illustrate the potential outcome of differential growth rates among individuals in the sub-canopy using the height and growth data at our disposal. These results have important implications for future forest growth: fast rates of height growth at an early sapling stage of development in the forest understory may confer advantages to subsequent recruitment into the canopy.

5.3.4 Discrete analysis of growth and crown morphology

Mean light availability is significantly higher in open than closed canopy environments for all species and most study locations (Tables 5.1-5.4). For summary statistics and analyses presented here and in Tables 5.1-5.4, all individuals alive at the end of the study period are included (except those with missing values such as leader length). Therefore, RHG here is a broad measure of overall change in height over the 2.5-year period, including both positive and negative changes in height.

All species exhibit elevated relative growth rates in open canopy regimes (Tables 5.1-5.4) however, this is consistent across study locations only for black spruce. This may reflect in part the larger variation between open and closed canopy conditions for black spruce as compared to the other species. Balsam fir demonstrates greater RHG in canopy gaps than under closed canopy only for Forêt Montmorency, QC plots, where there is a marked difference in light conditions between open and closed canopy conditions. White spruce open canopy conditions were high radition sites comparable to those for black spruce, however, the average light availability under the closed mixed-conifer canopy where white spruce was monitored is generally higher than that under black spruce canopy where black spruce regeneration was monitored, and the difference in light conditions between the two canopy treatments may not be as dramatic as for black

spruce. Aspen open canopy conditions were high radiation sites, higher than or comparable to those for black spruce. However, there is more variation in mean RHG among aspen plots than for black spruce. Factors in addition to light availability, such as stem density, herbivory, and perhaps underground associations affect aspen RHG.

Within a species, RHG is similar across regions, with a few exceptions. White spruce growth in open plots is higher in Duck Mountains, MB than in other regions; black spruce growth in open plots is higher in the Ashuapmushuan Reserve, QC than in other regions; and balsam fir growth in open plots is higher in Forêt Montmorency, QC than in other regions. All of these plots exhibit extremely high mean %PPFD relative to other open plots of a given species, which may explain the high RHG observed. The extensive spruce budworm gaps at the Forêt Montmorency plots result from a disturbance regime typical in eastern forests, but not western ones. Inter-regional differences in light environments exist for balsam fir regeneration, and its response varies across study locations. Differences in light availability and corresponding RHG among regions for white and black spruce may be reflection of variation in site conditions, however, a longer study period is needed to determine if regional-level variation in sapling growth exists and what regional-level factors (eg. climate) are important

Crown morphology

Mean L:B ratios are >1 in open canopy environments for the two spruce species (Tables 5.1-5.4). The spruces exhibit stronger apical dominance in disturbed and post-harvest sites, and weaker apical dominance under closed canopies. Differences in L:B ratio between open and closed canopy conditions are significant for all study locations of black spruce, and two of four study locations of white spruce. There is a significant difference in balsam fir L:B ratio between gaps and closed canopy conditions only in Forêt Montmorency, QC. These results generally support the idea that shade-tolerant coniferous species exhibit weak apical dominance in low light environments (as saplings forage horizontally for higher-light microsites), but restore apical dominance in high light conditions following natural disturbance or harvesting (eg. Williams et al. 1999).

Results are similar for live crown ratio: mean plot live crown ratio is significantly greater in high than low light regimes for most study locations for black and white

spruce, and only for Forêt Montmorency for balsam fir. Mean plot live crown ratio is not significantly different between open and closed canopy conditions for aspen.

5.3.5 Linear regression

Apart from a few exceptions, the coefficients of determination are generally very low for linear regression models (for each species/study location/canopy treatment combination) predicting RHG (saplings exhibiting overall decrease in height removed) by %PPFD (Table 5.5). One explanation for the poor predictive ability of %PPFD is that an average calculation of height growth over the three growing seasons may obscure the relationship between growth and light by ignoring any height fluctuations (resulting from herbivory, stem dieback, shifting of apical dominance from one branch to another, and other factors) that may have occurred between the spring of 2000 and the fall of 2002 for a given sapling. Although these confounding factors are considerable for aspen and fir, they are not as influential for spruce regeneration. A further explanation for the poor relationship between light and height growth is the relatively narrow range of light conditions available within each canopy treatment. Moreover, only saplings alive at the end of the study period were used for growth analysis, excluding many of those growing under the lowest light conditions. Therefore, the range of light conditions for each regression model may be too narrow to elucidate a clear relationship between light availability and height growth. Furthermore, light may not be a limiting factor in many cases, in particular for white and black spruce growing under open canopy conditions and perhaps balsam fir growing under large gaps at Forêt Montmorency, QC. The limited variation in light availability within a canopy treatment, and unlimited light availability in some of our open canopy treatments, may also explain the relatively poor ability of light to predict variation in both live crown ratio and L:B ratio, and RDG for aspen (however, the diameter measurements taken were not very sensitive). Moreover, light measurements were made only once for each sapling, over the course of several seconds, at midday, in cloudy weather. These measurements may not reflect year-round light conditions. Light does predict live crown ratio consistently among regions for aspen regeneration in open sites; nonetheless, there remains much residual variation for these models.

5.3.6 Plot-level comparisons of mean RHG and %PPFD

There exists variation in the mean RHG and %PPFD among replicate plots within a canopy regime and study location (Figures 5.14-5.17). However, plots for a given canopy treatment and study location generally form groups in the RHG-%PPFD plane. Variation among permanent plots within a given study location is most notable: (1) for "open canopy" replicates of trembling aspen in Duck Mountains, MB, where plot 'DM83S' has a markedly lower mean %PPFD and corresponding mean RHG than either of the other two permanent plots (Figure 5.14); (2) for open canopy permanent plots of balsam fir regeneration in Forêt Montmorency, QC where mean RHG of plot 'FM4, QC' is higher than that for the other three plots (Figure 5.15); (3) among open canopy permanent plots in the Ashuapmushuan Reserve, QC, where plot 'AR3, QC' has a much lower mean RHG than the other three replicates (Figure 5.16); and (4) among open canopy sites of white spruce regeneration within Duck Mountains, MB, where plot 'DMI, MB' has a substantially lower mean RHG than other open canopy replicates (Figure 5.17). Outlying permanent plots for Duparquet, QC, are largely a result of low sample size (limited by %PPFD data) (see Appendix 3 for sample sizes and standard deviations of mean values presented for each permanent plot).

For aspen plot 'DM83S' in Duck Mountains, MB (Figure 5.14), both mean RHG and %PPFD are lower than for other replicates, suggesting that growth may be lower in this plot as a result of lower light availability for those individuals monitored. Higher mean RHG of balsam fir plot "FM4, QC" than that of other open canopy replicates in Forêt Montmorency, QC, may reflect the significantly smaller initial mean height of trees sampled in this plot (mean height/standard deviation in cm for open canopy plots 1 through 4 respectively are 64.29/31.31, 50.09/26.45, 67.20/26.19, and 46.56/22.04) (Figure 5.15). Smaller trees may have lower maintenance costs than taller trees, allowing for more allocation of photosynthate to height growth. Mean RHG of black spruce regeneration in permanent plot '3' (AR3, QC) of open canopy conditions in the Ashuapmushuan Reserve, QC is much lower than RHG means for the other three replicates (Figure 5.16). This may also be a result of significant differences in mean initial heights of saplings among permanent plots; saplings in that particular plot were

significantly taller at study onset ($P<0.0001$) (mean height/standard deviation in cm for plots 1 through 4 respectively are 48.66/21.75, 58.68/23.24, 85.98/24.70, and 44.70/18.071). Although RHG is a standardized measure that corrects for differences in absolute height among individuals, factors affecting growth may differentially affect differently sized individuals. Similarly, white spruce saplings in open canopy replicate 'DMI, MB' have a significantly smaller mean initial height than those at the other two high light replicates ($P<0.0001$) (mean height/standard deviation in cm for plots W, G, and I respectively are 65.01/26.60, 64.14/25.14, and 35.14/13.70). However, in this case RHG is *lower* for the plot with smaller saplings; this particular plot was frequently flooded as it was located close to the water table in a deserted gravel mine; it is conjectured that extreme conditions of frequent water logging and extremely high radiation levels, may have hindered sapling growth in this site.

5.3.7 Herbivory

Trembling aspen and balsam fir, the two species with the highest mortality rates, are also the only species to have undergone appreciable mammal herbivory. The average percentage of juvenile aspen browsed each year in a given canopy regime is relatively low for Duparquet, QC plots as compared to Alberta and Manitoba plots (Table 5.6). There may also be a difference in the importance of browsing species across plots or regions. Ungulate herbivores typically browse the leader and upper branches of both balsam fir and trembling aspen, whereas hare often girdle the base of aspen suckers, and browse on both lower and upper branches of balsam fir regeneration. The average percent of balsam fir browsed appears to be higher for Lac La Biche, AB, and Duck Mountains, MB plots than for either EMEND, AB or Québec plots. The dominant browse agent of balsam fir in Alberta is hare, whereas for other regions only herbivory by ungulates was reported. Differences in herbivore activity across study locations may be a reflection of localized conditions and herbivore population densities, or may suggest an overall difference in herbivore pressure on advance regeneration across regions. For both species, mean browse rates appear to be higher in closed canopy conditions than in canopy gaps or harvested sites.

Zamora et al. (2001) studied the impact of mammalian herbivory on sapling performance of Scots pine (*Pinus sylvestris* L.) in montane forests of southeast Spain. 72% of the monitored saplings (n=619) were browsed by livestock and wild ungulates (goats, sheep, and Spanish ibex) at some point in the 3-year study period. It was suggested that the time necessary to attain a stature great enough to escape herbivory, and to reach reproductive stage was delayed up to 12 years by ungulate herbivory in the montane Scots pine forests studied. The long-term effect of herbivore pressure on saplings in the North American boreal forest warrants further study.

5.4 Discussion

5.4.1 Height fluctuations of saplings in the understory

Trembling aspen and balsam fir saplings undergo annual height fluctuations that result from causes other than incremental growth of leader branches. Plots of mean aspen height over time illustrate that in some cases aspen saplings decrease in height between the end of one and start of a subsequent growing season; these decreases in height result partially from herbivory, and winter dieback. Pacala et al. (1994) note that sapling height should have increased 2-3 times faster than observed in their study of sapling growth of 10 species of conifer-hardwood and mixed oak forests of New England. The authors proposed that winter dieback of terminal leaders or browsing by deer were likely reducing effective height growth of saplings; for this reason, the authors presented data only for radial growth from harvested saplings. In our study, it was often observed that balsam fir saplings that had undergone herbivory or mechanical damage, resulting in damage to or removal of terminal leader branches, would compensate by a shift in apical dominance to a lateral branch. Changes in fir and aspen height over time were sometimes attributable in part to annual discrepancies in the leader branch measured. These results highlight the fact that for many saplings, particularly of aspen, and to a lesser degree fir, realized height growth differs from potential height growth in a given resource environment in the sub-canopy.

5.4.2 Inter-regional differences in sapling growth and crown morphology

The variation in sapling growth noted among regions may be the result of differences in plot-level rather than regional-level conditions. Claveau et al. (2002) compared growth and crown morphological responses of juvenile conifers of three different genera both in British Columbia and in Québec. They found that growth and morphological responses of saplings to different light classes were similar in both regions. Where differences were noted, they were attributable to site-specific differences between the study areas of the two regions.

Some of the variation in sapling growth observed among study locations can be considered a reflection of regional-level variation. As a result of differential disturbance regimes across the boreal forest, the canopy gaps in which balsam fir advance regeneration were monitored differ among study locations. In Québec study locations where balsam fir was monitored under vast spruce budworm-caused canopy gaps, the difference in growth and crown morphology between open and closed canopy plots is more dramatic than for other regions. The response of balsam fir to large spruce budworm-caused canopy openings is different than that which occurs under smaller canopy gaps. Similarly, Drobyshev and Nihlgård (2000) found that growth of Norway spruce (*Picea abies* (L.) Karst.) saplings was positively correlated with gap size.

Annual precipitation is also much higher in eastern forests (see Table 3.1, Chapter 3); higher growth rates of balsam fir in some Québec plots may reflect inter-regional differences in climate. Drobyshev and Nihlgård (2000) suggested that gap size was more important than climate in governing sapling growth. A continuation of our monitoring program for several more years may provide sufficient data to correlate regional climate data with sapling performance.

5.4.3 The effect of canopy opening on sapling growth and crown morphology

Black spruce exhibited higher growth rates (based on both mean growth rates and distributions of growth rates) in open canopy conditions than closed canopy conditions for all study locations. Trembling aspen demonstrated higher growth in open canopy

conditions for two of four study locations. White spruce, and balsam fir, the two species traditionally considered most shade tolerant of the four study species, demonstrated significantly higher mean growth per plot in open canopy conditions for only one study location each. Our results suggest that the more shade tolerant species (fir and white spruce) may respond less to canopy gaps than less shade tolerant species (aspen and black spruce). However, differences among species' responses may in part reflect differences in the type of high radiation environment selected (eg. natural gap for fir vs. fully harvested conditions for black spruce). In particular, differences in radiation between the selected open and closed canopy conditions vary among among species (eg. difference between a small canopy gap and adjacent closed canopy for fir vs. difference between a harvested site and closed understory for black spruce).

Results agree with previous studies, which have demonstrated that across species, growth rates of juvenile trees generally increase with increasing light availability associated with natural canopy gap formation, or mechanical canopy removal (Pacala et al. 1994, Kneeshaw et al. 1998, 2002, Walters and Reich 2000, Beckage and Clark 2003). However, the degree of response may differ among species: shade tolerant species may not respond to increased light with increased growth rates unless the increase in light is substantial (but not so high as to damage the sapling through photoinhibition).

For each species studied, our illustrated growth distributions suggest that very few individuals exhibit comparably fast effective height growth. If few individuals continue to outgrow their neighbours then future height distribution will change dramatically. This result has important implications for future forest growth: fast rates of height growth at an early sapling stage of development may confer advantages to subsequent recruitment into the canopy. Kenkel et al. (1997a) demonstrated that jack pine (*Pinus banksiana* Lamb.) survival through the self-thinning phase of stand development could be predicted at a relatively early stage: size at 15 years of age was found to be a good predictor of age at death. For our study, the comparably few saplings exhibiting the highest average relative growth rates over three growing seasons stand a good chance of continuing to outgrow their neighbours to reach maturity.

For shade-intolerant aspen, the low height growth exhibited under shaded conditions is attributable to insufficient radiation levels. Reduced height growth of shade-

tolerant coniferous species under shaded conditions (for some study locations) may reflect a strategy for survival in low light environments. Kobe et al. (1995) suggest that the allocation of a large amount of energy to attributes such as root growth, stem diameter, wood density, starch reserves, and defensive compounds for herbivore defense favours long-term survival in the understory, but precludes the allocation of photosynthate to rapid growth. In juvenile trees, interspecific differences in light-dependent growth and mortality (shade-tolerance) can be explained by differences in carbohydrate allocation among species (Kobe 1997, Canham et al. 1999).

Crown morphology

Although height and lateral extension growth in saplings are important for exploiting higher light microsites and potentially overtopping surrounding vegetation, they may not be the most sensitive measures for characterizing a “whole plant” response to its light environment (Williams et al. 1999). A more appropriate measure may be the L:B ratio, which determines the degree of apical dominance relative to lateral growth (Kneeshaw et al. 1998, Williams et al. 1999, Ruel et al. 2000). Within the Pinaceae, a positive correlation between L:B ratio and light availability is frequently observed (Ruel et al. 2000). Our results demonstrate that the L:B ratio is greater in high light environments for black spruce, but less consistently so for white spruce and balsam fir. It has been demonstrated that shade-tolerant species exhibit greater changes in sapling crown morphology across a light gradient than do shade-intolerant species (Williams et al. 1999). In our study, live crown ratio differed between open and closed canopy conditions for the shade-tolerant coniferous species but not for aspen.

For shade-tolerant conifers, the live crown ratio does not necessarily reflect the amount of foliage because individuals can grow horizontally. This ratio is significantly higher in open canopy conditions, however, indicating that the live crown ratio of conifer saplings is a function of light availability. Evidence suggests that crown morphology is more variable in fir than spruces (Messier et al. 1999). Although all coniferous species examined in our study demonstrated morphological variability in different light environments, this was generally less pronounced for balsam fir (the most shade-tolerant species). The one exception was balsam fir growing in large, high-light spruce budworm

gaps in Quebec; most other study locations of balsam fir advance regeneration had only small canopy gaps. As with height growth, variation in morphological plasticity observed among coniferous species in our study appear largely to reflect variation in the light environments selected for each species. However, interspecific variation in conifer response (through crown morphology) to variable canopy conditions may also reflect differences in their respective shade tolerance.

5.4.4 Light as a predictor of growth at the individual sapling level

Linear regressions of individual light availability (%PPFD) with RHG or crown morphological variables vary among species, study locations, and canopy treatments. The strongest relationship between %PPFD and growth is for conifers growing in low or high light environments for a few of the study locations, and for aspen growing in high light environments. Black spruce growth was not predicted by light availability. Light may be a poor predictor of growth if it is not a limited resource, or if there is insufficient variation in the light levels examined. For conifer saplings in open canopy treatments, light is not a limiting factor, except perhaps for balsam fir regeneration in small canopy gaps (Alberta, Manitoba, Duparquet). Conversely, %PPFD is a significant predictor of aspen growth in open canopy conditions, suggesting that light is a limiting factor for dense stands of aspen regeneration. Although light is also a limiting factor for aspen regeneration within closed canopy conditions, the variation in %PPFD in such conditions is likely insufficient to detect a trend between aspen growth and light availability. Within closed black spruce stands there is very little variation in mean light availability, making it difficult to detect a relationship between growth and light. White spruce regeneration in closed stands generally exhibits more variation in light availability than closed black spruce stands, and for some regions light proved a good predictor of sapling growth. Although variation in light availability for closed canopy plots of balsam fir regeneration is similar to that for black spruce, it is possible that the growth of shade-tolerant balsam fir may be more sensitive to small changes in light. George and Bazzaz (1999) examined the effect of increasing light availability on seedling RHG and found that within a group

of species of similar successional status, a trade-off between low light survival and the ability to respond to increasing light levels with fast height growth may exist.

Several studies have used nonlinear functions including Michaelis-Menton, Chapman-Richards, and Weibull functions, to describe the relationship between sapling growth and light (Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Wright et al. 1998, Wright et al. 2000). However, within the very narrow range of light availability under full canopy conditions (and in smaller canopy gaps), the relationship between sapling growth and light would most likely remain approximately linear (for all species examined, regardless of their relative positions along a shade tolerance continuum). Under high light conditions, sapling growth as a function of light may be more appropriately modelled using nonlinear curves incorporating an upper limit to growth at light saturation. However, our linear regressions of height growth versus light showed much scatter of points across the x-y plane in cases where regressions were poor, suggesting that nonlinear functions are not likely to elucidate a much clearer relationship than the linear functions employed.

In all cases, much of the variation in growth and crown morphology within a defined canopy treatment is unexplained by %PPFD. Claveau et al. (2002) suggest that the interaction between understory tree height growth and light availability may be complex. Taller saplings should have a greater chance of reaching canopy size and have an advantage of higher light availability than surrounding overtopped vegetation. However, at low light levels, whole-plant carbon balance must be maintained for survival, and plants adapted to low light conditions may not respond to increased light by increasing their height growth, since maintenance costs will increase with growth.

Pacala et al. (1994) observed a strong relationship between sapling growth and light availability. However, they found that while whole season light availability was a good predictor of growth for the year in which light was measured, their models had poorer fits when growth over multiple years was considered. Therefore, a possible explanation for the poor predictive ability of light in our study was our use of mean RHG (averaged over three growing seasons). However, exploratory regressions using RHG from individual years yielded similar results as those using average RHG over three growing seasons. Pacala et al. (1994) noted a strong discrepancy between diameter and

height growth (height growth predictions were 2-3 times those observed), which they attributed to winter dieback of terminal leaders and/or browsing by deer; therefore, they utilized radial growth data. In our study an attempt was made to minimize the effects of herbivory and dieback in growth analysis by excluding individuals with negative growth rates. However, for aspen and fir the effects of these factors were not entirely removed: herbivory and dieback previous to the start of the study were not accounted for, nor were fluctuations within the 2.5-year period, since RHG was averaged over the entire study period. Furthermore, individuals may have undergone herbivory and still showed positive overall height growth. These factors, together with disease, natural genetic variation, microclimate, and soil variation may account for the residual variation in our models that was unaccounted for by light. Moreover, our measures of %PPFD may not be representative of whole-season light availability, and don't measure light quality.

5.4.5 Variation among permanent plots

In general, permanent plots within a study location exhibited similar mean RHG and %PPFD; the few permanent plots that differ appreciably from others in the same study location and canopy treatment differ significantly in mean initial height of saplings monitored, or in other site conditions. Preliminary linear regressions of individual sapling size (height, diameter) as a function of relative growth rate (using height) suggested that for the size range of saplings examined in this study, there was no significant relationship between total height or diameter, and RHG. Although a negative relationship between sapling size and growth is not generally evident in our data, it may be manifest among permanent plots where mean sapling height differs substantially. Although RHG is a standardized measure that corrects for differences in absolute height among individuals, factors affecting growth may differentially affect differently sized individuals.

Taller saplings have larger maintenance costs than smaller saplings and as a result may be allocating photosynthate to functions other than height growth (eg. costs associated with the maintenance of woody tissue [Walters et al. 1993]). Similarly, Williams et al. (1999) found that saplings of Douglas-fir (*Pseudotsuga menziesii* var. *glaucia* (Beissn.) Franco) and lodgepole pine (*Pinus contorta* Dougl. ex Loud. var.

latifolia Engelm) <2 m exhibited higher RHG than saplings >2 m in low light environments receiving less than 30% of above-canopy photosynthetic photon flux density (400-700nm waveband). The authors suggested that higher maintenance costs for larger saplings resulted in less carbon availability for height growth in shaded environments.

5.4.6 Summary

Growth rates represent a tree's integrated response to current and past stresses and, therefore, indicate vigour and mortality risk (Pedersen 1998, Wyckoff and Clark 2000). This study provides much needed measures of height growth for advance regeneration of white and black spruce, balsam fir, and trembling aspen across the boreal forest. With the exception of a few study locations, growth rates appear similar among regions. Balsam fir height growth is similar in distribution for most study locations, but is much different in canopy gaps eastern forests where gaps are extensive, and which receive much more annual precipitation. The growth rates presented may be characteristic of each species, and provide useful and representative empirical estimates for use in growth and mortality functions in model simulations of forest stand dynamics. Across species and study locations mean RHG, %PPFD, L:B ratio, and live crown ratio are significantly higher in open canopy conditions than in shaded understory conditions. The distribution of RHG also differs between light environments: RHG distributions for shaded understory conditions are consistently significantly positively skewed, and differ significantly from mesokurtosis.

If present growth rates are indicative of future growth rates, height distributions of saplings will become more positively skewed and leptokurtic over time. These results have important implications for future forest growth: fast rates of height growth at an early sapling stage of development in the forest understory may confer advantages to subsequent recruitment into the canopy. Our study demonstrates that light is a reasonably good predictor of growth only if it is a limited resource, and only if there is sufficient variation in light availability among the saplings examined. Different height classes of saplings may show different growth response to light and other influential factors. More

detailed growth descriptions for individual saplings including factors contributing to stem loss or dieback would further our understanding of growth processes in shaded and unshaded conditions.

5.4.7 Synoptic model of factors affecting sapling growth and mortality

Based on results from this study, existing literature, and field observations, factors affecting sapling growth and survival (whole-plant responses) have been summarized in a conceptual model (Figure 5.18). This summary model illustrates how the results of our study contribute to a more comprehensive understanding of sapling growth, crown morphology, and mortality. The literature reviewed pertains to the global boreal forest or North American forests.

Predisposing factors, inciting stresses, shade tolerance, and intraspecific genetic variation

A suite of predisposing factors and inciting stresses (*sensu* Manion [1981]) may influence sapling growth and/or survival. *Among* species, genetic differences expressed as variation in shade tolerance (or evolutionary growth strategy) also influence sapling growth and mortality (Pacala et al. 1994, Kobe et al. 1995, Kobe and Coates 1997, Lin et al. 2001). Mode of reproduction may also be an important factor influencing interspecific differences in growth and/or survival. *Within* species, genetic variation may contribute to observed differences in sapling growth and mortality.

Canopy openness and individual-level light availability

Results from this study contribute novel information to the existing body of literature and also support previous studies. Light availability both at the plot level (canopy openness) and individual-sapling level is the predisposing factor focused upon in our study. Canopy openness affects mean RHG, distributions of RHG, and crown morphology. Mean height growth, L:B ratio, and live crown ratio are significantly higher in open canopy conditions for all species examined for some study locations, but not others. Growth distributions in closed canopy conditions are significantly positively skewed and leptokurtic. Fast growth at an early sapling stage (exhibited by only a small

proportion of individuals examined) may confer advantages to subsequent growth and survival. Previous studies have demonstrated a relationship between sapling height growth or crown morphology and light environment (Pacala et al. 1994, Kobe et al. 1995, Williams et al. 1999, Claveau et al. 2002). Canopy openness may also affect sapling mortality: survival time and mortality rates differ between open and closed canopy conditions if the difference in radiation levels between environments is sufficiently large, and if appreciable mortality occurs to detect any trends.

Crown morphology as a predictor of sapling survival

Individual-level variation in live crown ratio is a strong predictor of individual mortality risk: saplings in favourable growing conditions that permit the maintenance of high live crown ratios have low risk of mortality. In recent years forest ecologists have begun to examine the relationship between growth and mortality of juvenile trees (Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Kobe and Coates 1997, Walters and Reich 2000, Lin et al. 2001). An inverse relationship between growth and mortality is generally recognized, and has been demonstrated and applied in predictive models of growth-dependent mortality (Pacala et al. 1994, Kobe et al. 1995, Kobe 1996, Kobe and Coates 1997, Walters and Reich 2000, Lin et al. 2001). Several studies have shown that growth, but not size, is an important predictor of sapling mortality (Kobe et al. 1995, Kobe 1996, Lin et al. 2001). Growth rates integrate the effects of many factors affecting sapling performance, and therefore act as an index for mortality risk (Wyckoff and Clark 2000).

Interactions among factors

Hartvigsen et al. (1995) examined the interactive effects of fertilization, mite herbivory, and predation on cottonwood (*Populus deltoides* Marsh.) sapling performance. Results suggest that sapling performance is influenced by a complex interaction of "bottom-up" (nutrient availability) and "top-down" (herbivory and predation of herbivores) factors. Zamora et al. (2001) monitored ungulate herbivory, insect herbivory, and frost damage of apical shoots of Scots pine in Mediterranean montane forests. Compared to the effects of ungulate herbivory, those of insect herbivory and frost damage were negligible. Similarly, in our study ungulate herbivory appears to govern

growth and mortality more than factors such as insect and pathogen damage or frost damage. However, the combined effects light and other resource availability, herbivory, mechanical damage, and insect/pathogen damage on sapling performance needs to be unraveled for a better understanding of the relative influence of each factor.

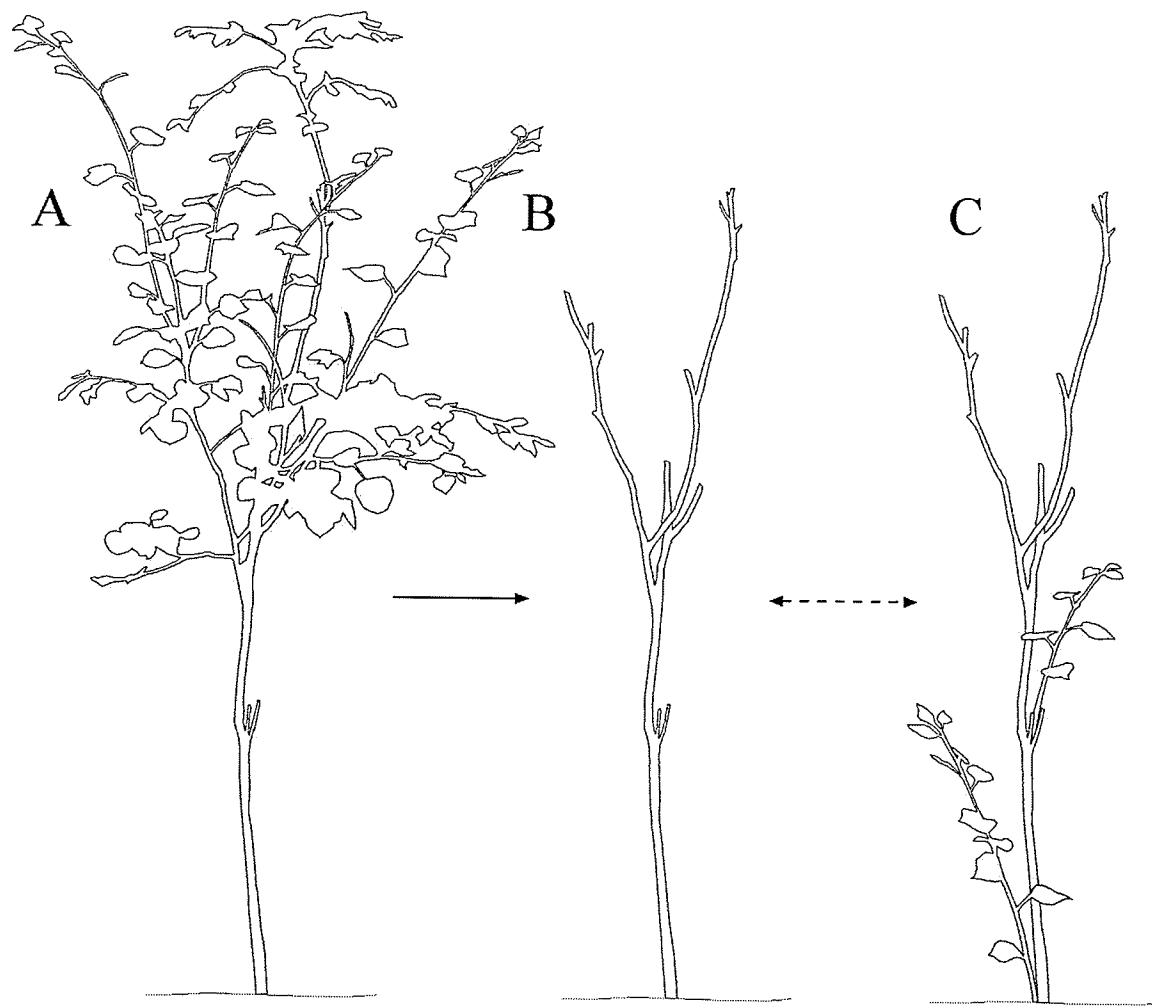


Figure 5.1. Dynamic states of aspen suckers within the size range sampled (0.3-2 m at study onset), growing in the shaded understory. An individual stem may shift in either direction between a fully leafed out form (A) and a suppressed form (B, C) in which the main axis appears dead, with either no shoots (B), or one or more basal or side shoots (C). This suppressed state of shade intolerant aspen suckers appears to result largely from low light availability; the ability of parent canopy trees to support the growth of aspen suckers in the shaded understory remains to be investigated (Cumming et al. 2000). Other prominent factors influencing overall vigour of aspen suckers include mammal and insect herbivory. Within the 2.5-year study period it was not uncommon for an individual sucker to remain in a suppressed state with no leaf tissue for one or more years (B), and then to re-sprout from either the base or just below ground (very common) or upper branches in a subsequent year (C). Main axes of some suckers appear very weathered and may be relatively old; individuals may repeatedly dieback and re-sprout year after year in the shaded understory.

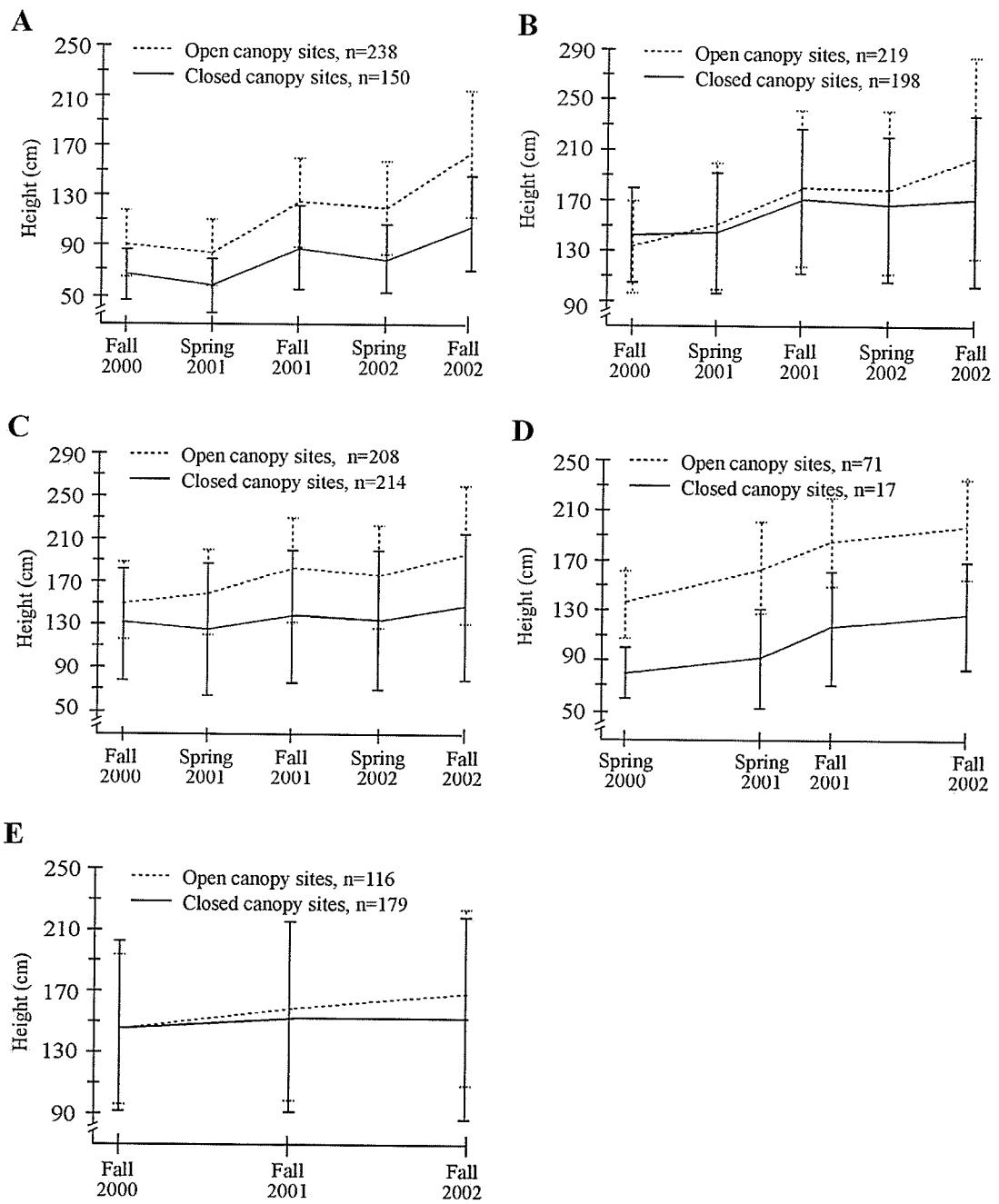


Figure 5.2. Mean height of aspen suckers over time in A.) EMEND, AB, B.) Lac La Biche, AB, C.) Duck Mountains, MB, D.) Manitoba Shield, MB, and E.) Duparquet, QC. Broken lines chronicle aspen height in open canopy (clearcut) conditions, and solid lines show mean sucker height in closed canopy hardwood forests. Standard deviation bars, which show dispersion about the mean, reflect variation in height among individual suckers. The time from spring to fall measures, and fall to spring measures are approximately 3-4 months, and 8-9 months respectively. All individuals alive at the end of the study are included (n) with the exception of a few stems with missing height measurements from a given year.

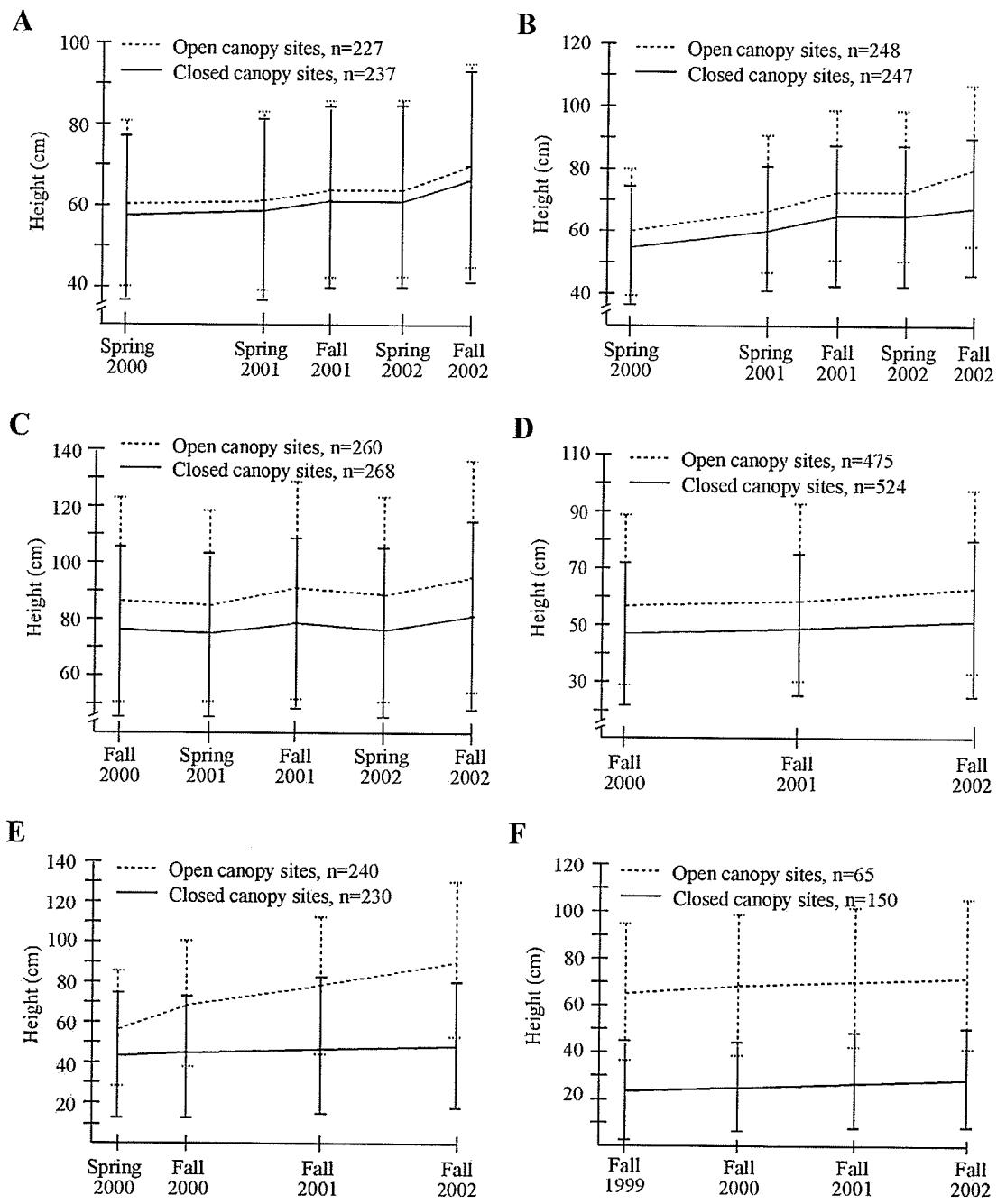


Figure 5.3. Mean height of balsam fir saplings over time in A.) EMEND, AB, B.) Lac La Biche, AB, C.) Duck Mountains, MB, D.) Duparquet, QC, E.) Forêt Montmorency, QC, and F.) Chicoutimi, QC. Broken lines chronicle sapling height in open canopy (natural gap) conditions, and solid lines show mean sapling height in closed canopy mixed coniferous forests. Standard deviation bars, which show dispersion about the mean, reflect variation in height among individual saplings. The time from spring to fall measures, and fall to spring measures are approximately 3-4 months, and 8-9 months, respectively. All individuals alive at the end of the study are included (n) with the exception of a few stems with missing height measurements from a given year.

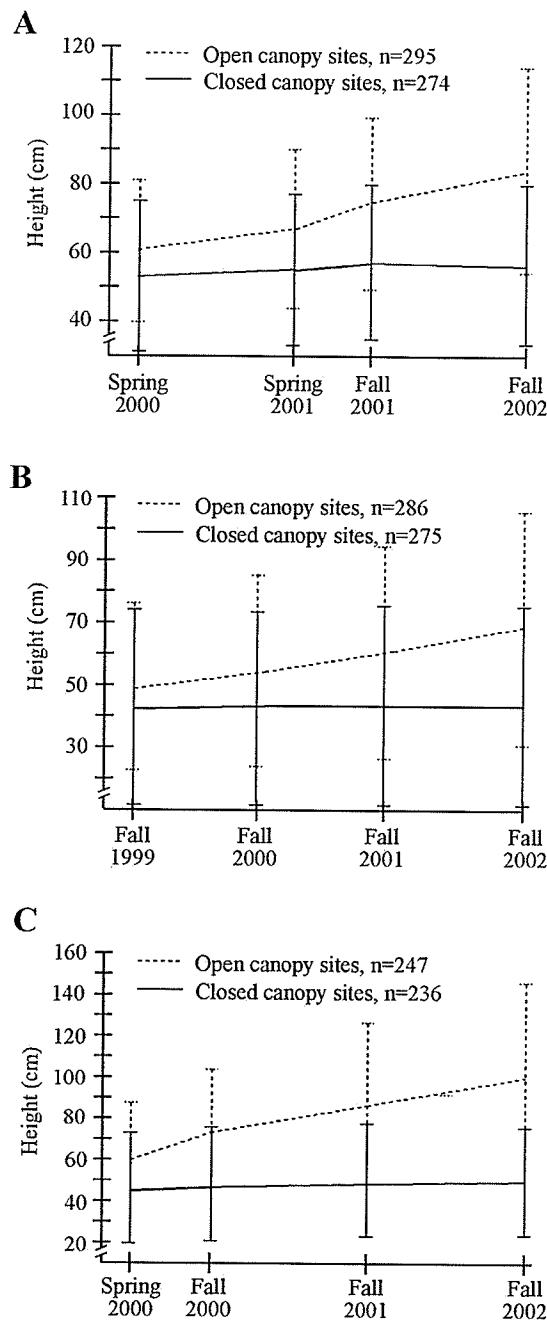


Figure 5.4. Mean height of black spruce saplings over time in A.) Manitoba Shield, MB, B.) Iroquois Falls, ON, and C.) Ashuapmushuan Reserve, QC. Broken lines chronicle sapling height in open canopy (carefully harvested) conditions, and solid lines show mean sapling height in closed canopy black spruce forests. Standard deviation bars, which show dispersion about the mean, reflect variation in height among individual saplings. The time from spring to fall measures, and fall to spring measures are approximately 3-4 months, and 8-9 months, respectively. All individuals alive at the end of the study are included (n) with the exception of a few stems with missing height measurements from a given year.

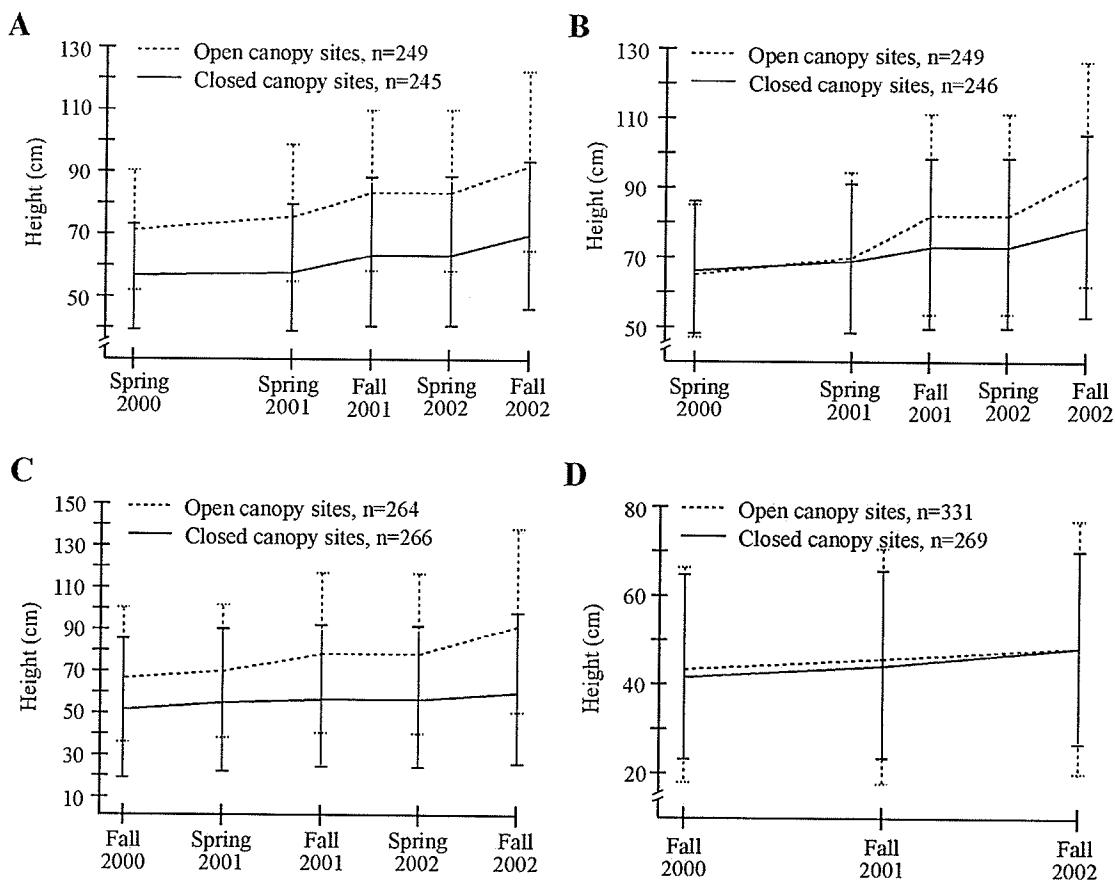


Figure 5.5. Mean height of white spruce saplings over time in A.) EMEND, AB, B.) Lac La Biche, AB, C.) Duck Mountains, MB, and D.) Duparquet, QC. Broken lines chronicle sapling height in open canopy (post-disturbance) conditions, and solid lines show mean sapling height in closed canopy mixedwood forests. Standard deviation bars, which show dispersion about the mean, reflect variation in height among individual saplings. The time from spring to fall measures, and fall to spring measures are approximately 3-4 months, and 8-9 months, respectively. All individuals alive at the end of the study are included (n) with the exception of a few stems with missing height measurements from a given year.

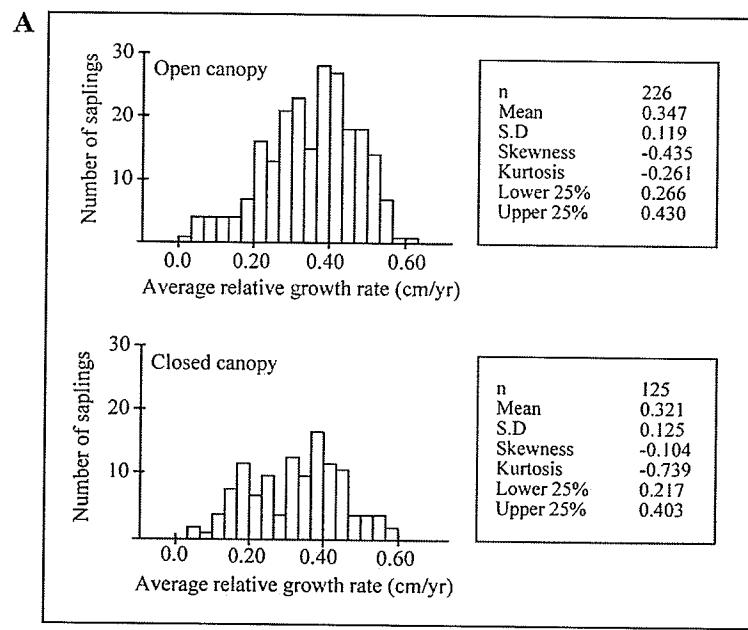


Figure 5.6 A. Frequency histograms of aspen relative growth rate (RHG, cm/year) for open and closed canopy conditions at EMEND, AB. Mean RHG is not significantly different between open and closed canopy plots ($P=0.324$, $n=4$). The open canopy histogram is significantly positively skewed; the closed canopy histogram is significantly platykurtic (at $\alpha=0.05$).

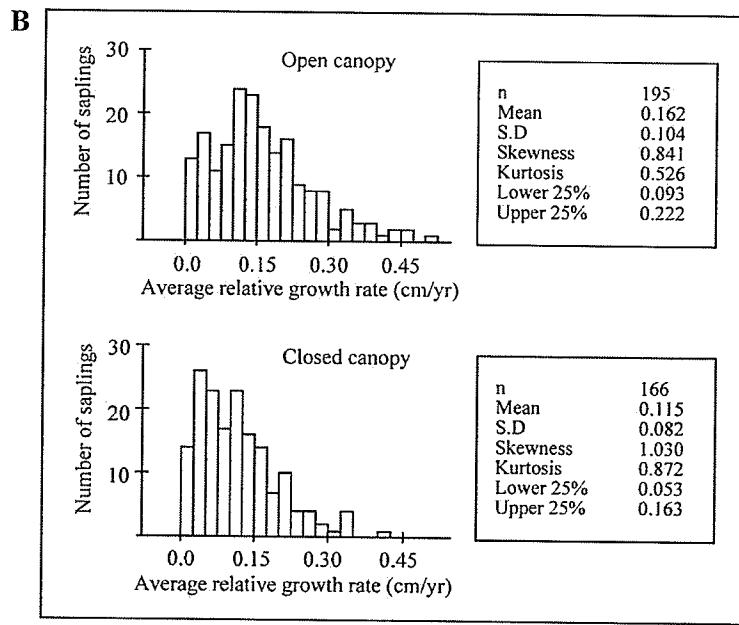


Figure 5.6 B. Frequency histograms of aspen relative growth rate (RHG, cm/year) for open and closed canopy conditions at Lac La Biche, AB. Mean RHG is not significantly different between open and closed canopy plots ($P=0.257$, $n=4$). Both open and closed canopy histograms are significantly positively skewed (at $\alpha=0.05$).

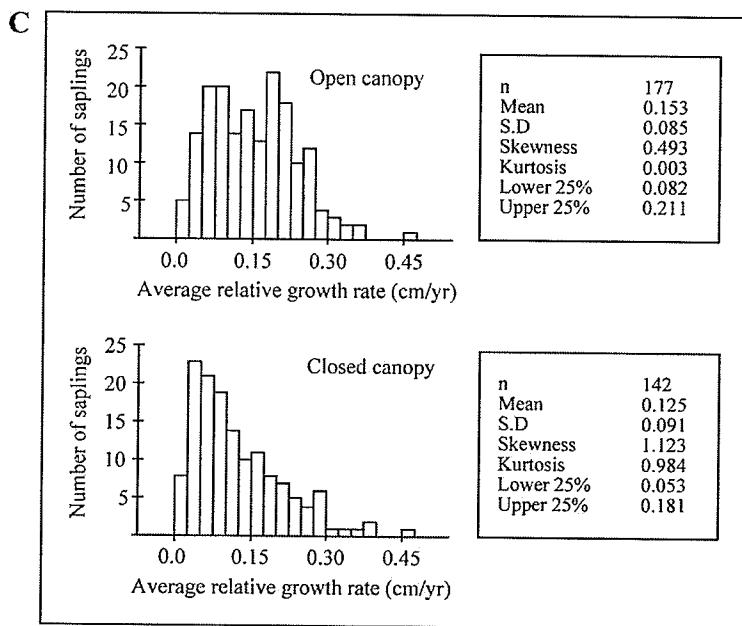


Figure 5.6 C. Frequency histograms of aspen relative growth rate (RHG, cm/year) for open and closed canopy conditions at Duck Mountains, MB. Mean RHG is not significantly different between open and closed canopy plots ($P=0.203$, $n=3$). Both open and closed canopy histograms are significantly positively skewed; the closed canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

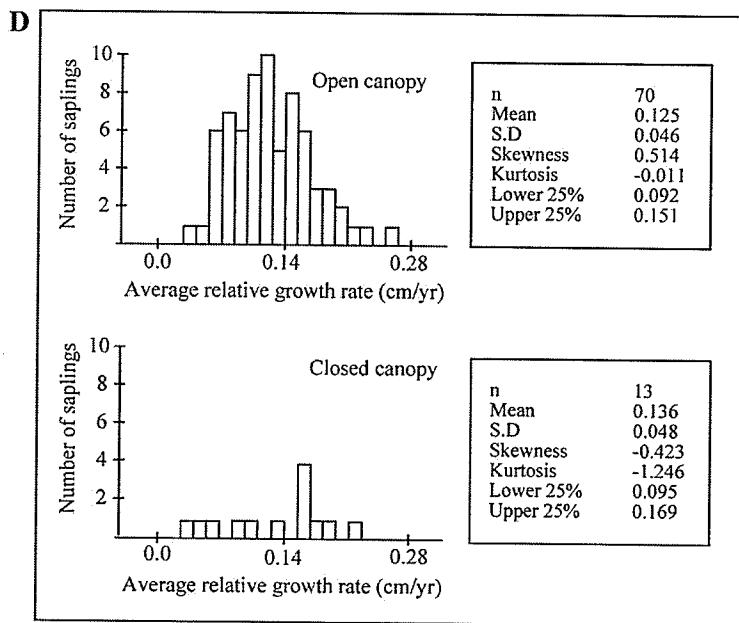


Figure 5.6 D. Frequency histograms of aspen relative growth rate (RHG, cm/year) for open and closed canopy conditions at Manitoba Shield, MB. Only one closed canopy plot replicate was left with live saplings at the end of the study period. Neither open nor closed distributions differ significantly from normality (at $\alpha=0.05$).

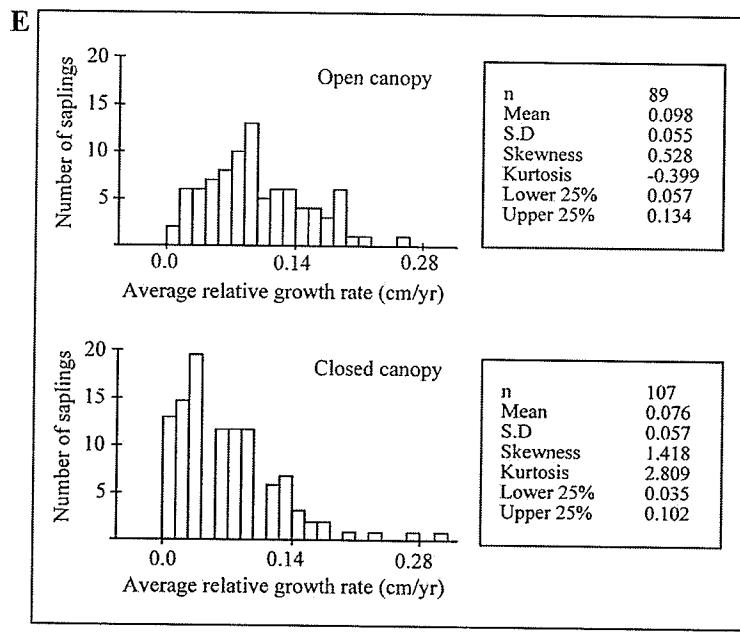


Figure 5.6 E. Frequency histograms of aspen relative growth rate (RHG, cm/year) for open and closed canopy conditions at Duparquet, QC. Mean RHG is not significantly different between open and closed canopy plots ($P=0.121$, $n=5$). Both open and closed canopy histograms are significantly positively skewed; the closed canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

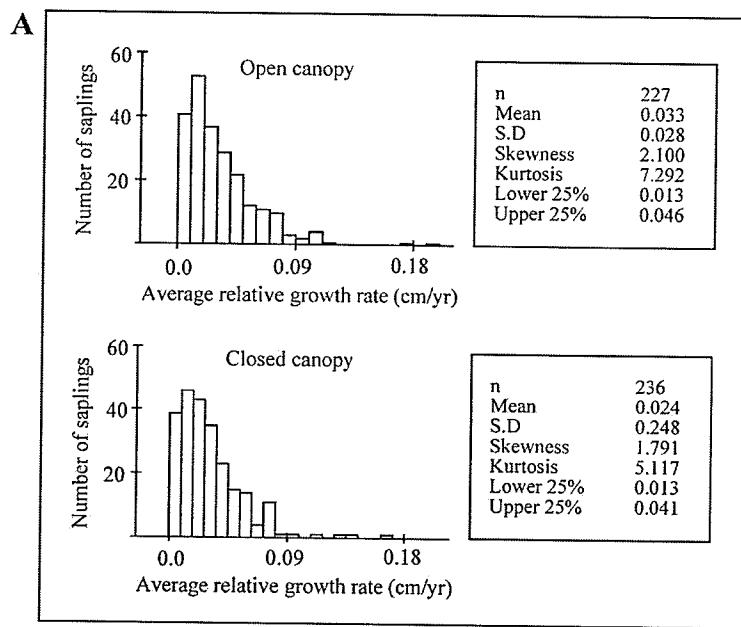


Figure 5.7 A. Frequency histograms of balsam fir relative growth rate (RHG, cm/year) for open and closed canopy conditions at EMEND, AB. Mean RHG is not significantly different between open and closed canopy plots ($P=0.700$, $n=4$). Both open and closed canopy histograms are significantly positively skewed and leptokurtic (at $\alpha=0.05$).

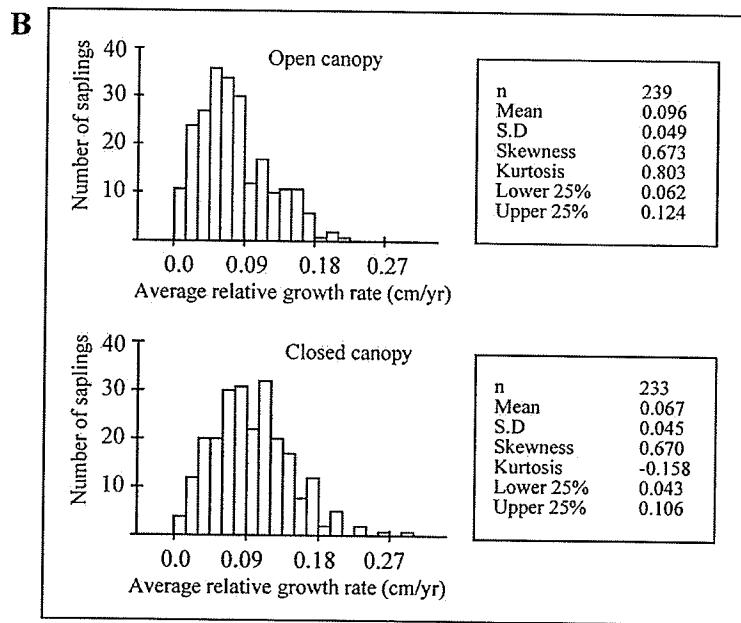


Figure 5.7 B. Frequency histograms of balsam fir relative growth rate (RHG, cm/year) for open and closed canopy conditions at Lac La Biche, AB. Mean RHG is significantly different between open and closed canopy plots ($P=0.094$, $n=4$). Both open and closed canopy histograms are significantly positively skewed; the open canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

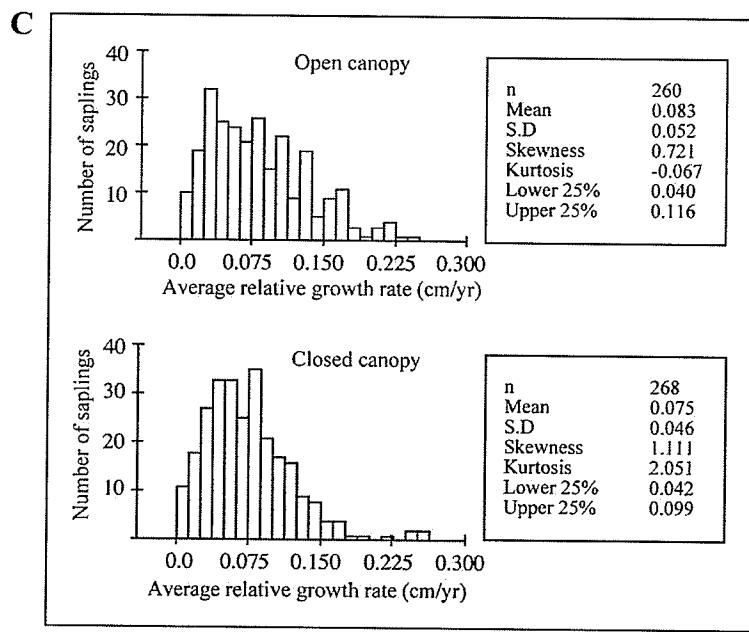


Figure 5.7 C. Frequency histograms of balsam fir relative growth rate (RHG, cm/year) for open and closed canopy conditions at Duck Mountains, MB. Mean RHG is not significantly different between open and closed canopy plots ($P=0.444$, $n=3$). Both open and closed canopy histograms are significantly positively skewed; the closed canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

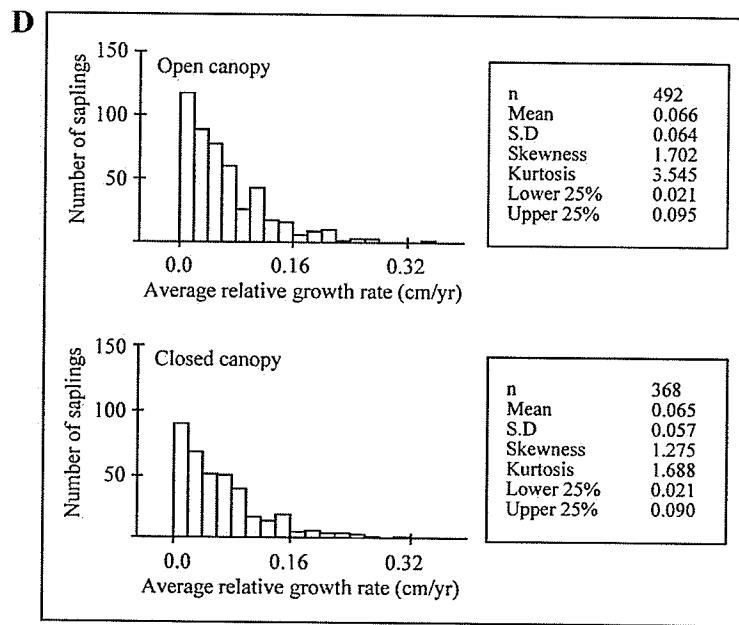


Figure 5.7 D. Frequency histograms of balsam fir relative growth rate (RHG, cm/year) for open and closed canopy conditions at Duparquet, QC. Mean RHG is not significantly different between open and closed canopy plots ($P=0.818$, $n=8$ and 6 for open and closed canopy plots respectively). Both open and closed canopy histograms are significantly positively skewed and leptokurtic (at $\alpha=0.05$).

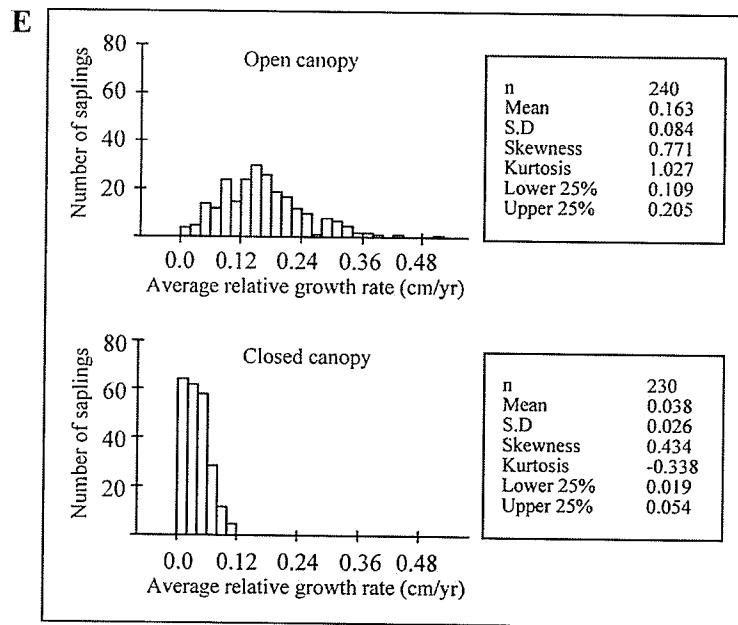


Figure 5.7 E. Frequency histograms of balsam fir relative growth rate (RHG, cm/year) for open and closed canopy conditions at Forêt Montmorency, QC. Mean RHG is significantly different between open and closed canopy plots ($P=0.003$, $n=4$). Both open and closed canopy histograms are significantly positively skewed; the open canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

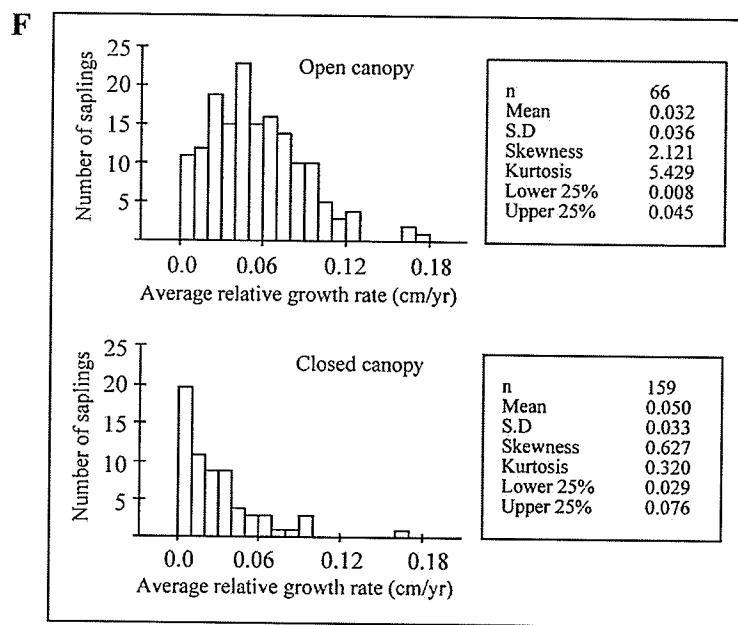


Figure 5.7 F. Frequency histograms of balsam fir relative growth rate (RHG, cm/year) for open and closed canopy conditions at Chicoutimi, QC. There was only one plot for open canopy conditions. Both open and closed canopy histograms are significantly positively skewed; the open canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

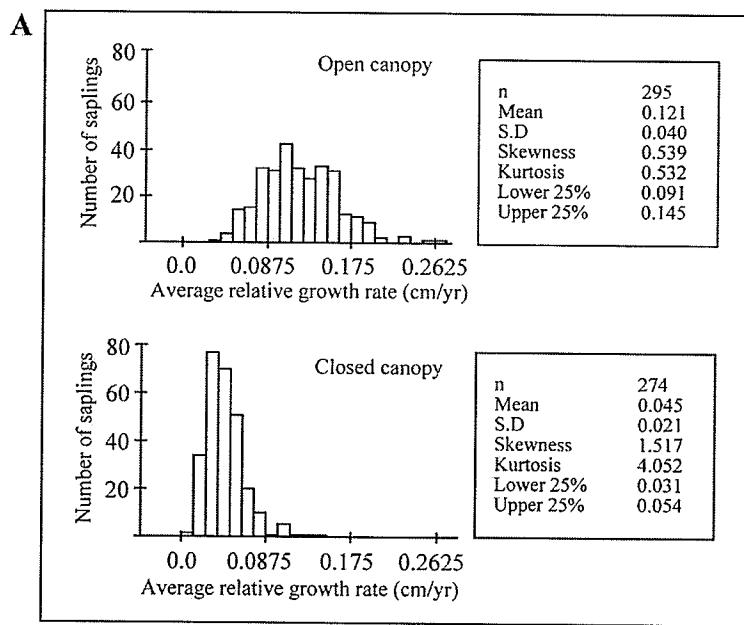


Figure 5.8 A. Frequency histograms of black spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at Manitoba Shield, MB. Mean RHG is significantly different between open and closed canopy plots ($P=0.0001$, $n=3$). Both open and closed canopy histograms are significantly positively skewed; the closed canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

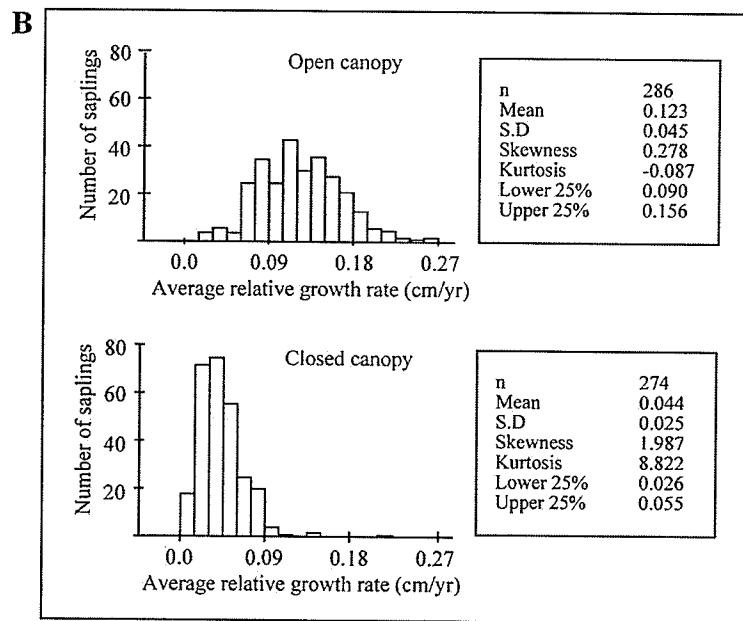


Figure 5.8 B. Frequency histograms of black spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at Iroquois Falls, ON. Mean RHG is significantly different between open and closed canopy plots ($P<0.0001$, $n=4$). Both open and closed canopy histograms are significantly positively skewed; the closed canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

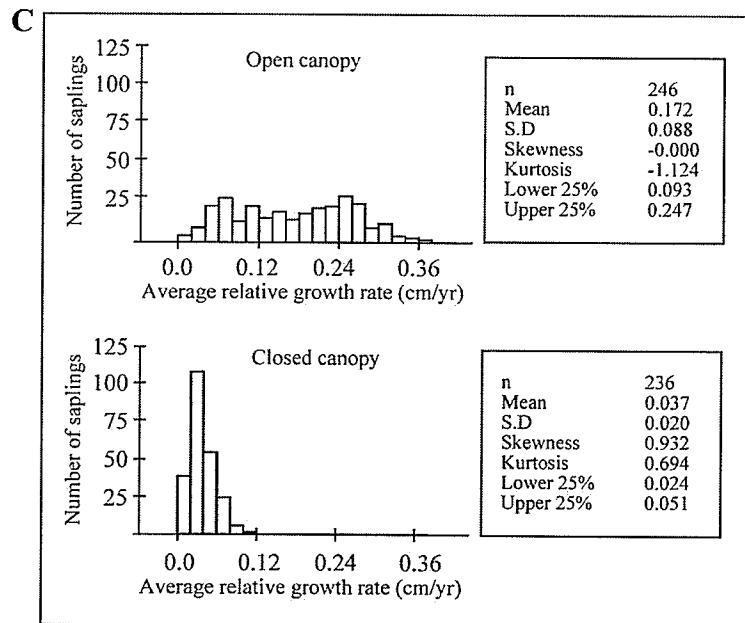


Figure 5.8 C. Frequency histograms of black spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at Ashuapmushuan Reserve, QC. Mean RHG is significantly different between open and closed canopy plots ($P=0.014$, $n=4$). Both open and closed canopy histograms are significantly positively skewed; the closed canopy histogram is significantly leptokurtic (at $\alpha=0.05$).

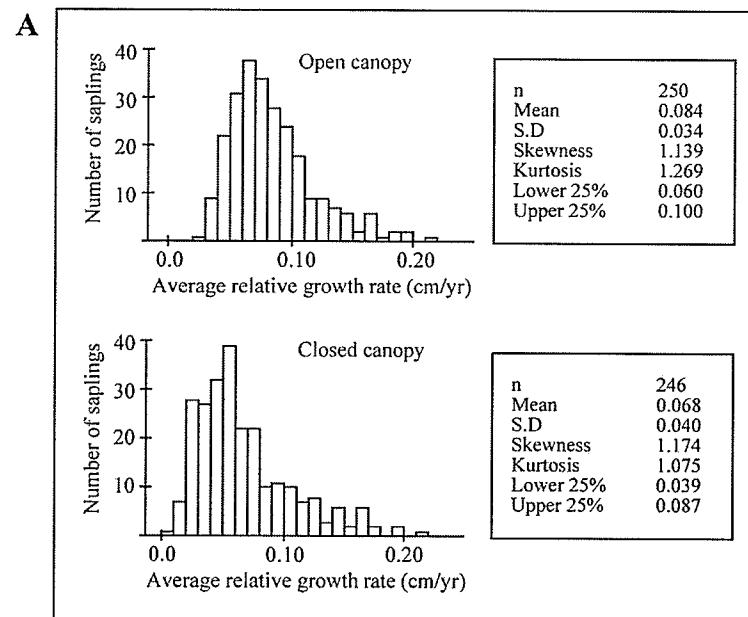


Figure 5.9 A. Frequency histograms of white spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at EMEND, AB. Mean RHG is not significantly different between open and closed canopy plots ($P=0.405$, $n=4$). Both open and closed canopy histograms are significantly positively skewed and leptokurtic (at $\alpha=0.05$).

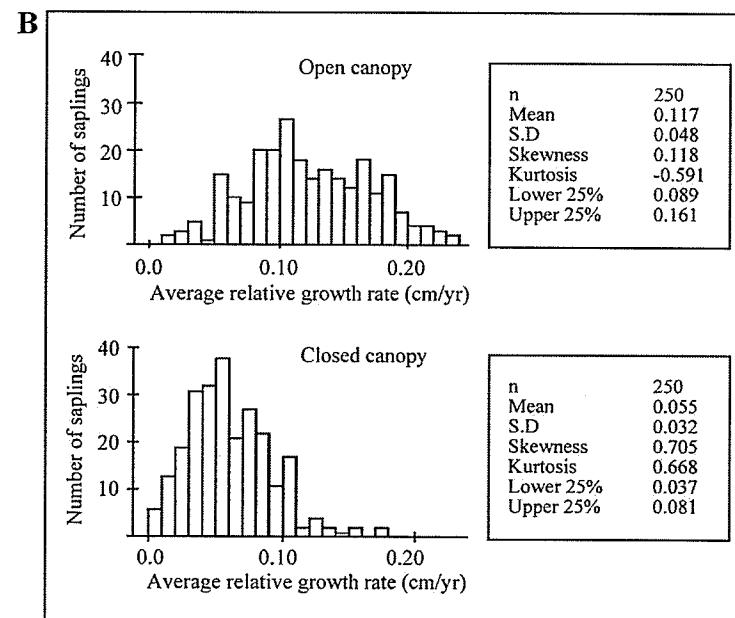


Figure 5.9 B. Frequency histograms of white spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at Lac La Biche, AB. Mean RHG is significantly different between open and closed canopy plots ($P=0.009$, $n=4$). The closed canopy histogram is significantly positively skewed.

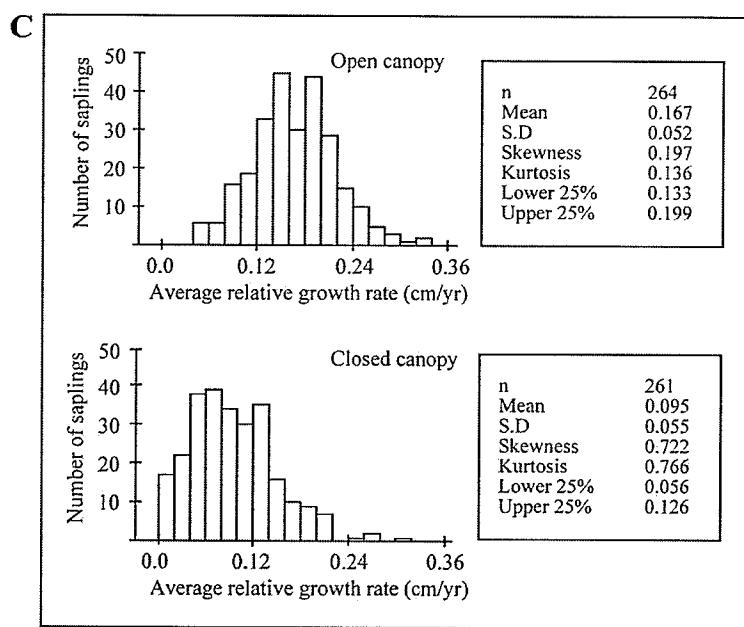


Figure 5.9 C. Frequency histograms of white spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at Duck Mountains, MB. Mean RHG is significantly different between open and closed canopy plots ($P=0.049$, $n=3$). Skewness and kurtosis are both significantly positive for closed canopy conditions.

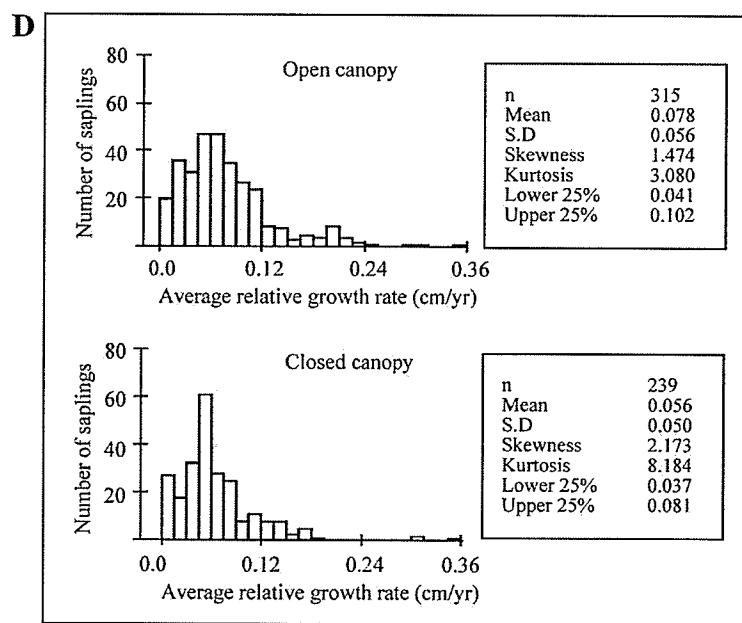
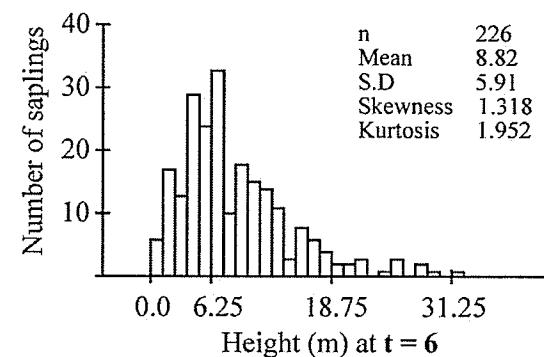
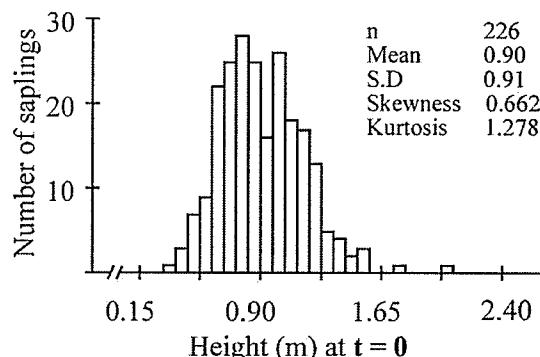


Figure 5.9 D. Frequency histograms of white spruce relative growth rate (RHG, cm/year) for open and closed canopy conditions at Duparquet, QC. Mean RHG is not significantly different between open and closed canopy plots ($P=0.379$, $n=3$). Both open and closed canopy histograms are significantly positively skewed and leptokurtic (at $\alpha=0.05$).

Open canopy



Closed canopy

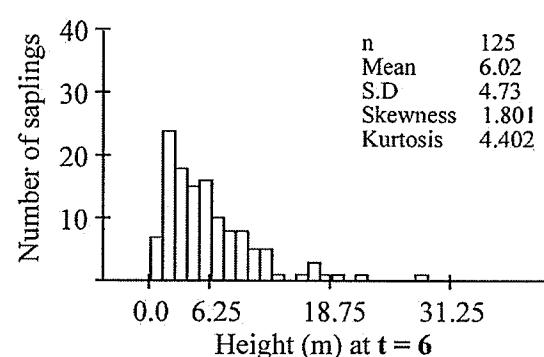
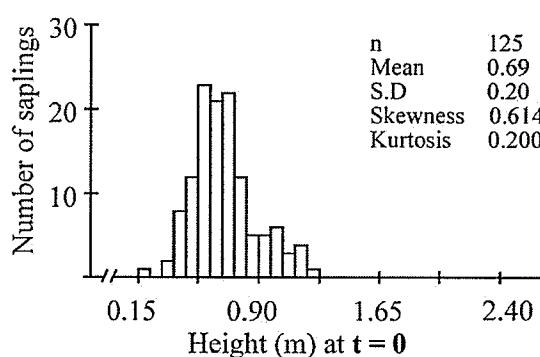
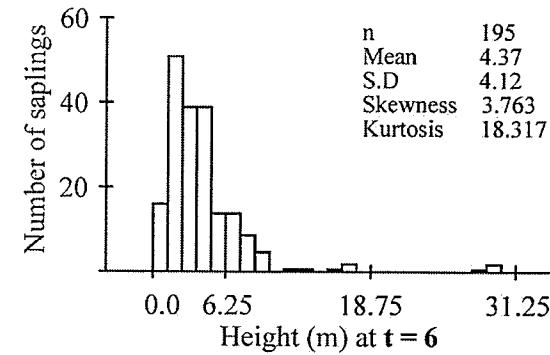
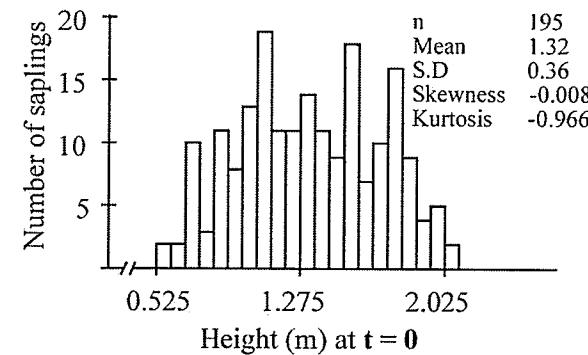


Figure 5.10 A. Frequency histograms of trembling aspen height at study onset (t=0) and after 6 years of projected exponential growth for open and closed canopy conditions in EMEND, AB. All four histograms are significantly positively skewed, however, only distributions at t=6 are significantly leptokurtic (at $\alpha=0.05$). Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

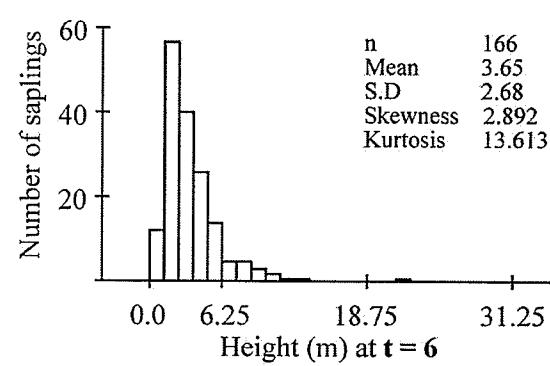
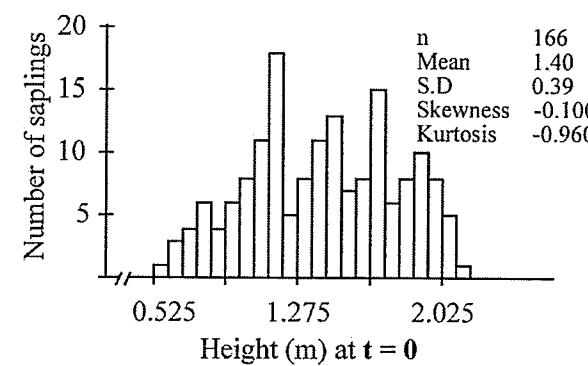
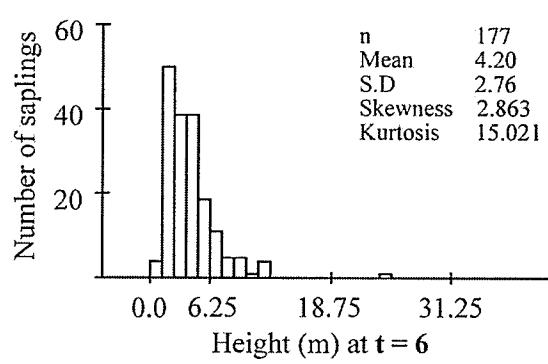
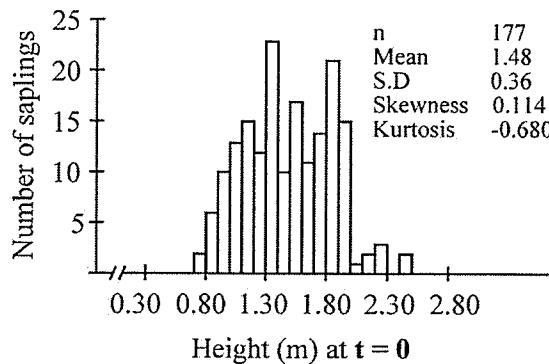


Figure 5.10 B. Frequency histograms of trembling aspen height at study onset (t=0) and after 6 years of projected exponential growth for open and closed canopy conditions in Lac La Biche, AB. Distributions at t=0 are significantly platykurtic, and at t=6 are significantly positively skewed and leptokurtic (at $\alpha=0.05$). Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

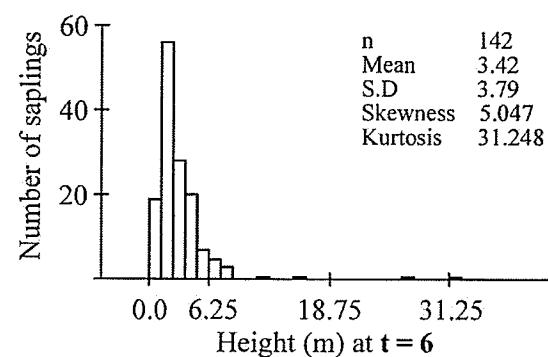
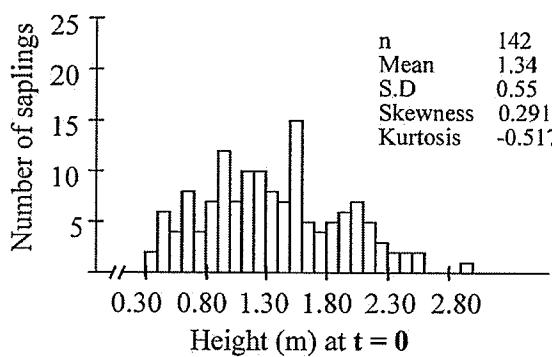
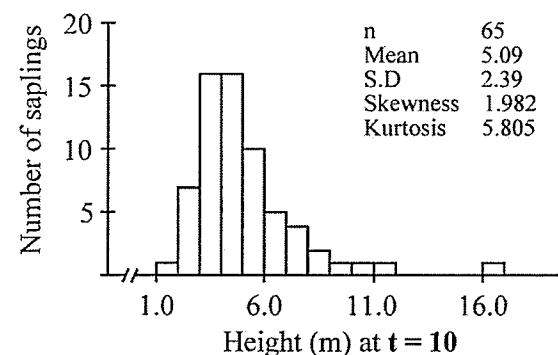
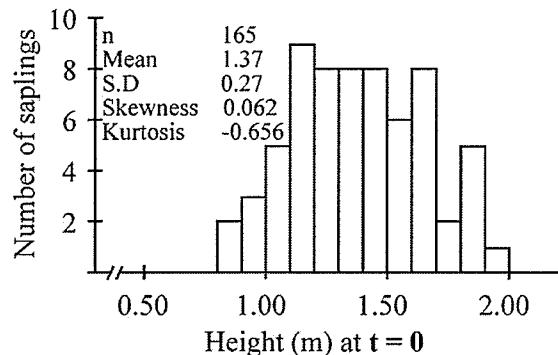


Figure 5.10 C. Frequency histograms of trembling aspen height at study onset ($t=0$) and after 6 years of projected exponential growth for open and closed canopy conditions in Duck Mountains, MB. Only distributions at $t=6$ are significantly positively skewed and leptokurtic (at $\alpha=0.05$). Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

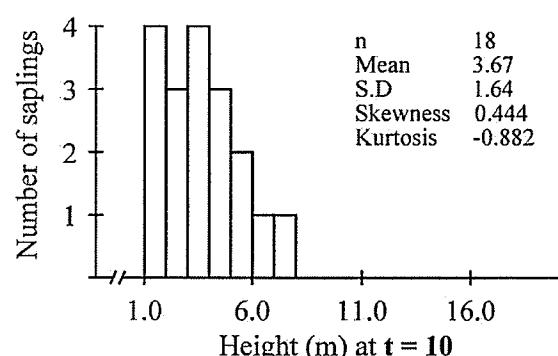
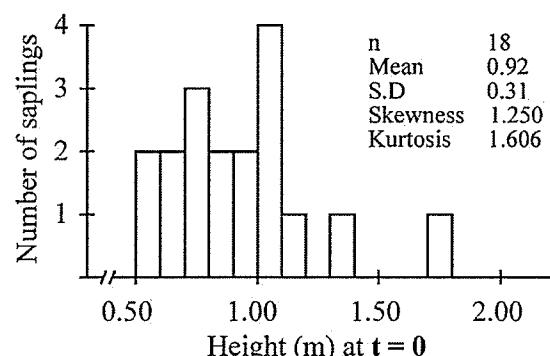
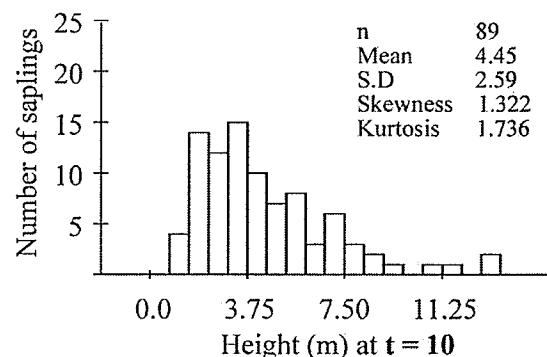
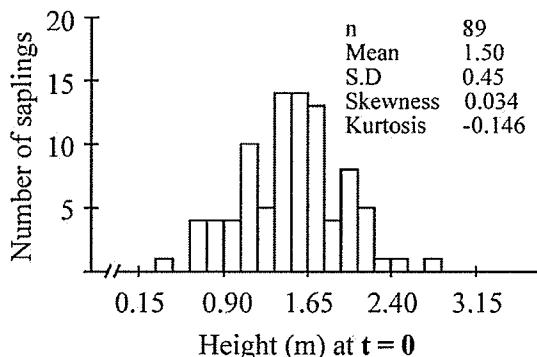


Figure 5.10 D. Frequency histograms of trembling aspen height at study onset ($t=0$) and after 10 years of projected exponential growth for open and closed canopy conditions in Manitoba Shield, MB. For open canopy conditions, height distribution is significantly positively skewed and leptokurtic only at $t=10$ (at $\alpha=0.05$). For closed canopy conditions, distribution at $t=0$ is significantly positively skewed and leptokurtic, and significantly platykurtic at $t=6$. Note scale differences.

Open canopy



Closed canopy

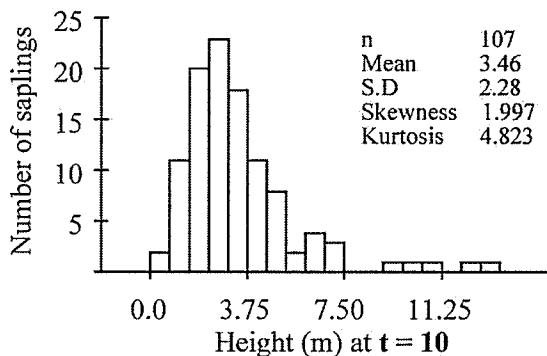
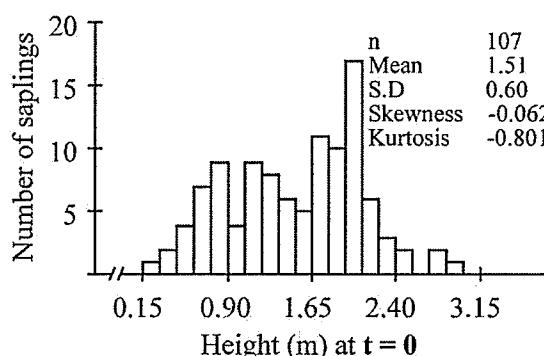
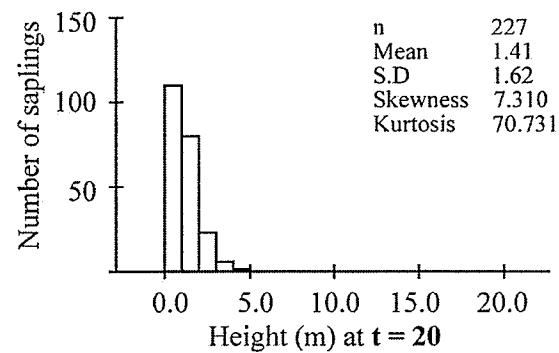
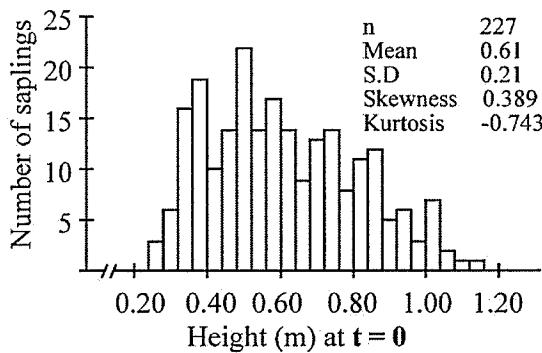


Figure 5.10 E. Frequency histograms of trembling aspen height at study onset ($t=0$) and after 10 years of projected exponential growth for open and closed canopy conditions in Duparquet, QC. Only distributions at $t=10$ are significantly positively skewed and leptokurtic (at $\alpha=0.05$). Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

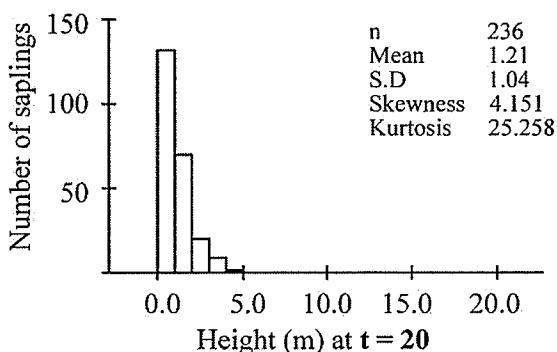
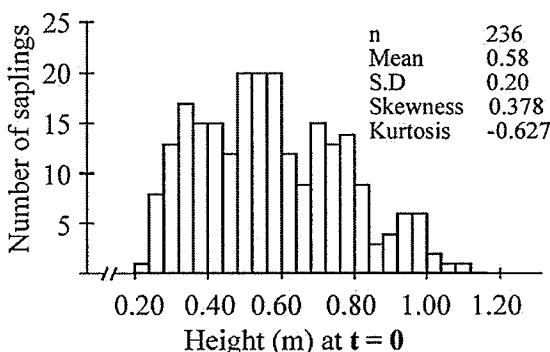
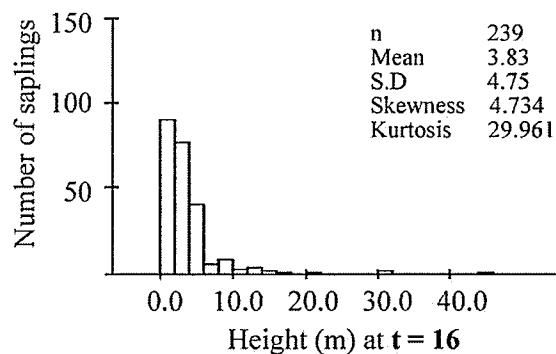
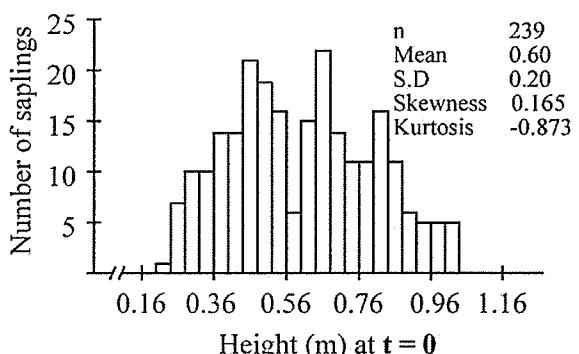


Figure 5.11 A. Frequency histograms of balsam fir height at study onset ($t=0$) and after 20 years of projected exponential growth for open and closed canopy conditions in EMEND, AB. All four distributions are significantly positively skewed; only distributions at $t=20$ are significantly leptokurtic (at $\alpha=0.05$). Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

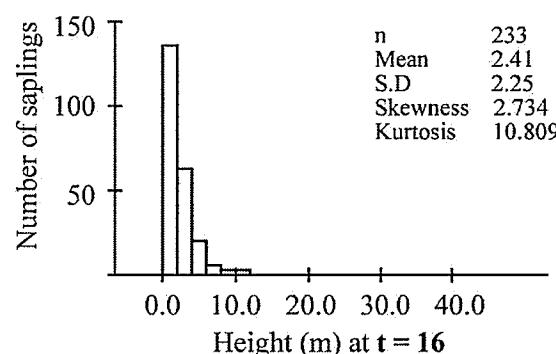
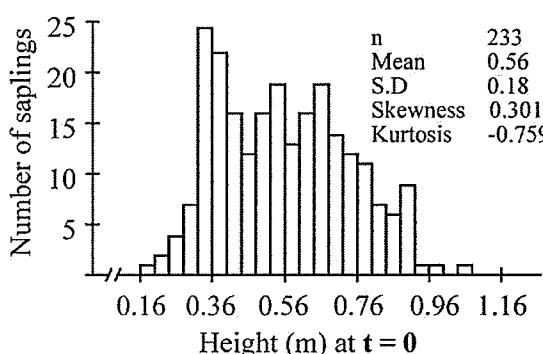
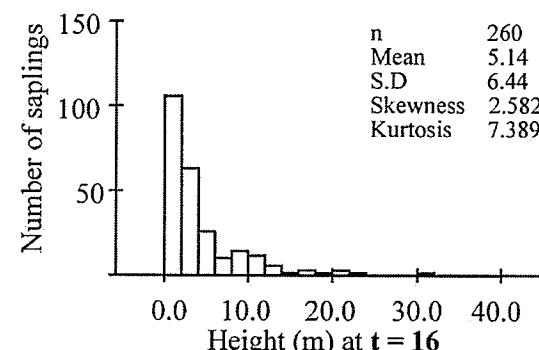
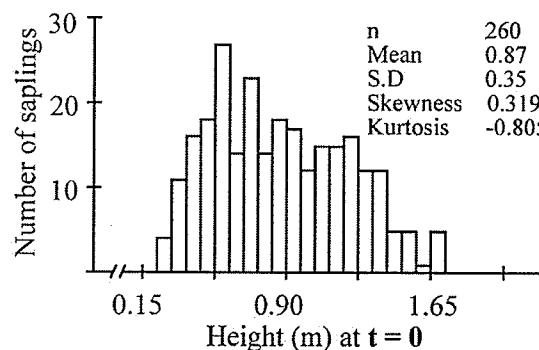


Figure 5.11 B. Frequency histograms of balsam fir height at study onset ($t = 0$) and after 16 years of projected exponential growth for open and closed canopy conditions in Lac La Biche, AB. Distributions are significantly positively skewed and leptokurtic only at $t = 16$ (at $\alpha = 0.05$). Kurtosis is significantly negative at $t = 0$ for open and closed canopy conditions. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

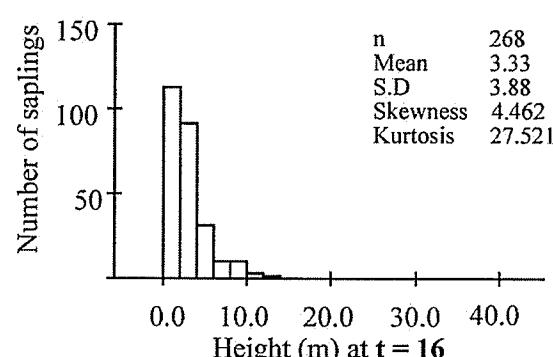
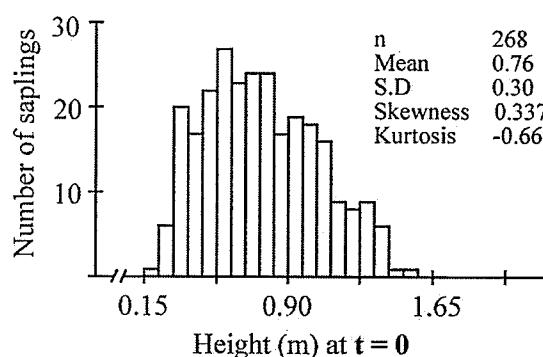
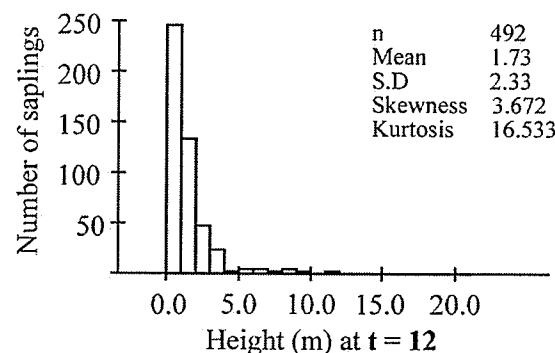
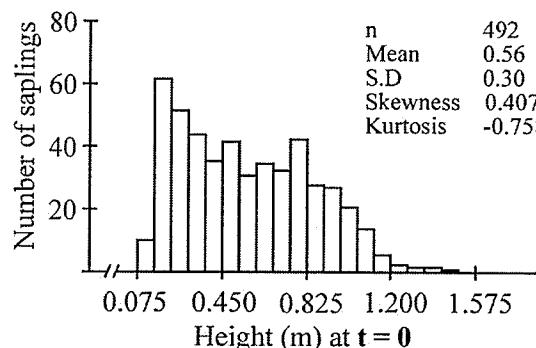


Figure 5.11 C. Frequency histograms of balsam fir height at study onset (t=0) and after 16 years of projected exponential growth for open and closed canopy conditions in Duck Mountains, MB. All four distributions are significantly positively skewed and leptokurtic (at $\alpha=0.05$), with the exception of the coefficient of kurtosis for closed canopy conditions at t=0. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

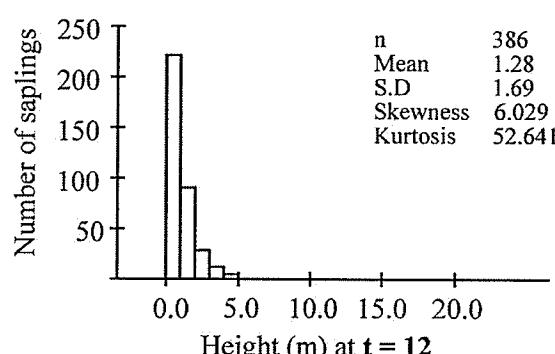
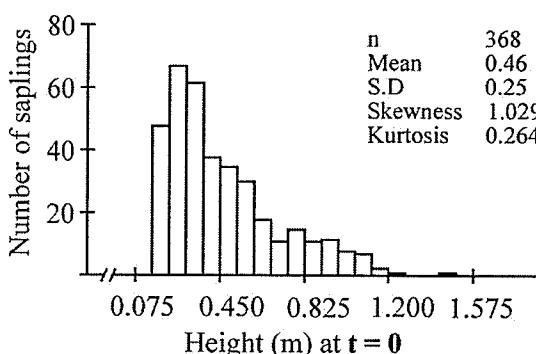
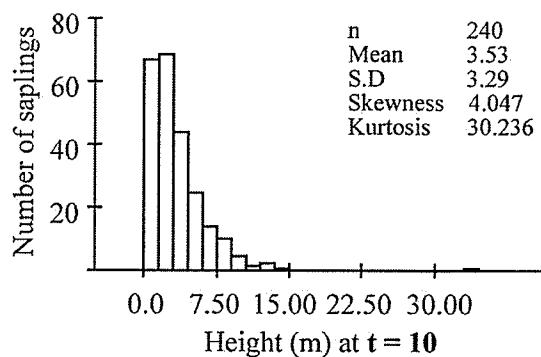
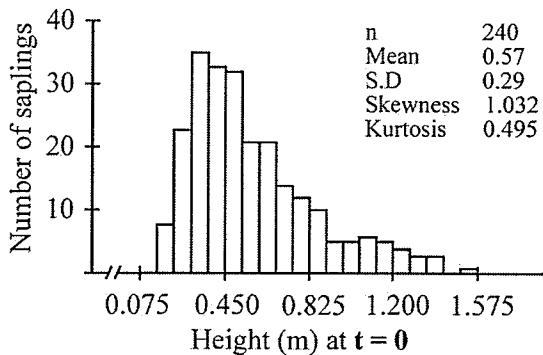


Figure 5.11 D. Frequency histograms of balsam fir height at study onset (t=0) and after 12 years of projected exponential growth for open and closed canopy conditions in Duparquet, QC. All four distributions are significantly positively skewed (at $\alpha=0.05$). Distributions at t=12 are significantly leptokurtic, and at t=0 significantly platykurtic for open canopy conditions and not significantly different from zero for closed canopy conditions. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

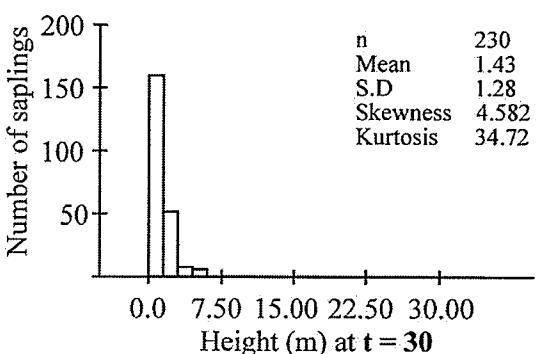
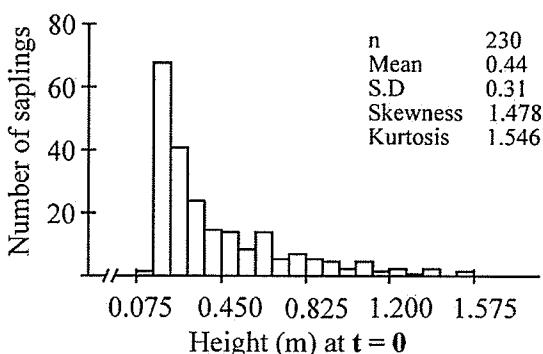
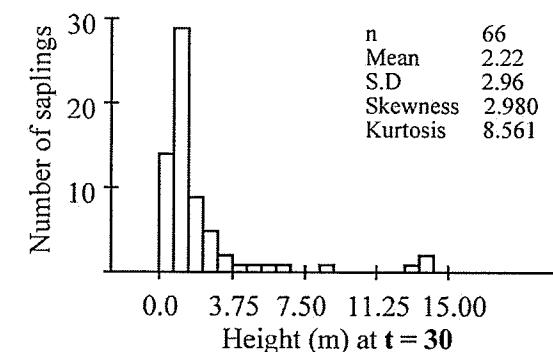
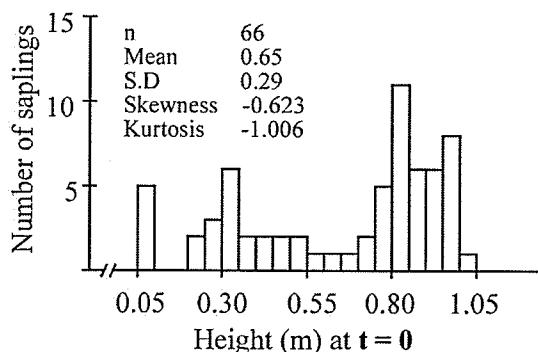


Figure 5.11 E. Frequency histograms of balsam fir height at study onset ($t=0$) and after 10 and 30 years of projected exponential growth for open and closed canopy conditions respectively in Forêt Montmorency, QC. All distributions are significantly positively skewed and leptokurtic (at $\alpha=0.05$), except kurtosis for open canopy conditions at $t=0$. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

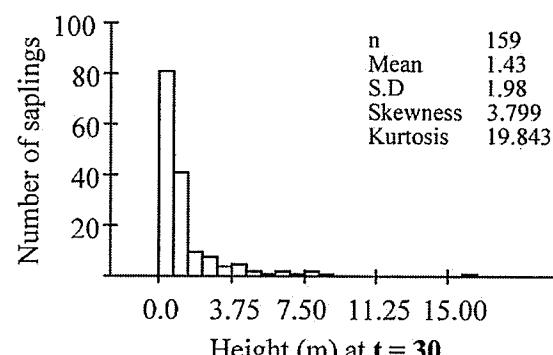
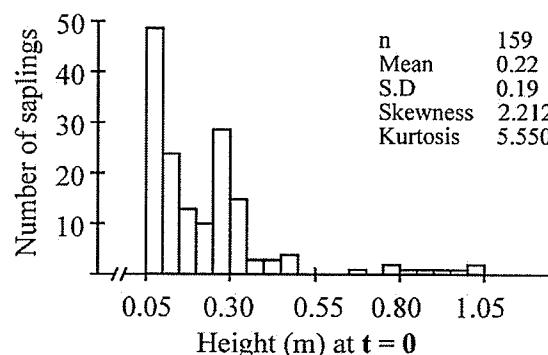
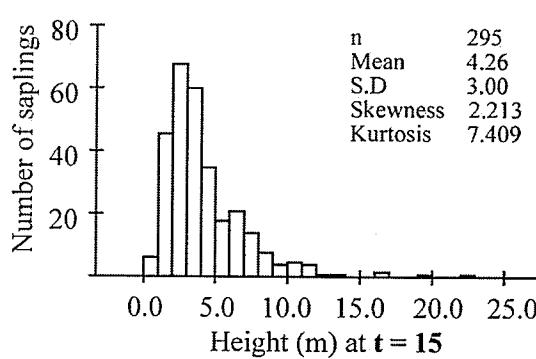
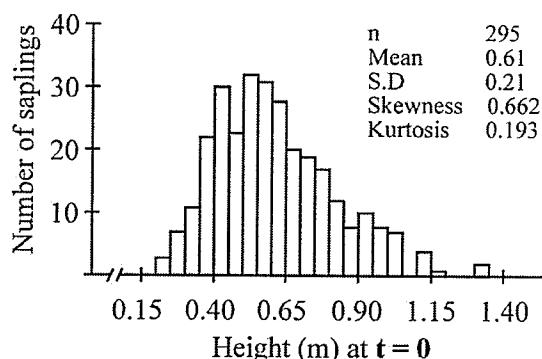


Figure 5.11 F. Frequency histograms of balsam fir height at study onset ($t = 0$) and after 30 years of projected exponential growth for open and closed canopy conditions near Chicoutimi, QC. All distributions are significantly positively skewed and leptokurtic (at $\alpha = 0.05$), except for open canopy conditions at $t = 0$ where skewness is significantly negative, and kurtosis not significantly different from zero. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

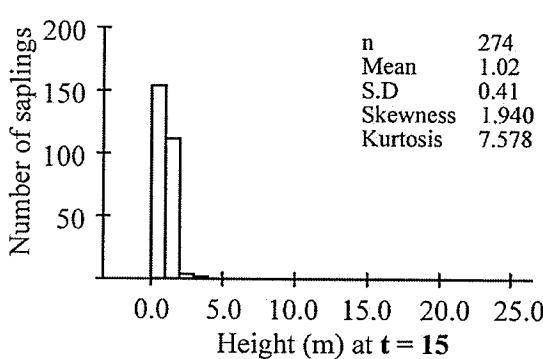
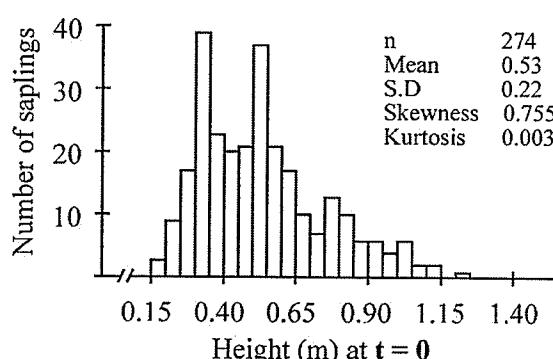
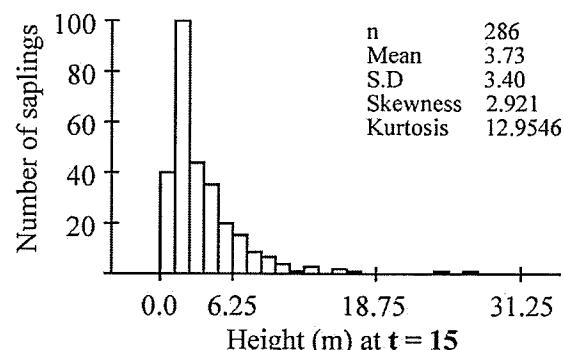
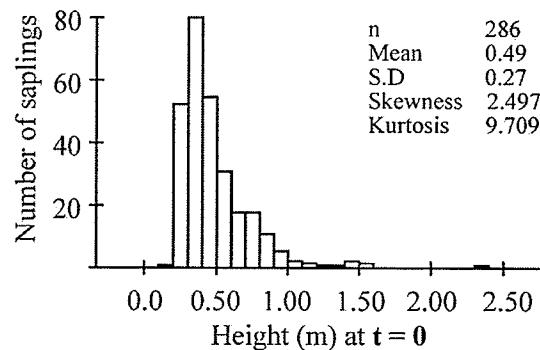


Figure 5.12 A. Frequency histograms of black spruce height at study onset ($t = 0$) and after 15 years of projected exponential growth for open and closed canopy conditions at Manitoba Shield, MB. All distributions are significantly positively skewed (at $\alpha = 0.05$), distributions at $t = 15$ are significantly leptokurtic. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

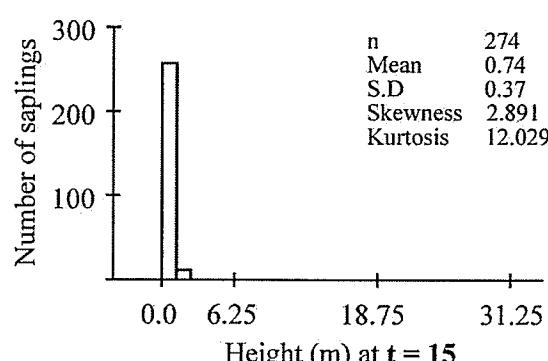
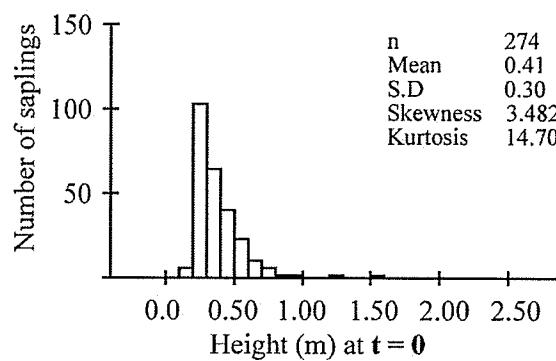
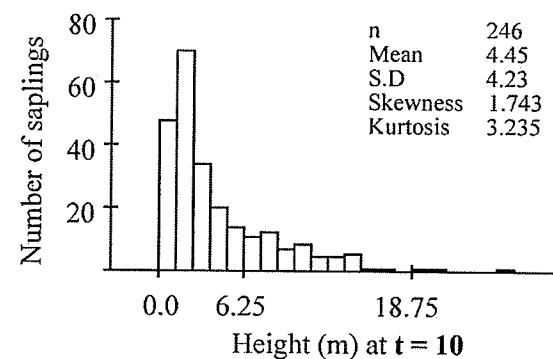
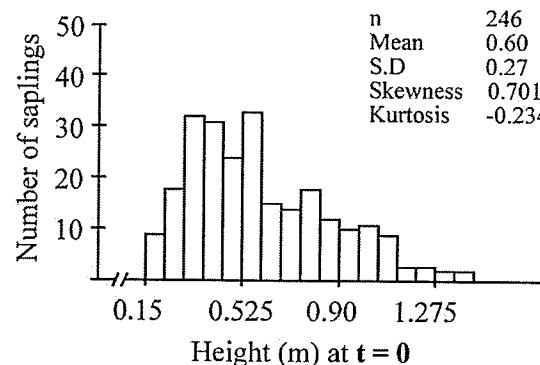


Figure 5.12 B. Frequency histograms of black spruce height at study onset ($t = 0$) and after 15 years of projected exponential growth for open and closed canopy conditions near Iroquois Falls, ON. All distributions are significantly positively skewed and leptokurtic (at $\alpha = 0.05$). Coefficients of skewness and kurtosis increase over time for open canopy conditions. Note scale differences.

Open canopy



Closed canopy

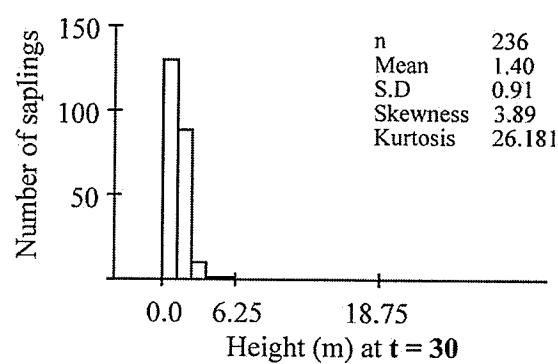
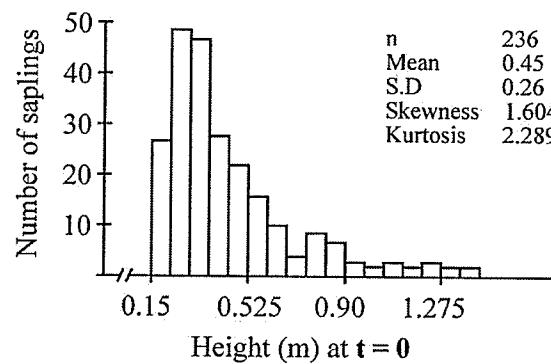
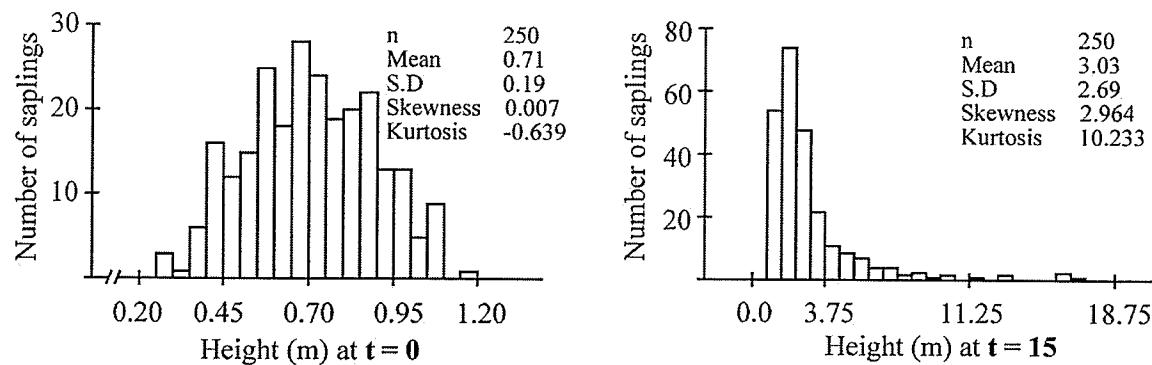


Figure 5.12 C. Frequency histograms of black spruce height at study onset (t=0) and after 10 and 30 years of projected exponential growth for open and closed canopy conditions respectively in the Ashuapmushuan Reserve, QC. All distributions are significantly positively skewed and leptokurtic (at $\alpha=0.05$), except for open canopy conditions at t=0 where the coefficient of kurtosis is not significantly different from zero. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

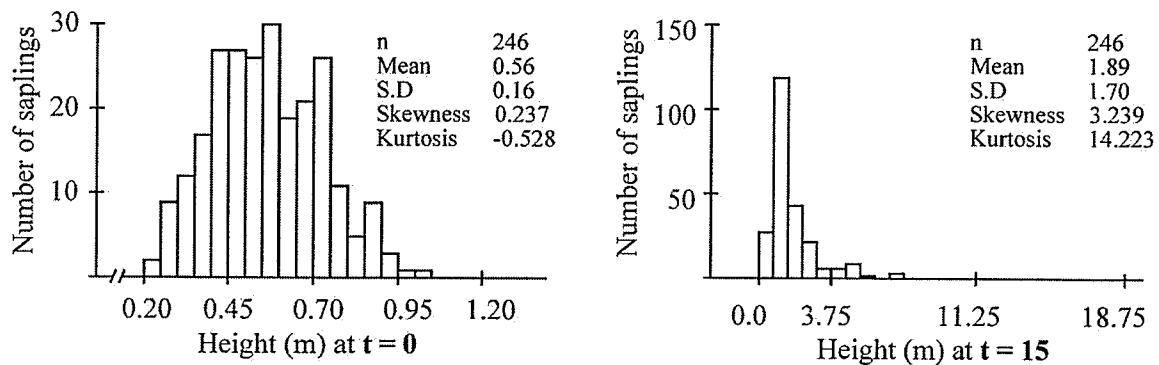
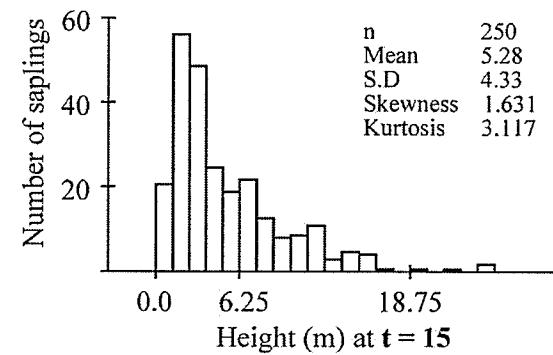
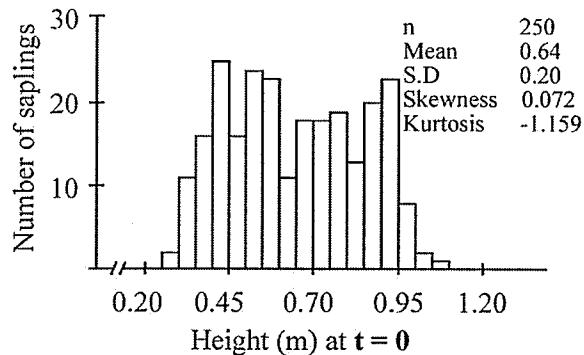


Figure 5.13 A. Frequency histograms of white spruce height at study onset ($t=0$) and after 15 years of projected exponential growth for open and closed canopy conditions in EMEND, AB. Distributions at $t=15$ are significantly positively skewed and leptokurtic (at $\alpha=0.05$). Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

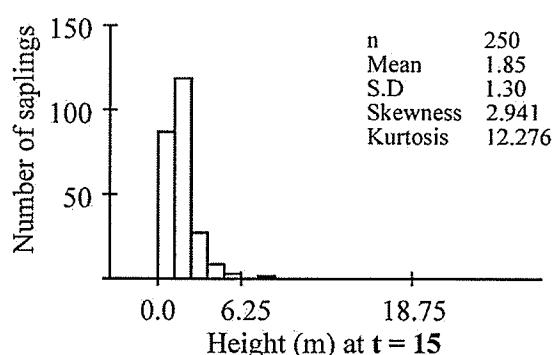
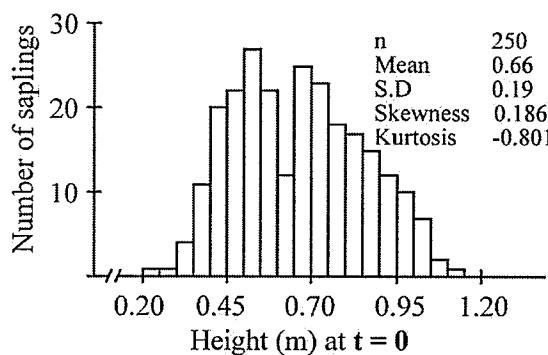
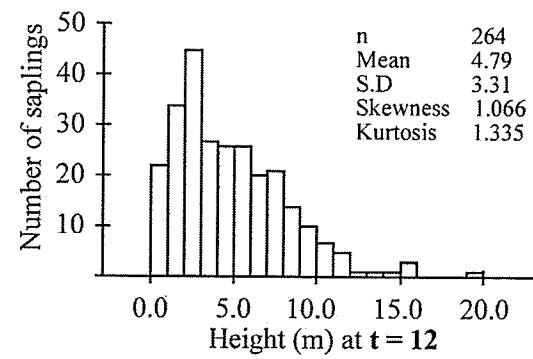
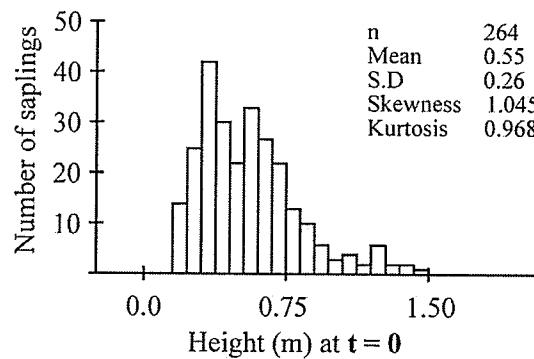


Figure 5.13 B. Frequency histograms of white spruce height at study onset ($t=0$) and after 15 years of projected exponential growth for open and closed canopy conditions in Lac La Biche, AB. Distributions at $t=15$ are significantly positively skewed and leptokurtic (at $\alpha=0.05$); distributions at $t=0$ are significantly platykurtic. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

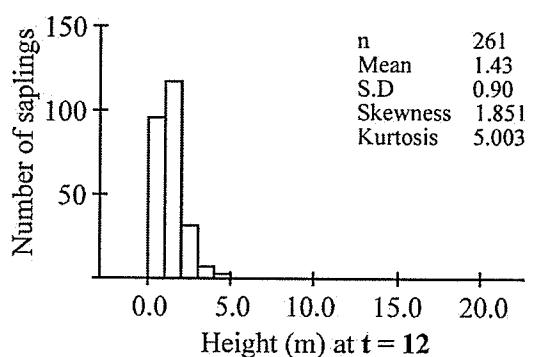
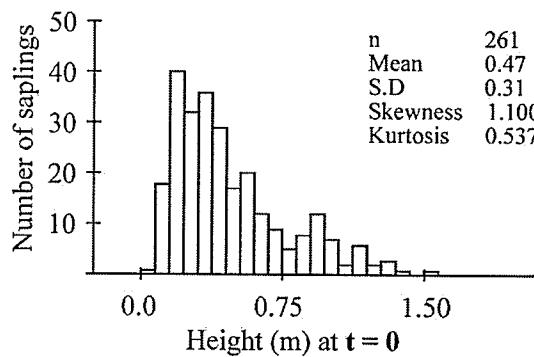
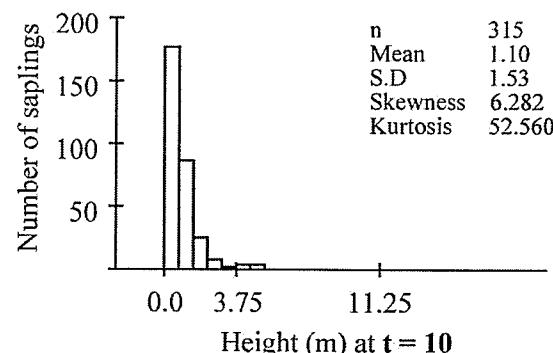
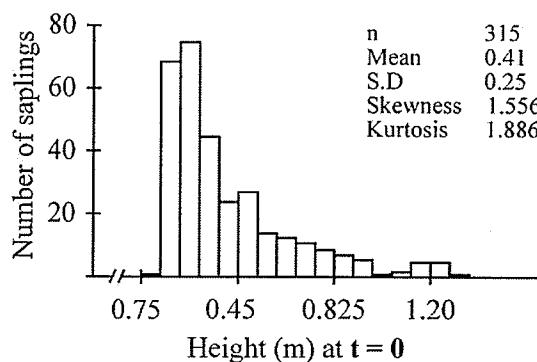


Figure 5.13 C. Frequency histograms of white spruce height at study onset ($t=0$) and after 12 years of projected exponential growth for open and closed canopy conditions in Duck Mountains, MB. All distributions are significantly positively skewed and leptokurtic (at $\alpha=0.05$) except for closed canopy conditions at $t=0$, where kurtosis is not significantly different from zero. Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

Open canopy



Closed canopy

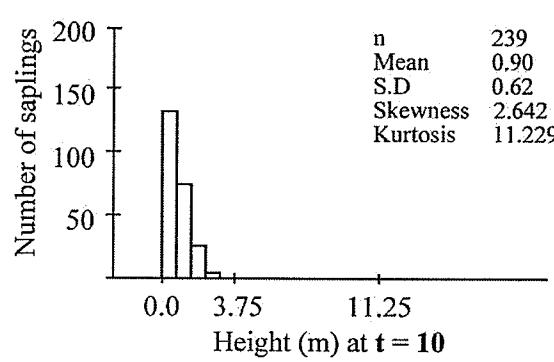
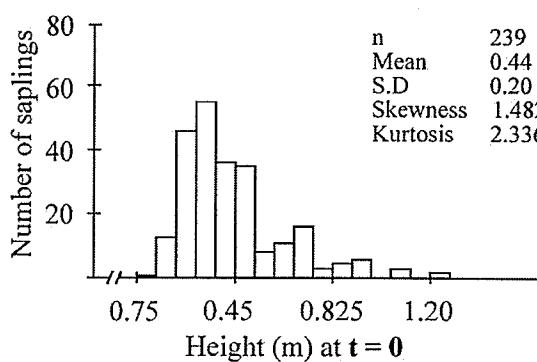


Figure 5.13 D. Frequency histograms of white spruce height at study onset ($t = 0$) and after 10 years of projected exponential growth for open and closed canopy conditions in Duparquet, QC. All distributions are significantly positively skewed and leptokurtic (at $\alpha = 0.05$). Coefficients of skewness and kurtosis increase over time for both open and closed canopy conditions. Note scale differences.

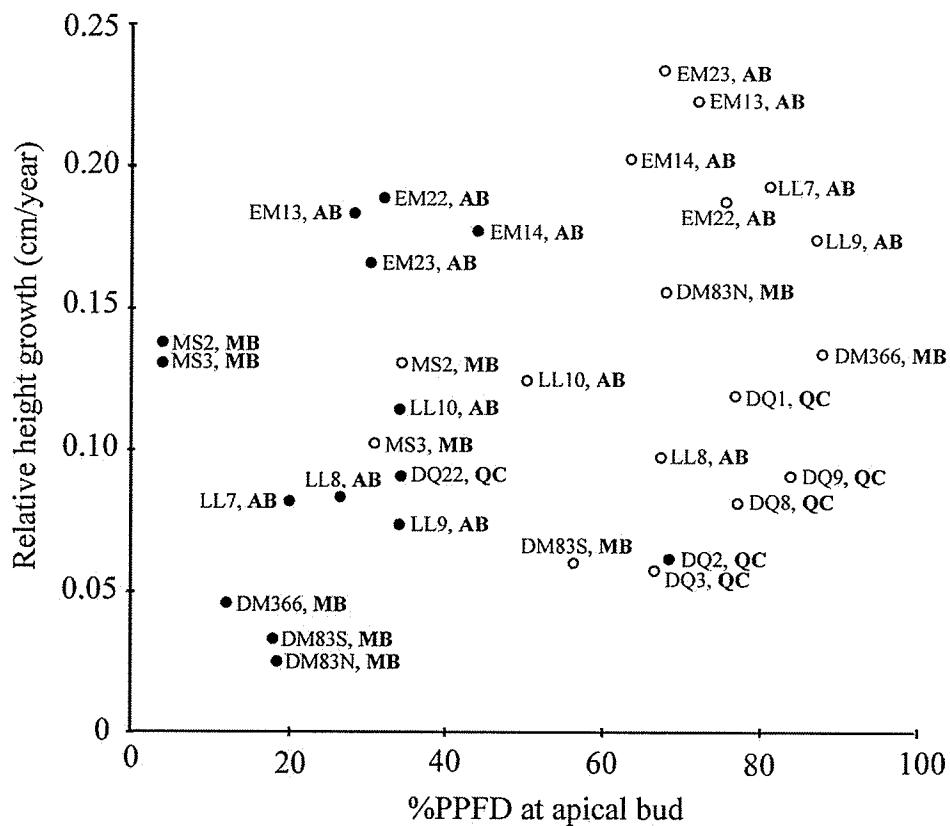


Figure 5.14. Scatterplot of mean RHG by mean %PPFD for all permanent plots of trembling aspen. Individual points represent permanent plot replicates for each canopy (light) treatment and region combination. Open circles represent high light, open canopy plots and shaded circles represent low light, closed canopy plots. Note differences in y and x-axis scales between this figure and Figures 5.15 and 5.16 for balsam fir and black spruce respectively. Both RHG and %PPFD are bimodal in distribution when considered across both canopy treatments, resulting in two separate groups of points in the upper right and lower left corners of the plots, corresponding to open and closed canopy treatments respectively. Only saplings exhibiting a positive RHG for the overall study period are included for averages of each permanent plot. Sample size (n) and standard deviation for each permanent plot, and clarification of point labels are provided in Appendix 3.1.

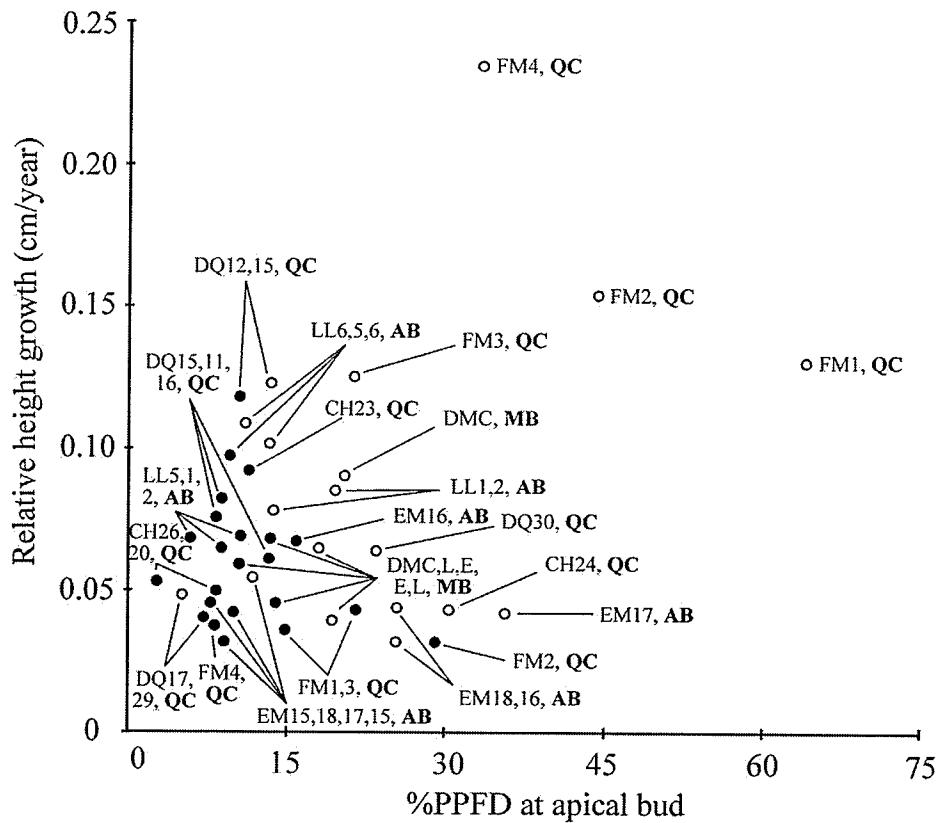


Figure 5.15 Scatterplot of mean RHG by mean %PPFD for all permanent plots of balsam fir. Individual points represent permanent plot replicates for each canopy (light) treatment and region combination. Open circles represent high light, open canopy plots and shaded circles represent low light, closed canopy plots. Note differences in y and x-axis scales between this figure and Figures 5.14, 5.16, and 5.17 for trembling aspen, black spruce and white spruce respectively. Both RHG and %PPFD are bimodal in distribution when considered across both canopy treatments, resulting in two separate groups of points in the upper right, and lower left corners of the plots, corresponding to open and closed canopy treatments respectively. Only saplings exhibiting a positive RHG for the overall study period are included for averages of each permanent plot. Sample size (n) and standard deviation for each permanent plot, and clarification of point labels are provided in Appendix 3.2.

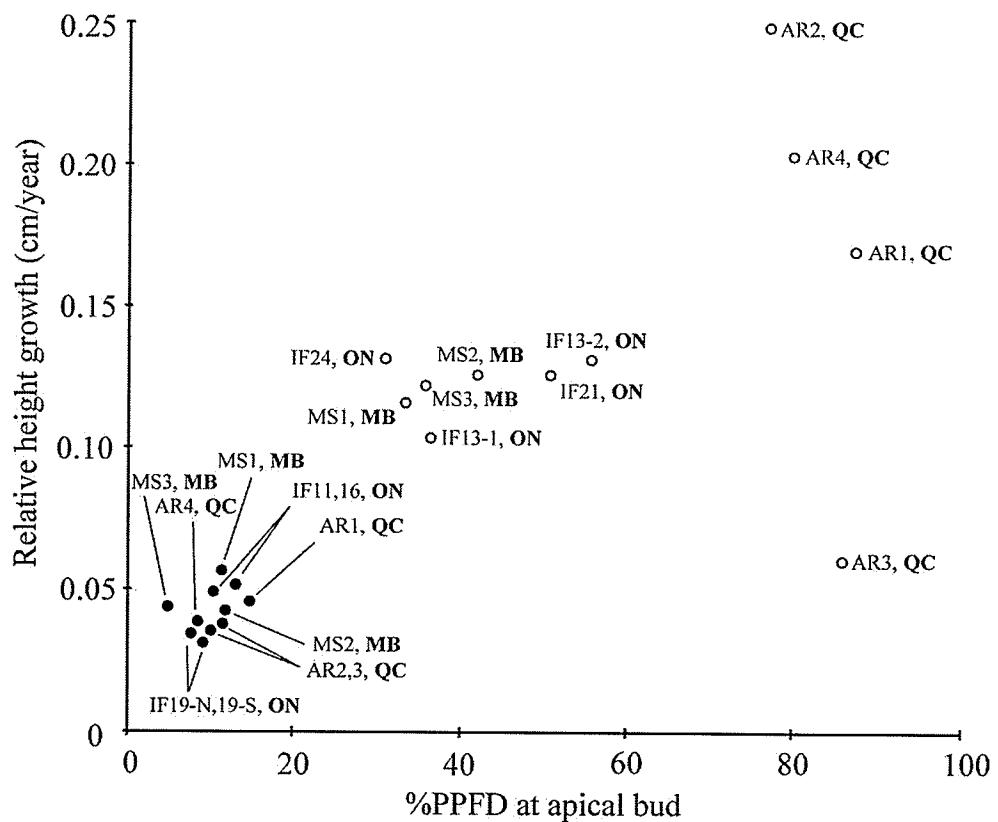


Figure 5.16. Scatterplot of mean RHG by mean %PPFD for all permanent plots of black spruce. Individual points represent permanent plot replicates for each canopy (light) treatment and region combination. Open circles represent high light, open canopy plots and shaded circles represent low light, closed canopy plots. Note differences in y and x-axis scales between this figure and Figures 5.15 and 5.17 for balsam fir and white spruce respectively. Both RHG and %PPFD are bimodal in distribution when considered across both canopy treatments, resulting in two separate groups of points in the upper right, and lower left corners of the plots, corresponding to open and closed canopy treatments respectively. Only saplings exhibiting a positive RHG for the overall study period are included for averages of each permanent plot. Sample size (n) and standard deviation for each permanent plot, and clarification of point labels are provided in Appendix 3.3.

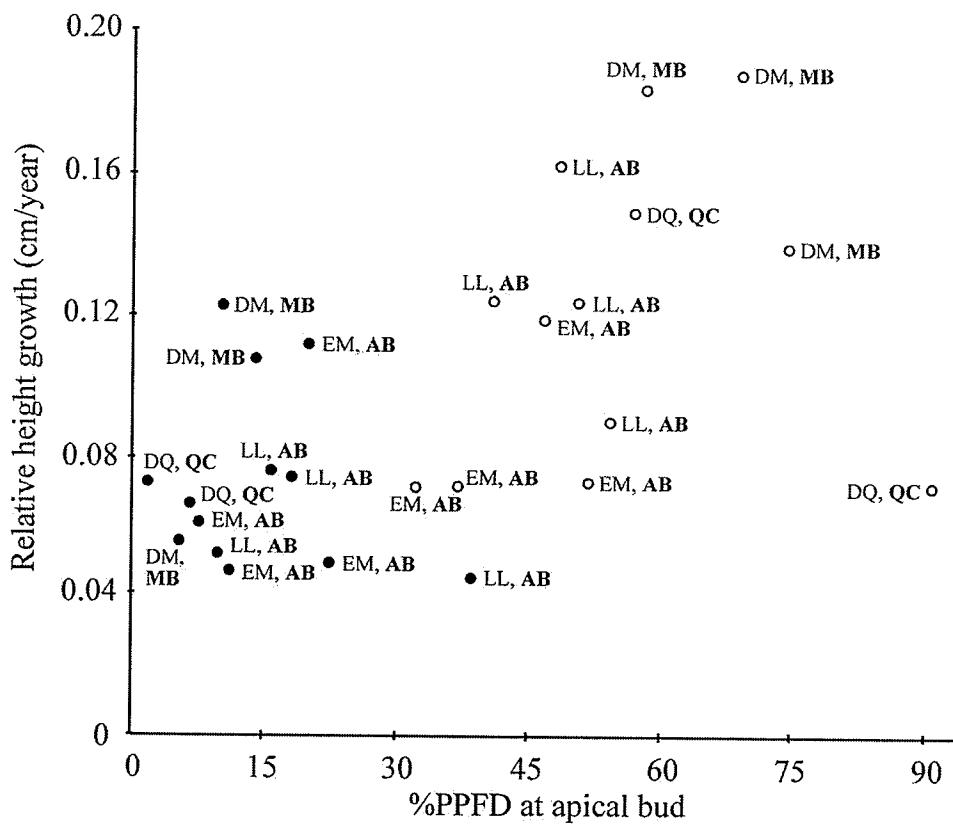


Figure 5.17. Scatterplot of mean RHG by mean %PPFD for all permanent plots of white spruce. Individual points represent permanent plot replicates for each canopy (light) treatment and region combination. Open circles represent high light, open canopy plots and shaded circles represent low light, closed canopy plots. Note differences in y and x-axis scales between this figure and Figures 5.14, 5.15 and 5.16 for trembling aspen, balsam fir and black spruce respectively. Both RHG and %PPFD are bimodal in distribution when considered across both canopy treatments, resulting in two separate groups of points in the upper right, and lower left corners of the plots, corresponding to open and closed canopy treatments respectively. Only saplings exhibiting a positive RHG for the overall study period are included for averages of each permanent plot. Sample size (n) and standard deviation for each permanent plot, and clarification of point labels are provided in Appendix 3.4.

Influential factors

Sapling response

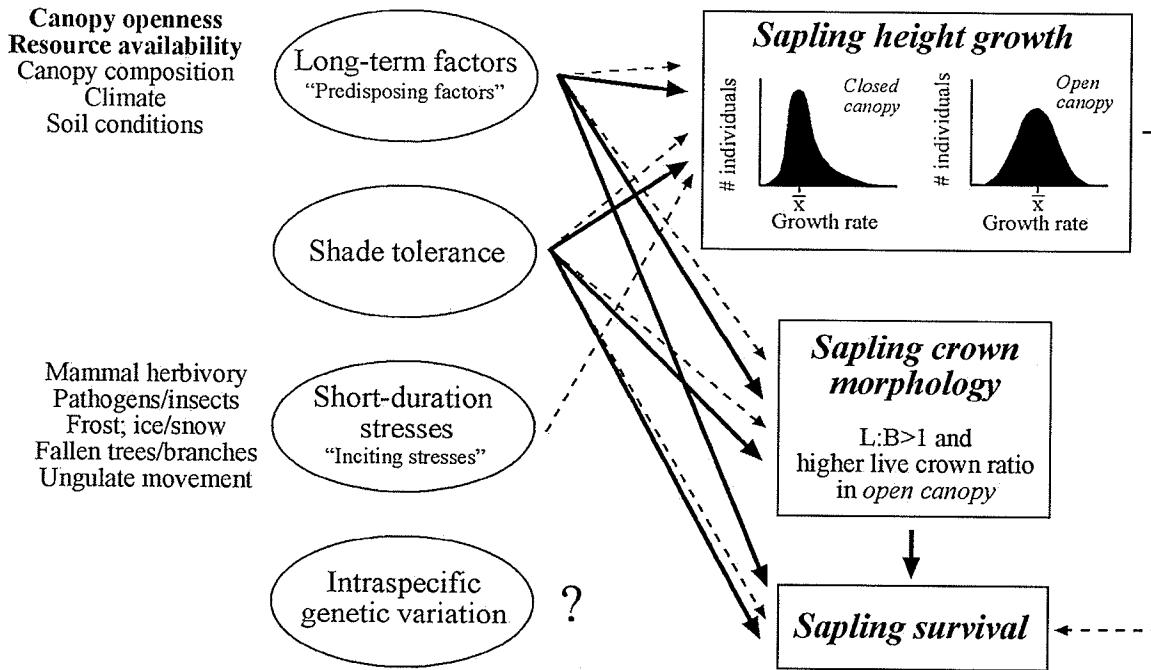


Figure 5.18. A synoptic model of the factors affecting sapling height growth, crown morphology and survival based on results from this study, field observations, and literature pertaining to boreal or North American species. A suite of predisposing factors and inciting stresses (*sensu* Manion [1981]) may influence sapling growth and/or survival. *Among* species, genetic differences expressed as variation in shade tolerance also influence sapling growth and mortality (Pacala et al. 1994, Kobe et al. 1995, Kobe and Coates 1997, Lin et al. 2001). *Within* species, genetic variation may also contribute to observed differences in sapling growth and mortality. These factors may interact to influence sapling performance. Factors whose influence on sapling growth or mortality have been assessed either in this study or in the reviewed literature have arrows illustrating their documented influence. Solid arrows show relationships demonstrated in the current study, broken arrows show relationships demonstrated in previous studies. Light environment both at the plot level (canopy openness) and individual-sapling level (resource availability) is the predisposing factor focused upon in this study. Mean RHG, distributions of RHG, crown morphology, and in some cases, mortality, differ significantly between open and closed canopy conditions. Live crown ratio is a robust predictor of individual mortality risk. Our results and observations suggest that factors interact in a complex way to influence individual sapling performance within a species and common environment. The combined effects of factors such as light availability, herbivory, mechanical damage, and insect/pathogen damage on overall sapling performance need unraveled for a better understanding of the relative influence of each factor. See section 5.4.7 for a more detailed discussion.

Table 5.1. Summary statistics for %PPFD, RHG, RDG, initial live crown ratio, initial L:B ratio, initial height and initial basal diameter of trembling aspen for each study location and canopy condition. Summary values were derived from all saplings that were alive at the end of the study period; therefore, the RHG values presented incorporate changes in sapling height over time resulting from factors other than physiological growth, such as stem dieback, or herbivory. P values are shown in brackets for t-test comparisons made between canopy conditions using mean values for each plot replicate. Statistically significant differences among light environments are highlighted. t-tests were not performed for initial height and diameter, which were used as selection criteria for plot establishment.

Study location	Canopy	# ind	# plots	%PPFD			RHG (cm/year)			RDG (cm/year)			Initial live crown ratio			Initial height (cm)		Initial diameter (cm)		
				n=#ind		P	n=#plots		n=#ind		P	n=#plots		n=#ind		P	n=#plots		mean	sd
				mean	sd		mean	sd	mean	sd		mean	sd	mean	sd		mean	sd		
EMEND, AB*	open	238	4	68.81	8.52	0.0001	0.19	0.12	0.6078	-	-	-	-	0.73	0.13	0.0877	90.19	25.80	1.19	0.31
	closed	156	4	34.03	10.92		0.15	0.13	-	-		0.62	0.14	-	-		67.98	19.91	0.09	0.28
Lac La Biche, AB*	open	220	4	71.91	19.86	0.0027	0.13	0.11	0.4234	-	-	-	-	0.60	0.14	0.1132	131.09	37.05	1.66	0.58
	closed	202	4	26.76	9.62		0.05	0.12	-	-		0.47	0.16	-	-		140.19	37.69	1.71	0.54
Duck Mountains, MB	open	208	3	69.66	30.13	0.0071	0.12	0.11	0.0421	0.06	0.0372	0.50	0.15	0.8828	150.73	36.57	1.43	0.44		
	closed	216	3	15.44	5.64		0.04	0.19		0.004		0.50	0.18		132.01	54.25		1.28	0.54	
Manitoba Shield, MB	open	71	2	32.21	9.72	-	0.12	0.06	-	0.11†	0.2982	0.51***	0.15	-	136.17	28.60	1.33	0.34		
	closed	20	1**	2.82	2.18		0.14	0.13		0.13		0.56***	0.22		81.11	18.47		0.79	0.22	
Duparquet, QC	open	134	5	71.95†	21.49	-	0.09	0.18	0.0338	0.06	0.1430	0.59	0.20	0.1745	143.77	50.70	1.56	0.66		
	closed	223	5	43.96†	22.57		0.00	0.21		0.03		0.57	0.17		148.27	58.31		1.25	0.51	

* Only one diameter measurement was available for Alberta plots, therefore RDG was not calculated.

** No t-tests comparing mean values between plot replicates were performed for Manitoba shield as saplings were alive at the end of the study only for one of the two closed canopy replicates.

*** Live crown ratio values for Manitoba Shield plots were measured in 2002, whereas this ratio was determined during the first year of the study for other regions.

† Summary statistics for %PPFD readings for Duparquet plots are based on 102 measurements (n) in open plots and 90 in closed plots. RDG summary statistics for Manitoba shield open canopy plots are based on 65 measurements.

Table 5.2. Summary statistics for %PPFD, RHG, initial live crown ratio, initial L:B ratio, initial height and initial basal diameter of balsam fir for each canopy regime and region. Summary values were derived from all saplings that were alive at the end of the study period; therefore, the RHG values presented incorporate changes in sapling height over time resulting from factors other than physiological growth, such as stem dieback, or herbivory. P values are shown in brackets for t-test comparisons made between canopy regimes for sapling response in growth and crown morphology, and for %PPFD availability. Statistically significant differences among light environments are highlighted. T-tests were not performed for initial height and diameter, which were used as selection criteria for plot establishment.

Study location	Canopy	# ind	# plots	%PPFD			RHG (cm/year)			Initial live crown ratio			Initial L:B ratio†			Initial height (cm)		Initial diameter (cm)							
				n=#ind		P	n=#plots		n=#ind		P	n=#ind		P	n=#plots		n=#ind		P	n=#plots		mean	sd	mean	sd
				mean	sd		mean	sd	mean	sd		mean	sd		mean	sd	mean	sd		mean	sd				
EMEND, AB	open	228	4	23.93	12.57	0.0372	0.05	0.03	0.8359	0.84	0.14	0.4226	1.02	2.73	0.5646	60.96	20.50	1.35	0.50	57.52	19.69	1.20	0.44		
	closed	156	4	10.61	4.99		0.05	0.03		0.80	0.17		0.79	1.48											
Lac La Biche, AB	open	250	4	14.32	8.77	0.0305	0.09	0.05	0.0901	0.82	0.12	0.1307	0.87	1.25	0.4048	59.69	19.82	1.20	0.42	55.42	17.80	1.01	0.41		
	closed	248	4	8.88	4.75		0.06	0.04		0.74	0.15		0.74	0.62											
Duck Mountains, MB	open	260	3	19.29	7.97	0.0044	0.07	0.06	0.7139	0.71	0.13	0.6807	1.05	0.50	0.9368	77.79	30.92	1.45	0.73	68.37	26.95	1.27	0.50		
	closed	269	3	12.63	5.04		0.06	0.05		0.68	0.15		0.992	0.76											
Duparquet, QC*	open	578	6	13.03	10.22	0.2930	0.05	0.12	0.3393	0.61	0.22	0.4919	0.99	2.16	0.4917	56.83	29.84	1.00	0.45	46.71	24.55	0.90	0.41		
	closed	477	8	10.39	4.95		0.04	0.14		0.67	0.21		0.87	1.96											
Forêt Montmorency, QC	open	240	4	40.67	20.34	<0.0001	0.16	0.08	0.0137	0.84††	0.15	0.0213	1.15	0.43	0.0024	56.75	27.89	0.81	0.44	43.89	31.32	0.65	0.50		
	closed	230	4	18.44	10.56		0.04	0.03		0.61††	0.23		0.47	0.49											
Chicoutimi, QC**	open	65	1	30.77	9.30	-	0.04	0.04	-	-	-	-	-	-	-	-	-	-	-	60.53	31.26	0.85	0.52		
	closed	159	3	8.82	3.23		0.07	0.05		-	-		-	-		-	-	-	-						

* # of individuals for %PPFD for Duparquet plots are n=179 and n=368 for open and closed plots respectively.

** Only one plot replicate of open canopy conditions for Chicoutimi, and no crown morphology measures available.

† As a result of some saplings missing leader and/or lateral branches for the first year of the study, L:B summary statistics are based on fewer measurements than the # individuals reported. EMEND: n=156 and 189 for open and closed plots respectively; Lac La Biche: n=231 for open plots; Duck Mountains: n=229 and 242 for open and closed plots respectively; Duparquet: n=254 and 245 for open and closed plots respectively; Forêt Montmorency: n=218 for closed plots.

†† Live crown ratio values for Forêt Montmorency plots are from 2002 (n=235, 218 for open and closed canopy conditions respectively); for other plots values of live crown ratio are from the first year of the study.

Table 5.3. Summary statistics for %PPFD, RHG, initial live crown ratio, initial L:B ratio, initial height and initial basal diameter of black spruce for each canopy regime and region. Summary values were derived from all saplings that were alive at the end of the study period; therefore, the RHG values presented incorporate changes in sapling height over time resulting from factors other than physiological growth, such as stem dieback, or herbivory. P values are shown in brackets for t-test comparisons made between canopy regimes for sapling response in growth and crown morphology, and for %PPFD availability. Statistically significant differences among light environments are highlighted. T-tests were not performed for initial height and diameter, which were used as selection criteria for plot establishment.

Study location	Canopy	# ind	# plots	%PPFD			RHG (cm/year)			Initial live crown ratio			Initial L:B ratio			Initial height (cm)		Initial diameter (cm)			
				n=#ind		P	n=#plots		P	n=#ind		P	n=#plots		P	n=#ind		P	n=#plots		P
				mean	sd		mean	sd		mean	sd		mean	sd		mean	sd		mean	sd	
Manitoba Shield, MB	open	295	3	37.64	10.53	0.0012	0.12	0.04	0.0001	0.88	0.08	0.0104	1.48	0.58	0.0015	60.61	20.62	1.03	0.47		
	closed	274	3	9.79	4.74		0.04	0.02		0.69	0.17		0.97*	0.41		52.92	21.55		0.94	0.45	
Iroquois Falls, ON	open	288	4	46.50	19.32	0.0016	0.12	0.04	<0.0001	0.77	0.14	0.6129	1.35*	0.48	0.0100	49.32	26.58	0.88	0.55		
	closed	275	4	10.84	4.58		0.04	0.02		0.76	0.15		0.98*	0.44		42.79	30.24		0.69	0.66	
Ashuapmushuan Reserve, QC	open	246	4	82.55	17.22	<0.0001	0.18	0.09	0.0138	0.89	0.16	0.0213	1.68	0.65	0.0024	59.62	27.34	1.23	0.01		
	closed	237	4	12.29	4.16		0.04	0.02		0.67	0.21		0.999	0.61		45.22	25.97		0.64	0.42	

* As a result of some saplings missing leader and/or lateral branches for the first year of the study, L:B summary statistics for closed Manitoba Shield, MB plots are based on 274 measurements. L:B ratios in Ontario plots are based on 287 and 269 measurements for open and closed plots respectively.

Table 5.4. Summary statistics for %PPFD, RHG, initial live crown ratio, initial L:B ratio, initial height and initial basal diameter of white spruce for each canopy regime and region. Summary values were derived from all saplings that were alive at the end of the study period; therefore, the RHG values presented incorporate changes in sapling height over time resulting from factors other than physiological growth, such as stem dieback, or herbivory. P values are shown in brackets for t-test comparisons made between canopy regimes for sapling response in growth and crown morphology, and for %PPFD availability. Statistically significant differences among light environments are highlighted. T-tests were not performed for initial height and diameter, which were used as selection criteria for plot establishment.

Study location	Canopy	# ind	# plots	%PPFD			RHG (cm/year)			Initial live crown ratio			Initial L:B ratio**			Initial height (cm)		Initial diameter (cm)			
				n=#ind		P	n=#plots		n=#ind		P	n=#ind		P	n=#plots		n=#ind		P	mean	sd
				mean	sd		mean	sd	mean	sd		mean	sd		mean	sd	mean	sd		mean	sd
EMEND, AB	open	250	4	41.95	17.01	0.0021	0.08	0.04	0.4051	0.71	0.15	0.9544	1.06	0.34	0.1626	71.13	20.05	1.27	0.53		
	closed	250	4	14.45	7.89		0.07	0.04	0.71	0.18	0.92	0.92	0.32	0.1626	45.36	17.61	0.92	0.31			
Lac La Biche, AB	open	250	4	48.96	18.94	0.0062	0.12	0.05	0.0093	0.86	0.08	0.0099	1.15	0.30	0.0228	63.68	20.59	1.31	0.50		
	closed	245	4	21.13	12.66		0.06	0.03		0.76	0.12		0.96	0.29		65.68	20.55	1.10	0.40		
Duck Mountains, MB	open	264	3	67.19	15.90	0.0028	0.17	0.05	0.2250	0.87	0.09	0.0448	1.47	0.67	0.0484	54.98	26.45	1.36	0.64		
	closed	266	3	10.22	6.56		0.10	0.06		0.68	0.18		1.069	0.09		47.21	30.53	0.86	0.55		
Duparquet, QC*	open	331	3***	87.80	18.22	0.0592	0.07	0.07	0.3806	0.83	0.17	0.1882	0.93	0.85	0.8167	41.74	25.18	1.10	0.44		
	closed	270	3***	4.65	2.38		0.05	0.07		0.73	0.16		0.90	1.27		43.68	20.04	0.79	0.35		

* Sample sizes for %PPFD for Duparquet plots are n=195 and n=204 for open and closed plots respectively.

** As a result of some saplings missing leader and/or lateral branches for the first year of the study, L:B summary statistics are based on fewer measurements than the n values reported. For EMEND, n=237 and 234 for open and closed plots respectively, for Duck Mountains, n=250 and 223 for open and closed plots respectively, and for Duparquet, n=280 and 193 for open and closed plots respectively.

*** Only two plot replicates each for open and closed canopy conditions for t-tests comparing %PPFD for Duparquet.

Table 5.5. Coefficients of determination and significance levels for simple linear regressions of RHG, RDG, live crown ratio, and L:B ratio against %PPFD for natural regeneration of white spruce, black spruce, balsam fir, and trembling aspen. Significant regressions are highlighted. As a result of some saplings missing leader and/or lateral branches sample size (n) for L:B regressions are lower than those presented. All relationships are positive with the exception of the significant regressions for white spruce regeneration in Duparquet. r^2 values are presented as percentage ($r^2 \times 100\%$).

Species	Region	Canop y	RHG			RDG			Live crown ratio			L:B ratio		
			n	r^2	P	n	r^2	P	n	r^2	P	n	r^2	P
Trembling aspen	EMEND, AB	open	226	0.8	0.183	-	-	-	225	13.1	<0.0001	-	-	-
		closed	125	0.0	0.837	-	-	-	133	5.8	0.005	-	-	-
	Lac La Biche, AB	open	195	19.1	<0.0001	-	-	-	203	12.5	<0.0001	-	-	-
		closed	166	0.4	0.436	-	-	-	166	2.0	0.072	-	-	-
	Duck Mountains, MB	open	177	38.2	<0.0001	179	2.0	0.059	179	30.8	<0.0001	-	-	-
Balsam fir	MB	open	142	0.1	0.710	153	0.3	0.526	153	1.6	0.122	-	-	-
		closed	70	6.9	0.028	70	0	0.945	70	7.4	0.023	-	-	-
	Manitoba shield, MB	open	13	12.5	0.236	17	29.4	0.025	17	16.4	0.203	-	-	-
		closed	78	0.9	0.405	78	4.4	0.064	78	0.1	0.807	-	-	-
	Duparquet, QC	open	51	4.1	0.155	51	0.8	0.541	51	0.5	0.670	-	-	-
Balsam fir	EMEND, AB	open	227	0.0	0.974	-	-	-	227	0.8	0.186	156	0.4	0.407
		closed	236	16.6	<0.0001	-	-	-	236	9.2	<0.0001	189	4.8	0.002
	Lac La Biche, AB	open	239	7.2	<0.0001	-	-	-	250	1.8	0.032	231	0	0.949
		closed	233	9.0	<0.0001	-	-	-	248	5.2	0.000	243	8.0	<0.0001
	Duck Mountains, MB	open	260	15.6	<0.0001	-	-	-	245	15.7	<0.0001	234	10.7	<0.0001
		closed	268	3.6	0.008	-	-	-	241	10.5	<0.0001	251	1.7	0.041
Black spruce	Duparquet, QC	open	146	7.1	0.001	-	-	-	146	20.6	<0.0001	118	1.0	0.271
		closed	261	4.5	0.001	-	-	-	261	16.1	<0.0001	218	4.3	0.002
	Forêt Montmorency, QC	open	240	1.5	0.058	-	-	-	240	3.4	0.005	237	1.4	0.067
		closed	230	0.1	0.572	-	-	-	230	0.6	0.275	218	0.1	0.578
	Chicoutimi, QC	open	11	34.3	0.059	-	-	-	-	-	-	-	-	-
White spruce	Manitoba shield, MB	open	295	1.9	0.017	-	-	-	295	1.0	0.093	295	0.3	0.324
		closed	274	1.7	0.033	-	-	-	274	0	0.820	274	0.0	0.820
	Iroquois Falls, ON	open	286	6.3	<0.0001	-	-	-	288	0.9	0.109	287	0.0	0.990
		closed	274	0.6	0.191	-	-	-	281	0.1	0.672	269	0.0	0.991
	Ashuapmushuan Reserve, QC	open	246	0.6	0.234	-	-	-	246	0.3	0.385	246	0.3	0.385
White spruce	EMEND, AB	open	250	2.1	0.021	-	-	-	248	3.7	0.002	237	3.3	0.005
		closed	246	12.5	<0.0001	-	-	-	246	5.2	0.000	234	3.1	0.007
	Lac La Biche, AB	open	250	0.0	0.764	-	-	-	250	0.3	0.392	250	2.3	0.023
		closed	250	0.6	0.217	-	-	-	245	0.3	0.409	245	6.5	<0.0001
	Duck Mountains, MB	open	264	0.1	0.531	-	-	-	264	11.9	<0.0001	250	0.2	0.446
		closed	261	14.0	<0.0001	-	-	-	261	5.3	0.000	223	0.7	0.209
White spruce	Duparquet, QC	open	185	21.3	<0.0001	-	-	-	185	4.0	0.007	157	30.2	<0.0001
		closed	160	1.7	0.099	-	-	-	160	10.0	<0.0001	141	2.9	0.042

Table 5.6. Percentage of total number of monitored saplings of trembling aspen and balsam fir browsed each year. Values are means across the 2.5 years comprising the study period. Standard deviation therefore represents annual variation. The number of years that herbivory was monitored differs among other regions. Herbivory was only recorded in one year for balsam fir in Duparquet, therefore there is no estimated annual variation.

Species	Region	Canopy regime	Average % of saplings browsed	sd	agent
Trembling aspen	EMEND, AB	Open	16.93	5.60	mostly ungulate, some hare
		Closed	24.65	13.02	mostly ungulate, some hare
	Lac La Biche, AB	Open	20.86	3.46	mostly ungulate, some hare
		Closed	35.27	16.55	mostly ungulate, some hare
	Duck Mountains, MB	Open	32.94	7.65	ungulate
		Closed	42.32	5.61	ungulate
	Manitoba shield, MB	Open	1.68	2.90	ungulate
		Closed	19.50	12.49	ungulate
	Duparquet, QC	Open	11.19*	10.54	ungulate
		Closed	2.74	0.56	ungulate
Balsam fir	EMEND, AB	Open	2.53	4.39	mostly hare, some ungulate
		Closed	1.60	2.77	mostly hare, some ungulate
	Lac La Biche, AB	Open	14.13	19.31	mostly hare, some ungulate
		Closed	23.33	21.75	mostly hare, some ungulate
	Duck Mountains, MB	Open	21.54	13.55	ungulate
		Closed	23.75	23.10	ungulate
	Duparquet, QC	Open	1.90	0	ungulate
		Closed	1.40	0	ungulate
	Forêt Montmorency, QC	Open	0.40	0.80	ungulate
		Closed	0.53	1.05	ungulate

*Unusually high number of saplings reported browsed for one of the five open canopy permanent plots of aspen regeneration in Duparquet.

CHAPTER 6

MANAGEMENT IMPLICATIONS

6.1 Introduction: the use of advance regeneration in natural disturbance-based management

Natural disturbance-based management is commonly considered the best approach for maintaining the integrity and long-term sustainability of managed forests (Lieffers et al. 1996, Burton et al. 1999, McCarthy 2001, Chen and Popadiouk 2002, Harvey et al. 2002). Maintaining natural structure and composition of forests at both landscape and stand levels may necessitate both even-aged and uneven-aged harvesting strategies to reflect natural stand dynamics (McCarthy 2001, Harvey et al. 2002). Careful harvesting to protect advance regeneration is an even-aged silvicultural practice that has been used in recent years as a low-cost method for ensuring sufficient regeneration that is well-suited to a site (Ruel et al. 1995, Örlander and Karlsson 2000, Pothier 2000, Harvey and Brais 2002, Prévost and Pothier 2003). Furthermore, the use of uneven-aged silviculture to mimic natural disturbance in gap-driven systems is being newly explored in boreal forests in North America (Coates and Burton 1997, McCarthy 2001).

Careful logging practices have been widely implemented in the boreal forests of Ontario and Québec (Bergeron et al. 1999, Ruel et al. 2000, Kneeshaw et al. 2002). This practice emulates in many ways spruce budworm outbreaks, which are an integral part of the disturbance regime of eastern boreal forests (though not of western ones). It has been suggested that forest ecosystem management should not simply mimic natural disturbance: the dynamics of natural disturbance should also be considered in developing strategies for promoting natural forest structure and composition while meeting other industry objectives (Bergeron et al. 1999). Careful logging should also be explored as a silvicultural tool in western boreal regions where disturbance regimes differ. Both even-aged careful logging as practiced in eastern regions and uneven-aged, or "classic selection" silvicultural approaches should be explored in western regions. For example, a combination of careful and partial harvesting is a more sustainable strategy for logging western boreal riparian ecosystems than is clearcutting (Timoney and Peterson 1996).

Management considerations for careful harvesting

Important considerations in attempting to utilize advance regeneration in forest management include ensuring adequate abundance of advance regeneration and its ability to respond positively to overstory removal, protecting it from damage during harvesting, and minimizing mortality risk associated with increased radiation, drought, and frost injury following overstory removal (Groot and Carlson 1996, Greene et al. 1999, Örländer and Karlsson 2000, Ruel et al. 2000).

Light availability, together with stand basal area and forest floor characteristics, affect pre-harvest densities of advance regeneration (Greene et al. 1999). In the eastern boreal forest, Kneeshaw and Bergeron (1996) recommend that management strategies based on conifer advance regeneration should focus on mixed conifer-deciduous stands. The low density of conifer seedlings and saplings in hardwood stands, and strong competition from shade-intolerant species in large gaps of coniferous stands, limit the utility of advance regeneration strategies in these stands.

In addition to abundance of natural regeneration, post-harvest survival is an important consideration when assessing the potential of a site for careful harvesting. Interspecific variation in mortality should be considered: advance regeneration of balsam fir is often more abundant than spruce, but our results indicate that fir has consistently higher mortality rates than spruce (though fir mortality is still low). Ruel et al. (1995) demonstrated that amount of sapling suppression prior to release, and logging damage during harvest are needed to assess mortality immediately following release. The optimal shelterwood density for growth and survival of Norway spruce (*Picea abies* (L.)) saplings – of similar size to the spruce examined in our study – in southern Sweden was 80-160 stems/ha (Örländer and Karlsson 2000). In promoting the growth of coniferous advance regeneration, it has been suggested post-harvest light availability should be high enough to ensure a L:B ratio > 1 (Klinka et al. 1992). A partial harvesting approach to careful logging of high-quality sites may optimize the response of advance regeneration, both by limiting post-harvest exposure and by minimizing the growth of competing vegetation.

The growth of advance regeneration is slow in the first few years following clear-cut harvesting, but increases rapidly thereafter (Kneeshaw et al. 2002). Advance regeneration growing in moister sites may show less reduction in height growth in the

initial few years following harvesting. Post-harvest advance regeneration growth is not appreciably reduced in smaller cuts and partial cutblocks, since changes in the “exposure” environment of advance regeneration are minimized (Kneeshaw et al. 1998, 2002, Örländer and Karlsson 2000). Our study supports previous findings that shade-tolerant coniferous advance regeneration demonstrates a “plastic” crown morphology that allows it to respond positively to overstory removal provided that proper management strategies are employed to minimize stress during and after harvesting.

6.2 Empirical population estimates of growth and mortality rates for trembling aspen, balsam fir, black spruce, and white spruce, in low and high light environments

Foresters base many of their projections of future stand conditions and silvicultural interventions on current stocking (abundance) of advance regeneration, and the probability that trees will die over a given period of time. An understanding of the rates and causes of mortality under different conditions will improve the reliability of such projections, and is therefore critical to ensuring the long-term sustainability of boreal forest. As forest management becomes more complex, simulation models that test alternative management approaches are increasingly important (Claveau et al. 2002). Interspecific differences in sapling mortality are critical in determining forest composition during secondary succession (Pacala et al. 1994, Kobe et al. 1995, Kobe and Coates 1997), and light availability is a crucial parameter influencing stand development (Claveau et al. 2002).

Our study has provided much-needed empirical growth and mortality rates for boreal forest species of different shade-tolerances, growing under different light environments in various regions of the Canadian boreal forest. For coniferous species, low mortality rates in conjunction with elevated growth rates under higher light environments suggest that advance regeneration will form an important component of future stands following gap-formation or careful harvesting. Comparably high mortality of aspen suckers in the understory implies an alternative strategy for canopy replacement: a continuous turnover of short-lived aspen suckers ensures a constant supply of advance regeneration. Growth distributions of natural regeneration in shaded understory

conditions have important implications for future forest growth: fast rates of height growth at an early sapling stage of development in the forest understory may confer advantages to subsequent recruitment into the canopy.

Our study has addressed the potential for geographic variation in growth and mortality rates of advance regeneration across the Canadian boreal forest. With few exceptions resulting from unique localized site conditions, mortality rates are fairly consistent across regions. Growth responses of balsam fir differ substantially between geographic regions where spruce budworm dynamics dominate systems and regions in which smaller-scale gap formation governs the dynamics of infrequently burned forests.

6.3 Growth and mortality compared in high and low light environments

Growth and crown morphology differed between contrasting light environments for all species, for some study locations. Growth differences between open and closed canopy conditions were most pronounced and consistent among regions for black spruce. Differences in growth were not significant for balsam fir except under spruce budworm gaps. Shade tolerant fir may not respond to changes in light environment to the same extent as less shade tolerant black spruce or aspen. Balsam fir mortality was higher in low light conditions than in high light conditions under vast spruce budworm-caused canopy gaps (Quebec), but was higher in small gaps than closed forest in western regions (Manitoba, Alberta). Spruce mortality was consistently low across light conditions and study locations. Factors in addition to light were likely contributing to the higher balsam fir mortality. Aspen mortality was high in both open and closed canopy conditions, but the causes of mortality differed. The information presented can aid in the formulation of management approaches for given canopy conditions and geographic regions.

6.4 Individual-level predictors of mortality risk

To ensure adequate stocking of harvested stands, preserved advance regeneration must be maintained in a healthy state; specific field criteria are needed to assess the ability of advance regeneration to respond positively to overstory removal (Ruel et al.

2000). L:B ratio, live crown ratio, and pre-release height growth have all been found to be good indicators of post-release response for shade-tolerant coniferous species. Ruel et al. (2000) used results from a study by Kobe and Coates (1997) to determine tentative threshold light values at which mortality rates were 10% or less. They proposed that shade-tolerant species growing at < 10% of open canopy light, and shade-intolerant species growing at < 40% light, were not sufficiently vigorous to be used for restocking following careful harvesting. However, they also suggested that additional indicators may be required, and that specific threshold values may need to be developed for different regions.

We used survival analysis to provide estimates of the potential of an individual sapling to die in a given season, based on morphological measures and light availability. Cox PH models that have been derived for each study location and light environment can be used to derive threshold values of %PPFD (for aspen) initial height (for aspen), and live crown ratio (for aspen and fir) in a similar manner as was done by Ruel et al. (2000). Acceptable probabilities of mortality within a 2.5-year time frame can be decided upon, and corresponding threshold values of %PPFD and height (for aspen) and live crown ratio (for aspen and fir) can be computed. In order to predict variation in survival time for white and black spruce, a longer study period is required to gather sufficient censored data of sapling mortality.

6.5. The need for long-term data

To more fully characterize the growth and mortality of advance regeneration growing in low and high light environments, including determining the effects of influential factors not examined in this study, our permanent monitoring program must continue for at least an additional 3-4 years. Several additional years of monitoring are needed also to obtain statistically robust estimates of growth and mortality rates. Robust estimates of growth and mortality based on long-term data are critical to the development and reliability of boreal forest stand dynamic models and management strategies. This study provides some insight into the growth and mortality of advance regeneration under different light regimes, and across regions of the boreal forest. However, the time period

over which saplings were monitored provides only a brief "snapshot". A long-term "dynamic" scenario of growth and mortality of advance regeneration would further our understanding of these critical processes. Moreover, the mortality rates of advance regeneration of shade tolerant coniferous (particularly the spruce species examined) are far too low over a 2.5-year period to generate informative survivorship curves. Long-term data will also allow us to compare growth and mortality rates with local climate data for each study location. Our permanent plots are ideal for continued long-term monitoring over many years. Such long-term data would provide us with a more comprehensive understanding of ecology and long-term dynamics of these important tree species, and contribute to their sustainable management across the Canadian boreal forest.

6.6. Specific recommendations

Across the Canadian boreal forest harvesting practices that preserve advance regeneration should continue to be explored for improving the preservation of natural structure and composition of managed forests. In addition to even-aged harvests, uneven-aged approaches (classic selective silviculture) should be considered in systems dominated by small-scale gap disturbance. For example, Coates and Burton (1997) found that a gap-based partial cutting silvicultural system is effective in permitting timber extraction while maintaining natural old-growth forest structure in western forests of British Columbia.

This study has provided much needed mortality and growth rates for advance regeneration of white and black spruce, balsam fir, and trembling aspen across the boreal forest; with a few exceptions, rates are similar among regions. The growth and mortality rates presented are characteristic for each species; thus, they provide representative empirical estimates for use in simulations of forest stand dynamics to derive and test alternative management strategies.

It is recommended that our results predicting mortality risk from %PPFD, size, and in particular live crown ratio contribute to the development of morphological indicators for in-field assessment of survival time of saplings growing under different light environments. Threshold values for acceptable levels of sapling mortality within a

defined time interval should be pre-determined for a given species and level of abundance of advance regeneration (eg. 10% mortality over a three-year period). Using species-specific mortality rates and survival times for advance regeneration, in conjunction with developed indices of vigour incorporating live crown ratio (the most robust predictor of survival time according to our results), the response of regeneration at a given site can be predicted. Inter-regional differences for balsam fir should be taken into consideration for any future applications of the provided mortality rates and survival times.

Growth and mortality of advance regeneration in our established plots should continue to be monitored for at least several more years to gain further insight into conifer mortality and to obtain statistically robust estimates of growth and mortality rates. To more fully characterize these processes additional factors influencing sapling growth and mortality not yet addressed in this study should be investigated. Our observations suggest that herbivory is an extremely influential factor, which may differ across geographic study locations. Herbivory and other predisposing and inciting factors discussed in this paper, in particular, insect and pathogen damage, understory competition, soil conditions, and climate, should be examined.

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A



B



Appendix 1.1. Adjacent plots of trembling aspen regeneration in open canopy conditions (A) and closed canopy conditions (B), in Duck Mountains, MB.

A



B

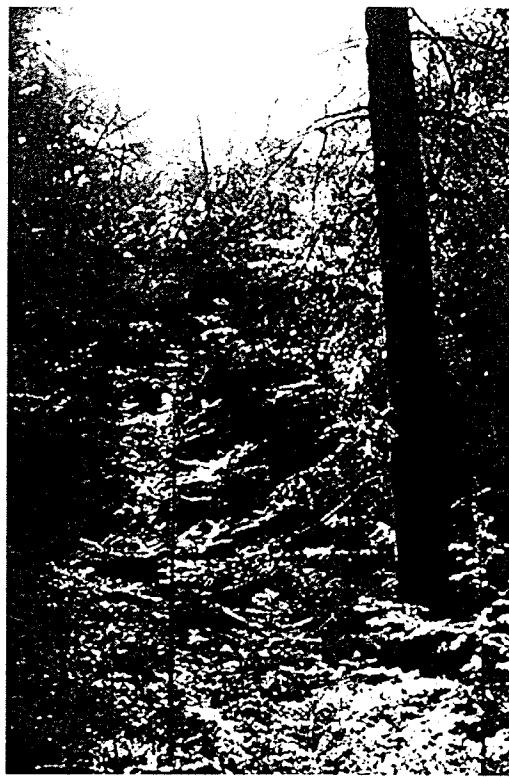


C



Appendix 1.2. Permanent plots of balsam fir advance regeneration in Forêt Montmorency, QC.
A.) Extensive canopy gap resulting from spruce budworm outbreak. B.) Advance regeneration of balsam fir growing under a spruce budworm gap. C.) Balsam fir advance regeneration growing in adjacent full canopy conditions.

A



B



Appendix 1.3. Open canopy (A) and closed canopy (B) permanent monitoring plots of balsam fir advance regeneration in Duck Mountains, MB.

A



B



Appendix 1.4. Adjacent plots of advance regeneration of black spruce under open canopy conditions (A) (note adjacent closed black spruce plot in background), and closed canopy conditions (B), in the Ashuapmushuan Reserve, QC.

A



B



Appendix 1.5. White spruce advance regeneration in open canopy conditions along a roadside near Lac La Biche, AB (A), and under closed canopy conditions in Duck Mountains, MB (B).

Appendix 2.1. Site descriptions including canopy and soil characteristics for permanent plots in EMEND, AB.

Site replicate	Canopy regime	Regeneration species	Elevation (m)	Slope (%)	Aspect (degrees)	Average canopy height (m)	Canopy basal area (m ² /ha)					Soil description	
							Trembling aspen	Balsam poplar	White spruce	Balsam fir	Black spruce	% coarse fragments	Description of soil horizons
EMEND13	open	trembling aspen	752	0	n/a							5	thin organic, mod Ah, mod B (C), effective texture C
EMEND14	open	trembling aspen	752	6	26							5	thick organic, mod Ah, thick B (SiCL), effective texture SiCL
EMEND22	open	trembling aspen	783	0	n/a							0	thick organic, mod Ah, thick B (C), effective texture C
EMEND23	open	trembling aspen	783	3	149							0	mod organic, thin Ah, thick B (SiC), effective texture SiC
EMEND13	closed	trembling aspen	801	0	n/a	24.8	13					5	mod organic, mod Ah, thick B (C), effective texture C
EMEND14	closed	trembling aspen	752	11	15	19.1		9	1			5	thin organic, thin Ah, thick Bm (SiC), effective texture SiC
EMEND22	closed	trembling aspen	783	0	n/a	20.1		5		1	2	0	mod organic, thin Ah, mod B (SiC), effective texture SiC
EMEND23	closed	trembling aspen	783	3	48	21.7		4	3	2		0	thin organic, thin Ah, thick B (SiC), effective texture SiC
EMEND15	open	balsam fir	848	10	257	21.8		8		9		5	mod organic, thin Ah, thick B (SiCL), effective texture SiCL
EMEND16	open	balsam fir	869	8	203	28.7		4		10		0	mod organic, thin Ah, thick B (SiC), effective texture SiC
EMEND17	open	balsam fir	849	3	70	22.4		4		11	1	5	thick organic, thin Ah, thick B (SiC), effective texture SiC
EMEND18	open	balsam fir	821	0	n/a	22.7		6		4		0	mod organic, thin Ah, thick B (SiC), effective texture SiC
EMEND15	closed	balsam fir	846	5	219	21.8		5		13	1	5	mod organic, mod Ah, thick B (C), effective texture C
EMEND16	closed	balsam fir	817	6	159	25.3		2		5		0	mod organic, mod Ah, thick B (C), effective texture C
EMEND17	closed	balsam fir	848	3	185	13.1				3	3	10	mod organic, thin Ah, thick B (C), effective texture C
EMEND18	closed	balsam fir	819	0	n/a	21.5		8		6	1	5	mod organic, mod Ah, thick B (SiC), effective texture SiC
EMEND19	open	white spruce	750	0	n/a							5	thin organic, thick Bt (C), effective texture C
EMEND20	open	white spruce	695	0	n/a							0	thin organic, thick Bt (C), effective texture C
EMEND21	open	white spruce	777	0	n/a							0	thin organic, thin Ah, thick Bt (C), effective texture C
EMEND24	open	white spruce	783	0	n/a							10	thin organic, thin Ah, thick B (SiC), effective texture SiC
EMEND19	closed	white spruce	762	3	21	24.9		3		11		5	thick organic, mod Ah, thick B (SiCL), effective texture SiCL
EMEND20	closed	white spruce	691	0	n/a	26.1		8	1	4		0	thin organic, mod Ah, thick B (CL), effective texture CL
EMEND21	closed	white spruce	737	0	n/a	26.4		9		2		0	mod organic, mod Ah, thick B (mottling) (CL), effective texture CL
EMEND24	closed	white spruce	788	0	n/a	19.9		12				0	thin organic, mod Ah, thick B (SiCL), effective texture SiCL

Appendix 2.2. Site descriptions including canopy and soil characteristics for permanent plots near Lac La Biche, AB.

Site replicate	Canopy regime	Regeneration species	Elevation (m)	Slope (%)	Aspect (degrees)	Average canopy height (m)	Canopy basal area (m ² /ha)					Soil description	
							Trembling aspen	Balsam poplar	White spruce	Balsam fir	Black spruce	% coarse fragments	Description of soil horizons
LLB7	open	trembling aspen	616	10	333	n/a			6			0	mod organic, thin Ae, mod Bf (SiL), effective texture SiL
LLB8	open	trembling aspen	603	12	196	n/a						0	no organic, no A, thick B (SiC), effective texture SiC
LLB9	open	trembling aspen	612	5	154	n/a						0	no organic, mod A, buried Ah, mod B (SiC), effective texture SiC
LLB10	open	trembling aspen	642	3	109	n/a						5	thick organic, thin Ah, thin Bm, thick B (CL), effective texture CL
LLB7	closed	trembling aspen	611	0	n/a	17.9	9					0	thin organic, mod Ah, thick B (CL), effective texture CL
LLB8	closed	trembling aspen	605	4	98	16.4	8	2				0	thin organic, thin Ah, very thick B (LS), effective texture LS
LLB9	closed	trembling aspen	605	0	n/a	19.1	8	1				0	thick organic, mod Ah, thick B (SiC), effective texture SiC
LLB10	closed	trembling aspen	642	7	37	25.6	6					0	thick organic, thick Ah, thick B (SiC), effective texture SiC
LLB1	open	balsam fir	622	4	203	22.4				2	2	5	thick organic, thin Ah, thin Bm, thick B (S), effective texture S
LLB2	open	balsam fir	622	0	n/a	20.3		1	5	4		0	thick organic, thin Ah, thick B (C), effective texture C
LLB5	open	balsam fir	632	0	n/a	23.7			1	3		5	thin organic, thin Ah, thick B (C), effective texture C
LLB6	open	balsam fir	595	5	78	21.8			2		11	0	thin organic, mod Ah, thick B (L), effective texture L
LLB1	closed	balsam fir	635	5	125	17.2	1		10	4	4	0	thick organic, mod Ah, thin Bm, mod B (SiCL), effective texture SiCL
LLB2	closed	balsam fir	638	3	122	18.7			1	5	2	0	thin organic, thin Ah, thick B (C), effective texture C
LLB5	closed	balsam fir	666	12	197	19.2	1			2		0	mod organic, thin Ah, thick B (C), effective texture C
LLB6	closed	balsam fir	668	0	n/a	24.0			1	1		5	mod organic, mod Ah, thick B (CL), effective texture CL
LLB3	open	white spruce	660	21	176	7.2						5	thin organic, thin Ah, thick B (mottling) (C), effective texture C
LLB4	open	white spruce	667	6	8	21.2		2				5	thin organic, thin A, thick B (mottling) (C), effective texture C
LLB11	open	white spruce	606	8	66	n/a						5	no organic, thin Ah, thin Bm, Thick C (SiL), effective texture SiL
LLB12	open	white spruce	643	10	235	n/a		3				15	thin organic, no A horizon, thick B (C), effective texture C
LLB3	closed	white spruce	663	3	8	19.8	5	2				5	mod organic, thin Ah, thick B (C), effective texture C
LLB4	closed	white spruce	660	6	243	20.4	14					5	mod organic, thin Ah, thick B (SiL), effective texture SiL
LLB11	closed	white spruce	610	0	n/a	21.3	4					0	mod organic, thin Ah, thick B (SiCL), effective texture SiCL
LLB12	closed	white spruce	642	6	217	15.2	3	3				0	thick organic, mod Ah, thick B (SiCL), effective texture SiCL

Appendix 2.3. Site descriptions including canopy and soil characteristics for permanent plots in Duck Mountains, MB.

Site replicate	Canopy regime	Regeneration species	Slope (%)	Aspect (degrees)	Average canopy height (m)	Canopy basal area (m ² /ha)						Soil description				
						Trembling aspen	Balsam poplar	White spruce	Balsam fir	Paper birch	Black spruce	Jack pine	% coarse fragments	LFH (cm)	Ah (cm)	Other horizons (cm)
Hwy 83N	open	trembling aspen	-1	252	n/a								0.0	5	2	14(Ae), >14(Btgj)
Hwy 83 S	open	trembling aspen	-8	28	n/a								0.0	4	3	15(AB), >15(Bt)
Hwy 366	open	trembling aspen	9	106	n/a								11.1	3	1	16(Btj), >16(Btgj)
Hwy 83N	closed	trembling aspen	-5	284	16.7	31.0	0.2						0.0	6	2	13(Ae), 11(Btgj)
Hwy 83 S	closed	trembling aspen	-9.5	216	17.6	19.1	7.9						0.0	5	2	11(AB), >11(Btgj)
Hwy 366	closed	trembling aspen	-6	100	21.9	30.7	7.1						10.2	3	5	>5(Bm)
Laurie Lake	open	balsam fir	-5	254	18.6	5.2		36.2	12.1				61.3	7	3	8(Ae), >8(Btgj)
East Blue Lake	open	balsam fir	-1	278	16.8		7.5	16.1	0.8				40.5	7	5	12(Ae), >12(Btg)
Childs Lake	open	balsam fir	-12	349	14.6	5.3	7.9	12.4		1.9			5.2	11	4	6(AB), >6Bg
Laurie Lake	closed	balsam fir	1.5	342	18.1		1.8	50.7	1.1		0.8		21.1	10	2	3.5(Ae), >3.5(Bt)
East Blue Lake	closed	balsam fir	-2	270	19.9	6.2	1.1	41.5					10.6	5	2	7(Ae), >7(Btg)
Childs Lake	closed	balsam fir	-11	351	18	16.9		11.4	5.5	1.2			9.2	9	4	2(AB), >6(Bgj)
Gravel pit	open	white spruce	-2.5	179	11.9	7.8	0.8	4.8			1.3		0.0	1.5	0.5	>0.5(C)
Interp trail	open	white spruce	-2.5	246	n/a								0.0	0	0	>0(C)
Wetlands	open	white spruce	n/a	n/a	9.8	3.5	1.0	3.5					3.9	5	19	34(Bm), >34(BC)
366 boundary	closed	white spruce	-2	6	14.2	22.2		11.1					0.0	10	7	22(Bg), >22(BC)
HWY 366 N	closed	white spruce	-1	278	15.6	8.3	7.2	12.6		12.2			0.0	6	14	20(AB), >20(Bm)
Childs	closed	white spruce	-6	292	11.6	10.1	0.2	4.2					4.4	4	1	B), 16(Bgj), >16(BC)

Appendix 2.4. Canopy and soil characteristics for permanent plots on the Canadian Shield in eastern Manitoba ("Manitoba Shield").

Site replicate	Canopy regime	Regeneration species	Average canopy height (m)	Canopy basal area (m ² /ha)	% coarse fragments (Ah)	LFH (cm)	Soil description			
							Soil horizons (cm)	pH	Salinity	Soil texture (Ah)
2	open	trembling aspen	20	34	8.4	3.5	10(Ah), 22(Bm), 35(Bc)	4.6(Ah)	0.62(Ah)	71.7(sand), 20.3(silt), 7.9(clay)
3	closed	trembling aspen	19	30	17.9	12	14(Ah), 25(Bm), 51(Bc)	6.0(Ah)	0.27(Ah)	63.0(sand), 23.1(silt), 24(clay)
2	open	trembling aspen	20	34	8.4	3.5	10(Ah), 22(Bm), 35(Bc)	4.6(Ah)	0.62(Ah)	71.7(sand), 20.3(silt), 7.9(clay)
3	closed	trembling aspen	19	30	17.9	12	14(Ah), 25(Bm), 51(Bc)	6.0(Ah)	0.27(Ah)	63.0(sand), 23.1(silt), 24(clay)
1	open	black spruce	17.6	26	0	1(L)	8(Of), 15(Om)	3.8(Om)		
2	closed	black spruce	18.3	24	0	2(L)	7(Of), 17(Om)	4.7(Om)		
3	open	black spruce	18	25	0	1(L)	10(Of), 18(Om)	3.1(Om)		
1	closed	black spruce	17.6	26	0	1(L)	8(Of), 15(Om)	3.8(Om)		
2	open	black spruce	18.3	24	0	2(L)	7(Of), 17(Om)	4.7(Om)		
3	closed	black spruce	18	25	0	1(L)	10(Of), 18(Om)	3.1(Om)		

Appendix 2.5. Canopy basal area and soil characteristics for permanent plots located near Duparquet and Lac Duparquet, QC.

Site replicate	Canopy regime	Regeneration species	Trembling aspen	Canopy basal area (m ² /ha)					Soil description			
				Balsam fir	Paper birch	White spruce	Jack pine	Eastern white cedar	Black spruce	White pine	% coarse fragments	LFH (cm)
1	open	trembling aspen									6	8(Ahc)
2	open	trembling aspen									8	8(Ah)
4	open	trembling aspen									7	5(Ah)
8	open	trembling aspen									9	
9	open	trembling aspen									6	6(Ahc)
3	closed	trembling aspen	2	10							5.5	4(Ae)
18	closed	trembling aspen	12								5	14(Ahc)
19	closed	trembling aspen	15	4		2					6	
22	closed	trembling aspen										
31	closed	trembling aspen	8								1.5	6(Ah)
4	open	balsam fir	4	1	3						7	5(Ah)
5	open	balsam fir	5		3	2					3	4(Ae)
15o	open	balsam fir									8	9(Ahc)
17	open	balsam fir	1		1						14	
23	open	balsam fir	5		3	3					5	4(Ae), 12(Af)
24	open	balsam fir	1		3	9					5	7(Ae)
25	open	balsam fir	1		1	1					13	12(Ae)
30	open	balsam fir			2			1		20	5	3(Ae)
6	closed	balsam fir		2	4	7					6	
11	closed	balsam fir			1		16				10	9
12	closed	balsam fir	5	6	1	3					7	5(Ah)
15f	closed	balsam fir				8.5		2			7	8(Ahc)
16	closed	balsam fir		1		9			2		9	6(Ae)
29	closed	balsam fir			3		21				5	
4	open	white spruce	4	1	3						7	5(Ah)
26	open	white spruce										
28	open	white spruce										
11	closed	white spruce									9	
22	closed	white spruce	7		2	1	1				6	7(Ae)
27	closed	white spruce									2	8(Ah)

Appendix 2.6. Soil characteristics for permanent plots in Forêt Montmorency, QC.

Site replicate	Canopy regime	Regeneration species	% coarse fragments	Soil description	
				Soil drainage	Soil texture
1	open	balsam fir	30	moderate drained	loamy sand
2	open	balsam fir	10	imperfectly drained	loamy sand
3	open	balsam fir	15	moderate drained	sandy loam
4	open	balsam fir	50	imperfectly drained	sandy loam
1	closed	balsam fir	50	moderate drained	loamy sand
2	closed	balsam fir	10	well drained	loamy sand
3	closed	balsam fir	0	imperfectly drained	loamy sand
4	closed	balsam fir	10	moderate drained	sandy loam

Appendix 2.7. Soil characteristics for permanent plots in the Ashuapmushuan Reserve, QC.

Site replicate	Canopy regime	Regeneration species	% coarse fragments	Soil description	
				Soil drainage	Soil texture
1	open	black spruce	35	well drained	loamy sand
2	open	black spruce	45	well drained	loamy sand
3	open	black spruce	10	non-well drained	sandy loam
4	open	black spruce	45	moderate drained	loamy sand
1	closed	black spruce	20	moderated drained	loamy sand
2	closed	black spruce	30	moderate drained	sandy loam
3	closed	black spruce	25	moderate drained	sandy loam
4	closed	black spruce	15	imperfectly drained	sandy loam

Appendix 2.8. Canopy characteristics for permanent plots north of Chicoutimi, QC.

Site replicate	Canopy regime	Regeneration species	Average canopy height (m)	Canopy basal area (m ² /ha)		
				Balsam fir	White spruce	Paper birch
Lib20	closed	balsam fir	15.3	32.2	1.1	3.8
Lib23	closed	balsam fir	15.7	37.3	0.5	0.2
Lib24	open	balsam fir	11.3	13.4	3.3	1.4
Lib26	closed	balsam fir	16.7	40.4	12.8	3.2

Appendix 3.1. Sample size (n) and standard deviation (SD) for mean relative height growth (RHG) and %PPFD for each plot of aspen regeneration as shown in Figure 5.14.

Study Location	Canopy type	Site code in figure	Site	RHG (cm/yr)		%PPFD	
				n	SD	n	SD
EMEND, AB	open	EM13, AB	EMEND13	57	0.13	57	7.27
		EM14, AB	EMEND14	55	0.14	55	7.91
		EM22, AB	EMEND22	56	0.11	56	6.55
		EM22, AB	EMEND23	58	0.09	58	7.87
	closed	EM13, AB	EMEND13	28	0.11	28	3.91
		EM14, AB	EMEND14	46	0.12	46	12.56
		EM22, AB	EMEND22	23	0.13	23	5.00
		EM22, AB	EMEND23	28	0.13	28	9.07
Lac La Biche, AB	open	LL7, AB	LLB7	52	0.11	52	12.43
		LL8, AB	LLB8	52	0.07	52	8.97
		LL9, AB	LLB9	57	0.09	57	12.72
		LL10, AB	LLB10	34	0.09	34	21.66
	closed	LL7, AB	LLB7	47	0.08	47	3.22
		LL8, AB	LLB8	50	0.06	50	8.95
		LL9, AB	LLB9	39	0.08	39	9.28
		LL10, AB	LLB10	30	0.11	30	6.61
Duck Mountains, MB	open	DM366, MB	Hwy 366	74	0.06	74	15.75
		DM83S, MB	Hwy 83S	63	0.10	63	32.48
		DM83N, MB	Hwy 83N	40	0.09	40	28.73
		DM366, MB	Hwy 366	48	0.10	48	6.50
	closed	DM83S, MB	Hwy 83S	46	0.08	46	4.89
		DM83N, MB	Hwy 83N	48	0.09	48	2.82
		MS2, MB	2	12	0.05	12	0.88
		MS3, MB	3	1	-	1	-
Manitoba Shield, MB	open	MS2, MB	2	43	0.05	43	10.42
		MS3, MB	3	27	0.04	27	8.15
	closed	DQ1, QC	1	31	0.05	31	21.01
		DQ2, QC	2	23	0.04	22	23.12
Duparquet, QC	open	DQ8, QC	8	15	0.05	9	15.91
		DQ9, QC	9	17	0.05	17	9.56
		DQ3, QC	3	18	0.04	16	26.24
		DQ18, QC	18	43	0.06	36	10.38

Appendix 3.2. Sample size (n) and standard deviation (SD) for mean relative height growth (RHG) and %PPFD for each plot of balsam fir regeneration as shown in Figure 5.15.

Study Location	Canopy type	Site code in figure	Site	RHG (cm/yr)		%PPFD	
				n	SD	n	SD
EMEND, AB	open	EM15, AB	EMEND15	63	0.02	63	2.74
		EM16, AB	EMEND16	56	0.02	56	9.78
		EM17, AB	EMEND17	59	0.02	59	8.97
		EM18, AB	EMEND18	49	0.04	49	12.89
	closed	EM15, AB	EMEND15	58	0.02	58	2.93
		EM16, AB	EMEND16	63	0.03	63	4.12
		EM17, AB	EMEND17	57	0.02	57	4.54
		EM18, AB	EMEND18	58	0.02	58	4.27
Lac La Biche, AB	open	LL1, AB	LLB1	61	0.05	61	13.52
		LL2, AB	LLB2	59	0.05	59	5.91
		LL5, AB	LLB5	58	0.05	58	6.09
		LL6, AB	LLB6	61	0.05	61	4.42
	closed	LL1, AB	LLB1	58	0.05	58	6.10
		LL2, AB	LLB2	56	0.04	56	4.99
		LL5, AB	LLB5	59	0.04	59	3.89
		LL6, AB	LLB6	60	0.04	60	3.39
Duck Mountains, MB	open	DML, MB	Laurie L.	85	0.03	85	5.79
		DME, MB	East Blue L.	87	0.05	87	8.16
		DMC, MB	Childs L.	88	0.05	88	9.40
		DML, MB	Laurie L.	73	0.05	73	4.32
	closed	DME, MB	East Blue L.	50	0.05	50	4.31
		DMC, MB	Childs L.	72	0.05	72	5.67
		DQ15, QC	15	61	0.07	77	3.63
		DQ17, QC	17	59	0.04	67	5.68
Duparquet, QC	open	DQ30, QC	30	33	0.05	35	14.92
		DQ11, QC	11	53	0.05	58	3.58
		DQ12, QC	12	33	0.09	88	4.60
		DQ15, QC	15	81	0.06	85	4.11
	closed	DQ16, QC	16	74	0.04	59	5.69
		DQ29, QC	29	54	0.02	78	4.03
		FM1, QC	1	57	0.07	57	16.64
		FM2, QC	2	62	0.07	62	18.07
Forêt Montmorency, QC	open	FM3, QC	3	59	0.05	59	4.05
		FM4, QC	4	62	0.09	62	9.70
		FM1, QC	1	56	0.02	56	0.03
		FM2, QC	2	56	0.02	56	13.55
	closed	FM3, QC	3	60	0.03	60	4.56
		FM4, QC	4	58	0.02	58	0.72
		CH24	24	58	0.03	35	2.96
		CH20	20	93	0.03	34	1.04
Chicoutimi, QC	closed	CH23	23	66	0.04	7	9.92
		CH26	26	8	0.03	7	1.15

Appendix 3.3. Sample size (n) and standard deviation (SD) for mean relative height growth (RHG) and %PPFD for each plot of black spruce regeneration as shown in Figure 5.16.

Study Location	Canopy type	Site code in figure	Site	RHG (cm/yr)		%PPFD	
				n	SD	n	SD
Manitoba Shield, MB	open	MS1, MB	1	95	0.03	95	9.67
		MS2, MB	2	110	0.04	110	11.95
		MS3, MB	3	90	0.04	90	7.34
	closed	MS1, MB	1	90	0.02	90	3.76
		MS2, MB	2	94	0.02	94	4.18
		MS3, MB	3	90	0.02	90	1.32
Iroquois Falls, ON	open	IF13-1, ON	13-1	68	0.05	68	14.75
		IF13-2, ON	13-2	69	0.04	69	15.05
		IF21, ON	21	79	0.04	79	21.39
		IF24, ON	24	70	0.05	70	12.46
		IF11, ON	11	69	0.03	69	2.69
	closed	IF16, ON	16	66	0.02	66	5.01
		IR19-S, ON	19-S	67	0.02	67	4.97
		IF19-N, ON	19-N	72	0.02	72	4.51
		AR1, QC	1	62	0.06	62	13.73
		AR2, QC	2	62	0.05	62	12.35
Ashuapmushuan Reserve, QC	open	AR3, QC	3	62	0.03	62	12.31
		AR4, QC	4	60	0.07	60	18.48
		AR1, QC	1	60	0.03	60	3.81
		AR2, QC	2	61	0.02	61	5.36
	closed	AR3, QC	3	59	0.02	59	2.37
		AR4, QC	4	56	0.02	56	2.78

Appendix 3.4. Sample size (n) and standard deviation (SD) for mean relative height growth (RHG) and %PPFD for each plot of white spruce regeneration as shown in Figure 5.17.

Study Location	Canopy type	Site code in figure	Site	RHG (cm/yr)		%PPFD	
				n	SD	n	SD
EMEND, AB	open	EM19, AB	EMEND19	62	0.04	62	15.17
		EM20, AB	EMEND20	61	0.02	61	16.51
		EM21, AB	EMEND21	63	0.02	63	11.67
		EM24, AB	EMEND24	63	0.03	63	16.91
	closed	EM19, AB	EMEND19	62	0.02	62	2.94
		EM20, AB	EMEND20	61	0.02	61	7.53
		EM21, AB	EMEND21	62	0.03	62	3.80
		EM24, AB	EMEND24	62	0.03	62	8.96
Lac La Biche, AB	open	LL3, AB	LLB3	60	0.04	62	8.29
		LL4, AB	LLB4	62	0.03	62	5.08
		LL11, AB	LLB11	61	0.03	62	8.81
		LL12, AB	LLB12	63	0.03	62	4.47
	closed	LL3, AB	LLB3	62	0.04	62	13.09
		LL4, AB	LLB4	62	0.04	62	13.99
		LL11, AB	LLB11	63	0.04	63	25.64
		LL12, AB	LLB12	62	0.04	61	18.12
Duck Mountains, MB	open	DMW, MB	Wetlands	88	0.04	88	14.81
		DMG, MB	Gravel pit	90	0.05	90	14.55
		DMI, MB	Interp trail	86	0.05	86	13.79
	closed	DMC, MB	Childs	89	0.05	89	3.09
		DM366, MB	HWY 366N	86	0.05	86	4.88
		DMB, MB	366 boundary	86	0.05	86	7.73
Duparquet, QC	open	DQ26, QC	26	173	0.04	150	8.22
		DQ28, QC	28	38	0.06	38	17.53
	closed	DQ11, QC	11	53	0.05	51	3.02
		DQ27, QC	27	158	0.05	122	0.84