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Differential Growth and Mortality of Advance Regeneration across the Canadian Boreal Forest

Developing better probabilistic function and field indicators of seedling mortality of important boreal tree species across the Canadian boreal forest

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May 2003

EXECUTIVE SUMMARY

Differential growth and mortality 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) was characterized for sites across the Canadian boreal forest over a three year period. Sites of advance regeneration were established in the spring of 2000 at locations across the Canadian boreal forest to ensure a western, central, and eastern representation of each species. Approximately 500 saplings for a given species were monitored in each region, in high and low light environments associated with the absence or presence of canopy cover. Sapling survival and various morphological and growth variables were recorded each year. A relative measure of light availability was recorded at the apex of each individual. Finite mortality rates have been established for each species, and apart from a few exceptions are generally consistent among study locations. Mortality is highest for aspen regeneration, followed by balsam fir, black spruce, and white spruce. When summer and winter mortality rates are standardized to unit time, mortality appears to be higher during the growing season. Survivorship curves for aspen and fir (the only two species showing appreciable mortality) differ among study locations. Moreover, differences in survival between high and low light environments are not consistent among study locations. Inter-regional differences are largely attributable to variation in local site conditions. Within a defined light regime (presence or absence of canopy cover) light availability has a small but significant effect on aspen mortality, but not on fir mortality. Crown morphology has a greater influence on survival than either light availability or size for both fir and aspen. In order to characterize mortality of white and black spruce a longer study period is necessary to gather sufficient censored data. The ability of light to predict growth within a define light regime is inconsistent among species and study locations. It appears that if light is a limited resource and there is sufficient variation in light availability, then light is a good predictor of sapling height growth over a three year period. Management strategies that preserve advance regeneration should continue to be explored as low-cost alternatives to planting, and for improving the preservation of natural forest structure and composition. Careful logging takes advantage of the natural plasticity that coniferous advance regeneration exhibits in response to light variation and is important for both clearcut and partial cut situations. Interspecific differences in mortality rates should be considered when assessing site potential for careful harvesting. Threshold values of live crown ratio can be derived for use as field indicators of survival for trembling aspen and balsam fir under different light conditions. The growth and mortality rates presented can be used in forest simulators to derive and test alternative management strategies.

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INTRODUCTION

Established seedling banks 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). Interspecific variation in light-dependent growth and mortality (shade tolerance) is generally considered to be a key factor underlying forest successional dynamics (Pacala et al. 1994; Walters and Reich 1996). Simulations of forest dynamics have demonstrated that interspecific differences in sapling mortality resulting from variation in species-specific shade-tolerance can have profound effects on forest dynamics and composition (Kobe et al. 1995). Moreover, differential growth and survival of juvenile trees within a species may have substantial effects on forest composition during secondary succession (Kobe 1996).

Fire cycles in the North American boreal forest have increased in length since the end of the Little Ice Age as a result of ensuing climate changes and changes in land use (Bergeron and Archambault 1993; Weir et al. 2000). As forests more commonly escape fire for long periods, small-scale disturbances and resulting gap dynamics become increasingly important in determining canopy composition (Kneeshaw and Bergeron 1996). Important environmental changes accompanying gap formation include higher light availability, lower air humidity, and higher water availability in the upper soil horizons (Drobyshev and Nihlgard 2000). The response of advance regeneration to environmental changes associated with canopy gap formation is of interest not only for interpreting stand dynamics, but also for refining silvicultural practices in which advance growth is preserved as immediate growing stock to renew forests (Ruel et al. 1995; Orlander 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). In an effort to produce a more comprehensive understanding of the ecology and sustainable management of economically important tree species occurring across the Canadian boreal forest, this long-term study addresses several important issues. To better understand the critical processes of growth and mortality of natural regeneration that has survived the initial years of extremely high mortality following germination, this study examines saplings at the crucial post-establishment phase of development. Existing studies of sapling mortality have been based on retrospective analyses. However, long-term monitoring of regeneration is necessary to better understand this important stage of stand development. A critical factor affecting growth of advance regeneration in the shaded understory is light availability (Lieffers et al. 1999). To address these issues, growth and mortality of advance regeneration are monitored in low (associated with closed canopy conditions) and high (either natural canopy gaps or post-harvest conditions) light environments, in order to compare long-term survival and growth of natural regeneration in different light environments. Finally, through a collaborative effort among several different research groups across the country, this study will increase our understanding of longitudinal variations and trends in boreal stand dynamics. This will in turn contribute to more unified theories of boreal stand development, and facilitate management implementation of this research across the country.

The main objective of this study is to characterize the growth and mortality of established natural regeneration of important boreal tree species including white spruce, black spruce (*Picea mariana* (Mill.) BSP), balsam fir, and trembling aspen (*Populus tremuloides* Michx.) in different light environments, across the Canadian boreal forest. The specific goals of this study are: (1) to summarize and explain any differential growth and mortality across geographic regions; (2) to examine interspecific differences in growth and mortality rates; (3) to determine the season of mortality; (4) to determine and compare species-specific growth rates, crown morphology, and mortality in open and closed canopy environments; (5) to determine the predictive ability of light, size, and crown morphology in explaining individual mortality; (6) to determine the extent to which light availability at the individual sapling level influences growth; and (7) to determine the ability of abiotic site-level characteristics, stand characteristics, and average light availability for saplings within a site, to predict average growth rates of a site.

METHODS

Study Area

Paired (low and high light regimes), replicated sites of natural regeneration of each the four studied species were established in early 2000 in northwestern Alberta at EMEND, in eastern Alberta near Lac La Biche, in west-central Manitoba in the Duck Mountains, in southeastern Manitoba on the Canadian shield (Manitoba shield), in northeastern Ontario near Iroquois Falls, in western Québec near Lac Duparquet and the town of Duparquet, in central Québec in the Forêt Montmorency north of Québec city, in the Ashuapmushuan reserve near Chibougamau, and north of Chicoutimi, Québec (Figure 1). Sites were located to ensure a western, central, and eastern distribution of each species. All study locations are within the closed-crown boreal forest. For closed canopy sites, 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 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.

Field Methods

Site establishment

Sites of abundant natural regeneration were chosen in adjacent high and low light environments. Only saplings above a certain size were chosen in order to avoid censusing mortality associated with early establishment. Since it is easier to evaluate height than age, size criteria were used to select saplings. Coniferous saplings between 0.2 and 1 m, and aspen suckers between 1 and 2 m in height, were selected for monitoring. To examine the effect of light environment on saplings, regeneration was selected in low light environments under closed canopy cover, and in high light environments (natural canopy gaps for fir, clearcuts for aspen, carefully harvested sites for black spruce, and disturbed areas for white spruce). In order to compare growth and mortality among regions, sites replicates were located on common soil deposit types across regions for each species. 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. Site conditions measured include basal area, average canopy height, soil stoniness, slope, and aspect.

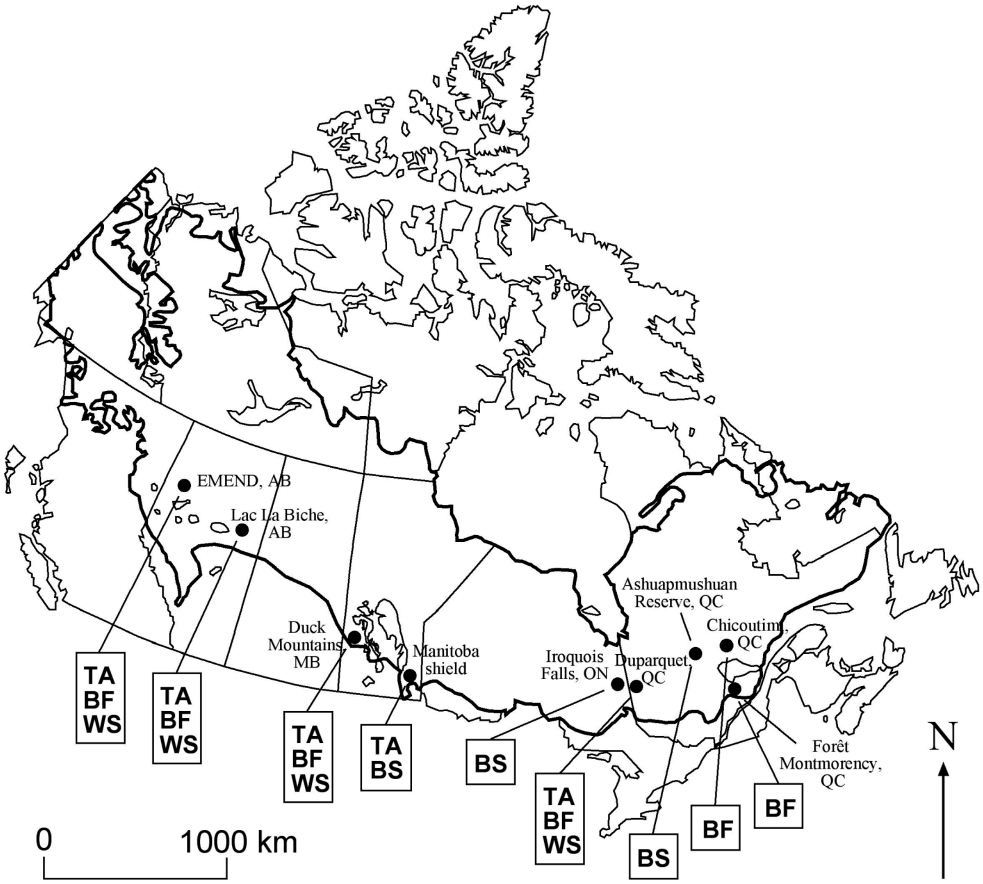

Figure 1. Locations of permanent monitoring sites for trembling aspen (TA), balsam fir (BF), white spruce (WS), and black spruce (BS) in boreal forests of Alberta, Manitoba, Ontario, and Québec. The broadly defined boreal forest is delineated by a bold line.

Based on estimated sapling mortality rates, an initial sample size of 500 saplings per species per region was selected. The intent was to provide a sufficient 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 paired sites of approximately 60-90 saplings per site were replicated for each species within each region.

Sapling measurements

For each individual sapling, mortality was censused in the spring and fall of every year, beginning at site establishment in the spring 2000 and ending in the fall of 2002. Growth and morphological variables were measured at the end of each growing season. Dimensions recorded include height, length of the leader branch, length of the longest branch subtending the leader (for coniferous species), depth of live crown, and basal diameter. Standardized response variables were derived from these measurements.

Light availability was the main factor of interest in predicting sapling growth and mortality. The percent photosynthetically active radiation (%PAR) available at the apical bud of each sapling was determined. Relative measures of %PAR were determined using hand-held quantum radiation sensors to measure the PAR (µmol/s/m^2) available at the apical bud, and simultaneously measuring the above canopy PAR availability with a quantum sensor and datalogger in the closest adjacent clearing receiving full light. %PAR measures can be considered a surrogate measure of the relative density of the stand (Williams et al. 1999).

Data Analysis

Mortality

Finite mortality rates

Species-specific finite annual mortality rates were established for open and closed canopy conditions for each region using Equation 1. Mortality rates were determined for each site replicate, and also for data pooled from all site replicates within a given canopy regime. Overall rates for open and closed canopy conditions were determined for the complete study period for all species. For trembling aspen and balsam fir, the only two species to exhibit appreciable mortality over the course of the study, seasonal rates were determined for total summer months and total winter months over the course of the study period. All rates were adjusted to a common time base of one year, using the following calculation:

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

where x is the time interval considered, *(# alive at t = x/# 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. A two-way factorial design was used to compare mortality rates among species and canopy regimes, and was performed using overall mortality rates from each region. A factorial model was also used to examine differences between open and closed canopy sites, and summer and winter mortality for each region, for aspen and fir. This analysis was performed using individual mortality rates for site replicates within each region. Analysis of variance was also used to compare mortality rates among regions, using mortality rates for site replicates in each region.

Survival analysis

Survival analysis includes statistical analyses in which the response variable of interest is time until an event occurs (Kleinbaum 1996). This analytical approach is well-suited to the present study of sapling mortality because the data form a time series, and are largely censored. Censoring 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 (Parmar and Machin 1995; Kleinbaum 1996; Krebs 1999). Therefore for each sapling we know time until death or time until censorship.

Kaplan-Meier (KM) survivorship curves were determined for aspen and fir - the only two species demonstrating appreciable mortality over the study period. The KM survival function estimates the probability of survival past time t conditional upon survival up to that time. Estimated KM survival probabilities are determined according to equation 2:

$$\hat{S}(t) = \prod_{i=1}^{t} \left(1 - \frac{d_i}{n_i}\right) \qquad [2]$$

where t is the number of time intervals over which mortality was censused, 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. These estimated survival rates differ from simple calculation 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 also because the number at risk at the beginning of each time period is considered. For each species, a separate curve was examined for each region, and for open and closed canopy conditions. A Log-Rank test was used for within-species comparisons of KM curves across regions, and to compare survival under low and high light within each region. In addition median survival times (time at which 50% cumulative mortality occurs) were determined.

Cox's Proportional Hazards (PH) nonparametric model (Equation 3) was used to predict the hazard ratio for saplings receiving different relative light, and with different initial size and morphology. The general form for the Cox proportional hazards model is:

$$h(t,\mathbf{X}) = h_0(t) \exp\left[\sum_{i=1}^{n} B_i X_i\right] \qquad [3]$$

where h(t, **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 **X**), $h_o(t)$ is the baseline hazard function, which is inversely related to S(t), and is an instantaneous probability of death per unit time, and $B_1, B_2, \ldots B_n$ are the coefficients for the n predictor variables $X_1, X_2 \ldots X_n$ respectively.

Cox hazard models were used to determine the hazard ratio (HR) for any two saplings. The HR is a measure of the relative survival of two individuals and is derived by dividing the 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 (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). The specific variables entered in a forward selection procedure into the model for each study location/light treatment include %PAR, height, diameter, and live crown ratio. All survival analysis was performed using SPSS 11.0 for Macintosh (SPSS Inc. 2002).

Growth and crown morphology

Derived response variables

In order to compare growth among saplings of different initial sizes, growth rates were standardized to unit size. The effective average relative height growth (RHG) over the three growing seasons examined was determined for each sapling of each species according to equation 4:

$$\mathrm{RHG} = \frac{\ln(\mathrm{height}_2) - \ln(\mathrm{height}_1)}{\mathrm{time}_2 - \mathrm{time}_1} \qquad [4]$$

where “time 2” corresponds to end of the study period and “time 1” corresponds to the beginning of the study. For aspen, relative diameter growth (RDG) was calculated using the same formula by substituting basal diameter measurements into equation 3. It has been suggested that as a result of the increasing proportion of non-photosynthetic tissue to photosynthetic tissue with increasing size and age in woody plants, that there may exist a decrease in RHG with increasing tree size (Brand et al. 1987). However RHG was not correlated with height for the size range of saplings monitored in our study. Furthermore, upon preliminary investigation RHG responded better to light availability than did the relative growth increment proposed by Brand et al. (1987).

Two measures of crown morphology were examined. The ratio of the leader branch length to the length of the longest lateral branch immediately subtending the leader (L:B ratio) is 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 used to compare crown morphology between open and closed canopy environments, and was examined for all four species.

Discrete analysis

Growth analysis was performed using only saplings that were alive at the end of the study period. Summary statistics for each species were computed for RHG, L:B ratio, live crown ratio, and %PAR for each canopy regime within a region. T-tests were performed on individual sapling response variables and %PAR measurements between open and closed canopy environments.

Linear regression

For each species and study location, simple linear regression models were examined for each light environment. Sapling response variables examined include RHG, RDG, L:B ratio, and live crown ratio, and the predictor variable of interest was light availability. Saplings that showed an overall decrease in height from the beginning to end of the study were excluded from regression analysis. This was done to account for some of the effects of herbivory or stem dieback, which would tend to obscure any relationship between light availability and growth. Live crown ratio and L:B ratio measurements for each region were used from the study year when light readings were taken. All response variables were approximately normally distributed.

For each species, mean RHG values for each individual site replicate were regressed against mean %PAR measures across all sites including both open and closed canopy. This regression examined inter-site replicate variation which had been treated the same as intra-site replicate variation for all preceding analyses. These regressions also examined variation between canopy regimes. Other site-level measures of canopy basal area, average canopy height, soil stoniness, slope, and aspect, were entered as potential predictor variables in multiple linear regression models.

RESULTS

Mortality

Survival tables

Advance regeneration of white spruce exhibited very little mortality over the three year monitoring period (Table 1). The ratio of the total number of white spruce saplings alive at the end of the study to the number alive at the beginning (finite survival) is 2126/2163 = 98.3%. Some 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. Black spruce advance regeneration also exhibited only slight mortality (1614/1648 = 97.9%) (Table 2). However, mortality more consistently occurred under closed canopy conditions and not in post-harvest sites. As compared with either of the spruce species, considerably more balsam fir saplings died over the course of the three year study period in both closed and open (gap) canopy sites (3016/3155 = 95.6%) (Table 3). Nonetheless in every region but Chicoutimi, Québec, there were some balsam fir site replicates in which no mortality occurred. In open canopy sites near Lac La Biche, Alberta, none of the monitored fir saplings died, and in closed canopy sites in Duck Mountains, Manitoba, only one sapling died over the study period. In contrast to advance regeneration of coniferous species, trembling aspen regeneration demonstrated appreciable mortality in both open (post-harvest) and closed canopy sites in all geographic regions (1688/2700 = 62.5%) (Table 4).

Mortality rates compared across species

Aspen mortality is significantly higher than that observed for any of the coniferous species (Figure 2). Of the coniferous species, balsam fir exhibits the highest mortality rates, followed by black spruce and white spruce. Aspen mortality rates for the overall study period range from 2.16% in open EMEND sites in Alberta, to 61.86% in closed sites of the Manitoba shield area (Table 5). The highest aspen mortality rates occur in both open and closed canopy sites in the Manitoba shield (36.75% and 61.86% in open and closed canopy sites respectively), and in open canopy sites in Duparquet, Québec (42.03%). Mortality rates for white spruce are the lowest, ranging from 0 to 2.20% within a given canopy regime of a region. Black spruce mortality rates range from 0 to 2.63%, and balsam fir mortality rates range from 0 in open canopy sites in Lac La Biche, Alberta, to 6.73% in closed canopy sites in Chicoutimi, Québec. Mortality rates are generally consistent among regions, with a few exceptions that can be explained by unique localized site conditions. The first outlying data are the low light treatment replicates of aspen regeneration in the Manitoba shield. Light availability under closed canopy conditions in these sites was much lower than that found in other regions, as a result of an appreciable balsam fir component in the canopy. Aspen regeneration in low light conditions occurred under a hardwood canopy in other regions. The second outlying data are balsam fir mortality rates for the Chicoutimi sites. The average height of monitored saplings in closed canopy Chicoutimi sites is somewhat smaller than that found in other regions, resulting in slightly higher overall mortality.

Table 1. Number of monitored white spruce saplings alive at each spring and fall census, beginning in the spring of 2000.

Study Location	**Canopy type**	**Site**	**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

Mortality rates compared between seasons and light environments

Trembling aspen

The only significant differences in seasonal mortality rates for aspen occur in the Manitoba shield and Duparquet, Québec sites (Figure 3). Mortality rates over the growing season are significantly higher than over the winter months for both regions. These two regions exhibited the highest overall mortality rates. As cumulative aspen mortality increases over time a similar trend of higher mortality over the growing season may become apparent in the Alberta and Duck Mountains, Manitoba sites as well. The only significant differences between mortality rates in open and closed canopy sites occurs in EMEND sites, where aspen growing in closed canopy sites demonstrates higher mortality rates, and in Duparquet sites where aspen growing in open canopy post-harvest conditions exhibits higher mortality.

Table 2. Number of black spruce saplings alive at each spring and fall census, beginning in the spring of 2000.

Study Location	**Canopy type**	**Site**	**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 sites were established in the fall of 1999, however no mortality occurred before the spring 2000 census.

Table 3. Number of balsam fir saplings alive at each spring and fall census, beginning in the spring of 2000.

Study Location	**Canopy type**	**Site**	**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
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 sites beginning in the fall of 1999. Four saplings from Lib20, two from Lib24, and two from Lib26 died before fall 2000.

Table 4. Number of trembling aspen saplings alive at each spring and fall census, beginning in the spring of 2000.

Study Location	**Canopy type**	**Site**	**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
	closed	2	82	73	68	59	24	19
		3	93	75	73	48	13	1
		Total	175	148	141	107	37	20
Duparquet, QC	open	1	103	82	63	45	40	28
		2	80	77	52	41	41	40
		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

Balsam fir

Balsam fir mortality rates were significantly higher in summer than winter months only for Forêt Montmorency, Québec (Figure 3). Although mortality rates appear to be higher in closed canopy sites than in canopy gaps for the easternmost Québec sites, the only significant difference in mortality rates between the two light environments occurs in the Duck Mountains sites in Manitoba, where rates are higher in sites with small canopy gaps.

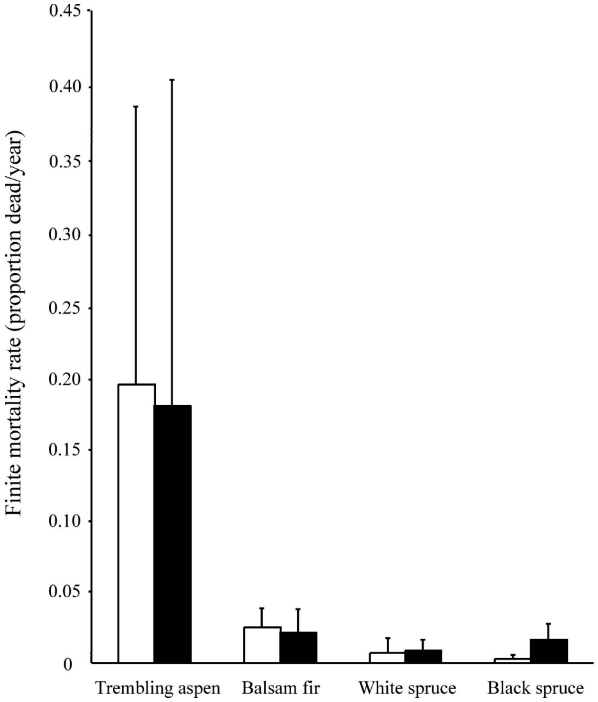

Figure 2. Finite annual mortality rates for advance regeneration growing under open conditions (unshaded bars) and closed conditions (shaded bars). Mortality rates were calculated using pooled data from all regions for each species. Rates were determined for the entire study period, from spring 2000 until fall 2002, and standardized to one year. Therefore, rates represent the proportion of saplings that die per year. For each species, a measure of standard deviation was calculated using distinct finite mortality rates determined for each region (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 regions). Standard deviation bars therefore summarize inter-regional variation. Aspen mortality pooled across regions is significantly higher than mortality for the three coniferous species (P=0.0008).

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). 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 sites is lower for Duparquet and Manitoba shield than for other regions. This mirrors the higher overall 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 sites was shorter. The Duparquet sites experienced high mortality over the first winter following site establishment, whereas Manitoba shield sites 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 sites. Under closed canopy conditions, the survival function decreases most dramatically in Manitoba shield sites, but otherwise functions are similar across regions.

Table 5. Finite mortality rates for each species, region, and canopy regime. Rates are the proportion of saplings that die per year. Raw data was pooled across site replicates within each canopy regime of a region. Standard deviations for each rate are derived from individual mortality rates calculated for each site replicate. There are significant differences in mortality rates between EMEND and Duparquet closed white spruce sites; between closed balsam fir sites in Chicoutmi and Duck Mountains, and Chicoutimi and Lac La Biche; and between open aspen sites in Duparquet and all other regions, and between both open and closed aspen sites in Manitoba shield and all other study locations.

Species	Region	Canopy regime	# site replicates	Mortality rate	Standard deviation
White spruce	EMEND, AB	open	4	0	0
		closed	4	0	0
	Lac La Biche, AB	open	4	0	0
		closed	4	0.0089	0.0108
	Duck Mountains, MB	open	3	0	0
		closed	3	0.0066	0.0077
	Duparquet, QC	open	3	0.0220	0.0213
		closed	3	0.0176	0.0166
Black spruce	Manitoba shield, MB	open	3	0	0
		closed	3	0.0016	0.0027
	Iroquois Falls, ON	open	4	0.0046	0.0061
		closed	4	0.0263	0.0121
	Ashuapmushuan Reserve, QC	open	4	0.0036	0.0072
		closed	4	0.0200	0.0126
Balsam fir	EMEND, AB	open	4	0.0401	0.0394
		closed	4	0.0253	0.0173
	Lac La Biche, AB	open	4	0	0
		closed	4	0.0036	0.0041
	Duck Mountains, MB	open	3	0.0166	0.0077
		closed	3	0.0016	0.0029
	Duparquet, QC	open	8	0.0348	0.0264
		closed	6	0.0146	0.0182
	Foret Montmorency,	open	4	0.0145	0.0179
		closed	4	0.0329	0.0143
	Chicoutimi, QC	open	1	0.0489	0
		closed	3	0.0673	0.0471
Trembling aspen	EMEND, AB	open	4	0.0216	0.0118
		closed	4	0.1891	0.0727
	Lac La Biche, AB	open	4	0.0535	0.0575
		closed	4	0.0531	0.0217
	Duck Mountains, MB	open	3	0.1080	0.0601
		closed	3	0.0853	0.0547
	Manitoba shield, MB	open	2	0.3675	0.0508
		closed	2	0.6186	0.2749
	Duparquet, QC	open	5	0.4203	0.0959
		closed	5	0.1937	0.0738

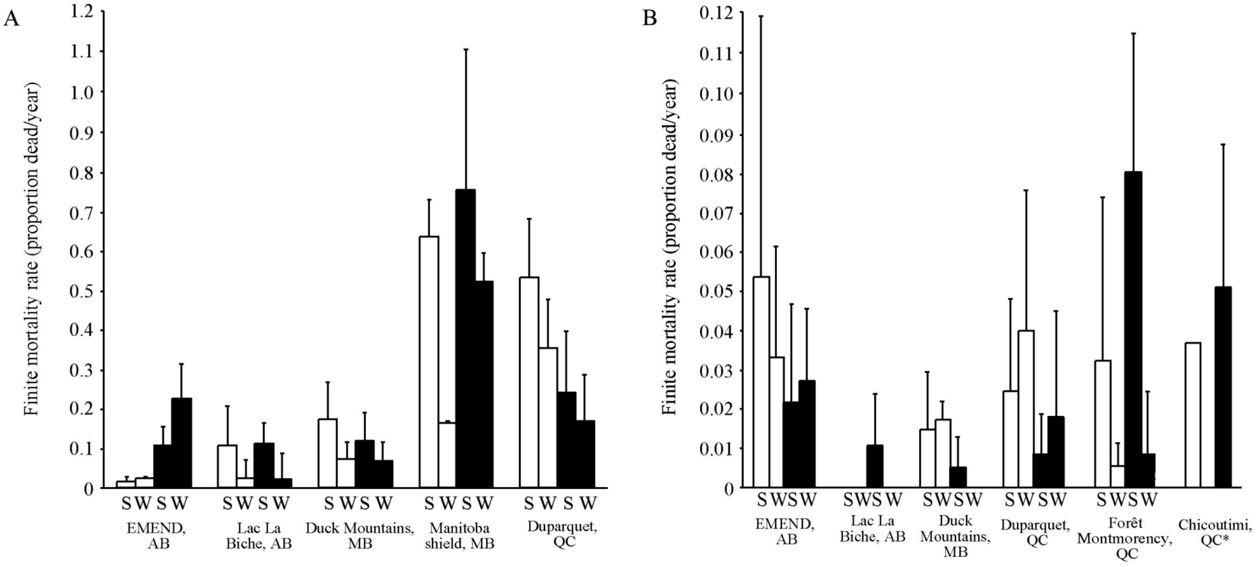

Figure 3. Finite mortality rates of trembling aspen (A) and balsam fir (B) natural regeneration for summer (S) and winter (W), adjusted to a common time base of one year. Unshaded bars represent mortality rates of natural regeneration growing in open canopy sites, and shaded bars summarize mortality rates under closed canopy conditions. Standard deviation measures were determined using mortality rates calculated for each site replicate within a region. Therefore, standard deviation bars represent variation among site replicates within each canopy treatment (open, closed) of a region. Note difference in scale of y-axis between figure 3A and 3B. Note also that finite mortality rates are not additive, however rates need only be reverted to instantaneous rates using equation 1 to render them additive. A.) Aspen mortality differs significantly between summer and winter in Manitoba shield (P=0.019) and Duparquet (P=0.039) sites. Significant differences in mortality between open and closed canopy sites occur for EMEND (P=0.001) and Duparquet (P=0.002) sites. There are no significant interactions between canopy condition and season of mortality for any of the regions. B.) Balsam fir mortality differs significantly between summer and winter only for Forêt Montmorency sites (P=0.005). Significant differences in mortality between open and closed canopy sites occurs only for Duck Mountain sites (P=0.028). There are no significant interactions between canopy condition and season of mortality for any of the regions. *Chicoutimi sites were monitored only in the fall to census annual mortality.

There are significant differences between KM curves for high and low light environments for aspen regeneration in EMEND (Log-Rank statistic=88.75; P<0.0001), Manitoba shield (Log-Rank statistic=101.37; P<0.0001), and Duparquet (Log-Rank statistic=97.38; P=0.0001) (Figure 5). Probability curves illustrate longer survival times in high light environments for EMEND and Manitoba shield, and in low light environments for Duparquet. The lack of a consistent trend in mortality between high and low light environments may be attributable to variation in the causes of mortality between light environments and among regions. Mortality of aspen suckers in open condition sites is primarily a result of self-thinning of very dense young stands, but may also result from interspecific competition from tall shrubs such as beaked hazelnut (*Corylus cornuta* Marsh.) that resprout following harvest. In contrast, understory aspen are generally much less dense in mature mixed hardwood stands, and are suppressed by light attenuation by the canopy and tall shrub layers. With decreased self-thinning of aspen suckers in post-harvest stands over time, mortality will be higher in closed canopy sites where the canopy and understory layers continue to attenuate light, resulting in high turnover of the aspen understory. Additional factors such as tree and branch windfall increase mortality in closed canopy conditions. Although mammal herbivory and pathogen/insect damage occur in both open and closed canopy sites (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 sites and regions.

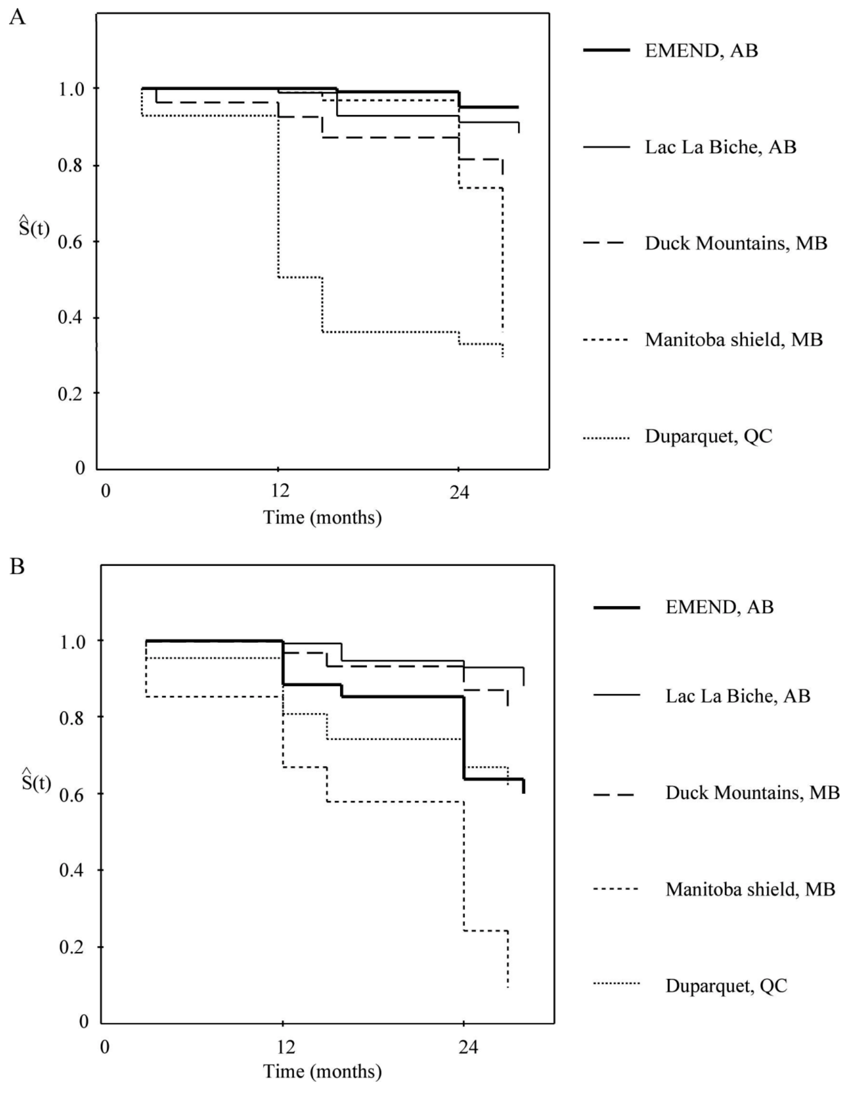

Figure 4. Kaplan-Meier estimated survival curves for natural regeneration of trembling aspen. Separate functions are shown for each region, for open (A) and closed (B) canopy sites. S(t) hat (estimated survival function) is the probability that a sapling's survival time is greater than time t. Monitoring began after the first growing season (t=3-4 months) following site establishment in the spring of 2000 (t=0). A.) Estimated survival functions for aspen regeneration in post-harvest open canopy sites. There is a significant difference among regional survivorship curves (Log-Rank statistic=590.0; P<0.0001). B.) Estimated survival functions for aspen regeneration growing under closed mixed hardwood canopy conditions. There is a significant difference among regional survivorship curves (Log-Rank statistic=412.6; P<0.0001).

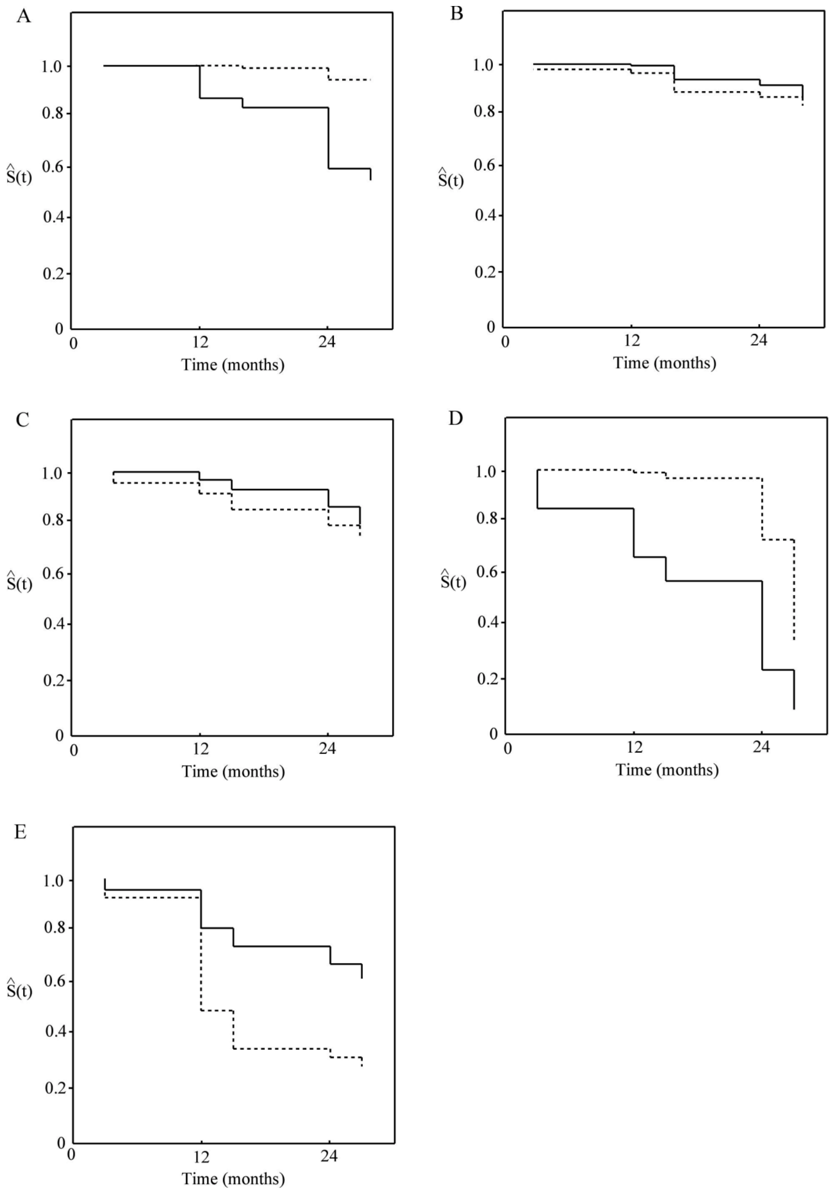

Figure 5. KM estimated survival curves for natural regeneration of trembling aspen. Separate survival functions are shown for open (broken line) and closed (solid line) canopy conditions for EMEND (A), Lac La Biche (B), Duck Mountains (C), Manitoba shield (D), and Duparquet (E). Log-Rank statistical tests of functions for open versus closed canopy are significant for EMEND (Log-Rank statistic=88.75; P<0.0001), Manitoba shield (Log-Rank statistic=101.37; P<0.0001), and Duparquet (Log-Rank statistic=97.38; P<0.0001).

Cox PH regression models of most study locations suggest that %PAR availability at the leader of aspen saplings is a good predictor of survival time for both open and closed canopy regimes (Table 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. In general, taller aspen saplings receiving more light, and in particular with higher live crown ratios have higher survival probabilities.

Table 6. Cox PH regression models for trembling aspen regeneration growing under either open (post-harvest) or closed canopy conditions, for each region of the study. The exponent of the variable coefficient *B* is the predicted 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 interval for exp(*B*) for all presented variables excludes 1.0, indicating that the population hazard ratio varies across different values of predictor variables. Variables were entered into models using a forward likelihood ratio test at a 5% significance level. All models have 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 (shown).

Region	Canopy regime	Model*	Variables in model	*B*	se	Wald statistic	df	P	exp(*B*)	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
	Closed	1	Height	-0.033	0.006	29.252	1	<0.001	0.968	0.956	0.979
		2	%PAR leader	-0.054	0.012	21.526	1	<0.001	0.947	0.926	0.969
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	%PAR 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	%PAR 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
			Live crown ratio	-4.564	0.888	26.406	1	<0.001	0.003	0.001	0.017
		2	%PAR leader	-0.043	0.006	47.306	1	<0.001	0.958	0.946	0.970
	Closed	1	Height	-0.009	0.003	8.151	1	0.004	0.941	0.986	0.997
			Live crown ratio	-2.227	0.714	10.159	1	0.001	0.103	0.025	0.416
		2	%PAR 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

*Two types of predictor variables were examined. Initial sapling dimensions of height, diameter and live crown ratio were examined to determine any relationship between sapling size and crown morphology and mortality (Model type 1). Percent PAR availability was examined in a separate model for each region and canopy type to investigate light availability as a causal factor of mortality. Percent PAR not used as postential variable for Duparquet data, for which light readings were available only for saplings alive at the end of the study period.

Balsam fir

KM estimated survival functions for balsam fir advance regeneration are significantly different among regions for both open canopy conditions (Log-Rank statistic=11.75; P<0.0019) and closed canopy conditions (Log-Rank statistic=27.41; P<0.0001) (Figure 6). Chicoutimi sites 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 Chicoutimi under both open and closed canopy conditions. However if sites are compared at two years following site establishment, the survival probability in closed canopy

Chicoutimi sites is still much lower than for other regions. This may be a result of the small initial size of some of the regeneration in Chicoutimi sites.

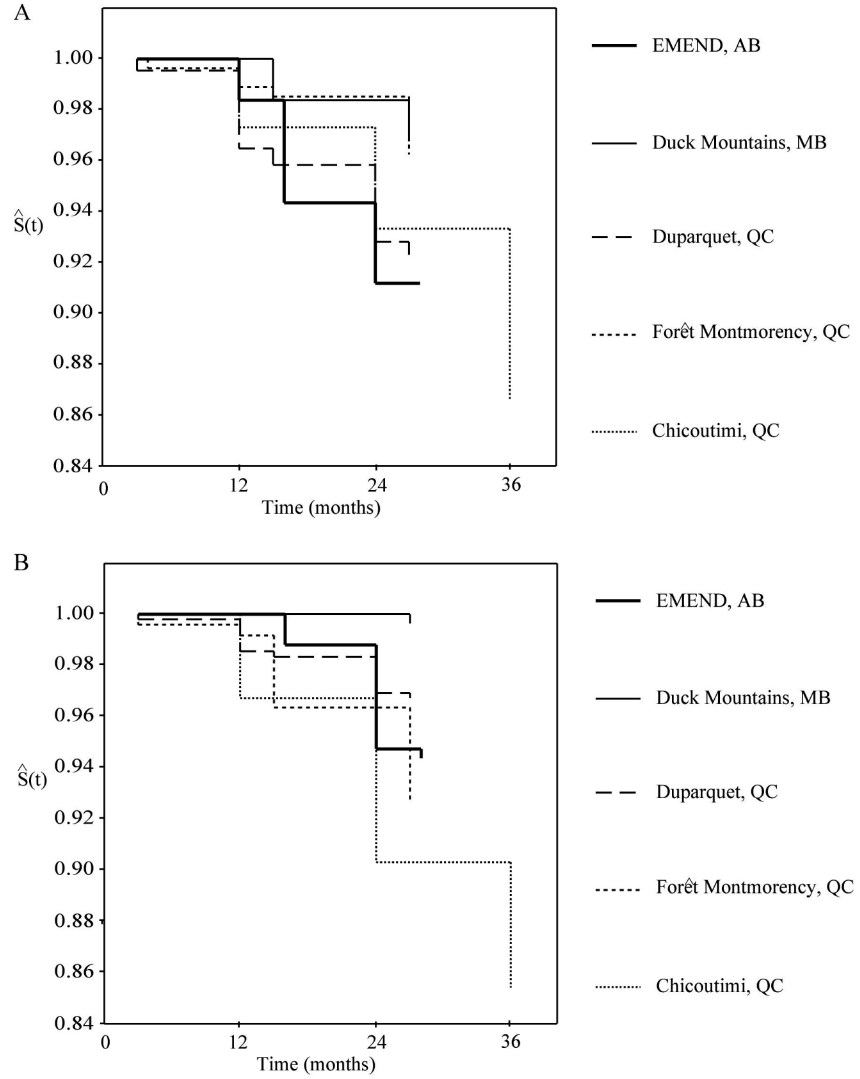

Figure 6. Kaplan-Meier estimated survivorship curves for advance regeneration of balsam fir. Note scale of y-axis differs from that for aspen survivorship curves (Figure 4). Separate functions are shown for each region, for open (A) and closed (B) canopy sites. S(t) hat (estimated survival function) is the probability that a sapling's survival time is greater than time t. A.) Estimated survival functions for balsam fir advance regeneration growing under canopy gaps. There is a significant difference among regional survivorship curves (Log-Rank statistic=11.75; P=0.019). B.) Estimated survival functions for balsam fir advance regeneration growing under closed canopy conditions. There is a significant difference among regional survivorship curves (Log-Rank statistic=27.41; P<0.0001). Chicoutimi sites were established in the fall of 1999, whereas other sites were established in the spring of 2000. Therefore, mortality in Chicoutimi sites has been monitored for approximately 36 months. In addition, Chicoutimi sites were monitored only in the fall, therefore no data is available for time periods between fall measurements (12, 24, and 36 months). Lac La Biche sites are not included in analyses because the observed mortality was negligible.

There are significant differences between KM curves of balsam fir regeneration in open and closed canopy conditions for Duck Mountains (Log-Rank statistic=7.52; P<0.0061), Duparquet (Log-Rank statistic=10.02; P=0.0016), and Forêt Montmorency (Log-Rank statistic=4.07; P=0.0436) (Figure 7). Balsam fir survival time is longer under closed canopy regimes for Duck Mountains and Duparquet sites, whereas in the Forêt Montmorency sites survival time is longer under canopy gaps. Canopy gaps in the Forêt Montmorency region are large, the result of large spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreaks. By 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 difference in light conditions between gaps and closed canopy sites in Forêt Montmorency is so dramatic that an overall difference in mortality of balsam fir regeneration at a very coarse scale is evident. 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.

Within a given canopy regime, light is not consistently a good predictor of survival time for balsam fir (based on the small number of fir saplings that died). This suggests that although light availability may influence fir mortality at a "coarse" spatial scale (e.g. comparing two dramatically different light environments), it does not predict variation in survival time within a given light regime. Live crown ratio is a good predictor of fir survival time for all canopy regimes and regions except Forêt Montmorency and Chicoutimi (Table 7). Cox regressions were not performed on Lac La Biche or closed canopy Duck Mountains sites because mortality in these sites is negligible. All models presented have significant likelihood ratio and Wald test statistics at the 0.05 significance level.

Growth and Crown Morphology

With a few exceptions, mean relative growth rates are quite consistent across regions, indicating that they are useful estimates of height growth under different light conditions for each species. Because relative growth rates are standardized by sapling size, they can be used to compare growth rates among sites and regions with different-sized individuals.

Light, RHG, and crown morphology compared across light environments and regions

Light

Light availability is significantly different between open and closed canopy regimes for all regions (Tables 8-11).

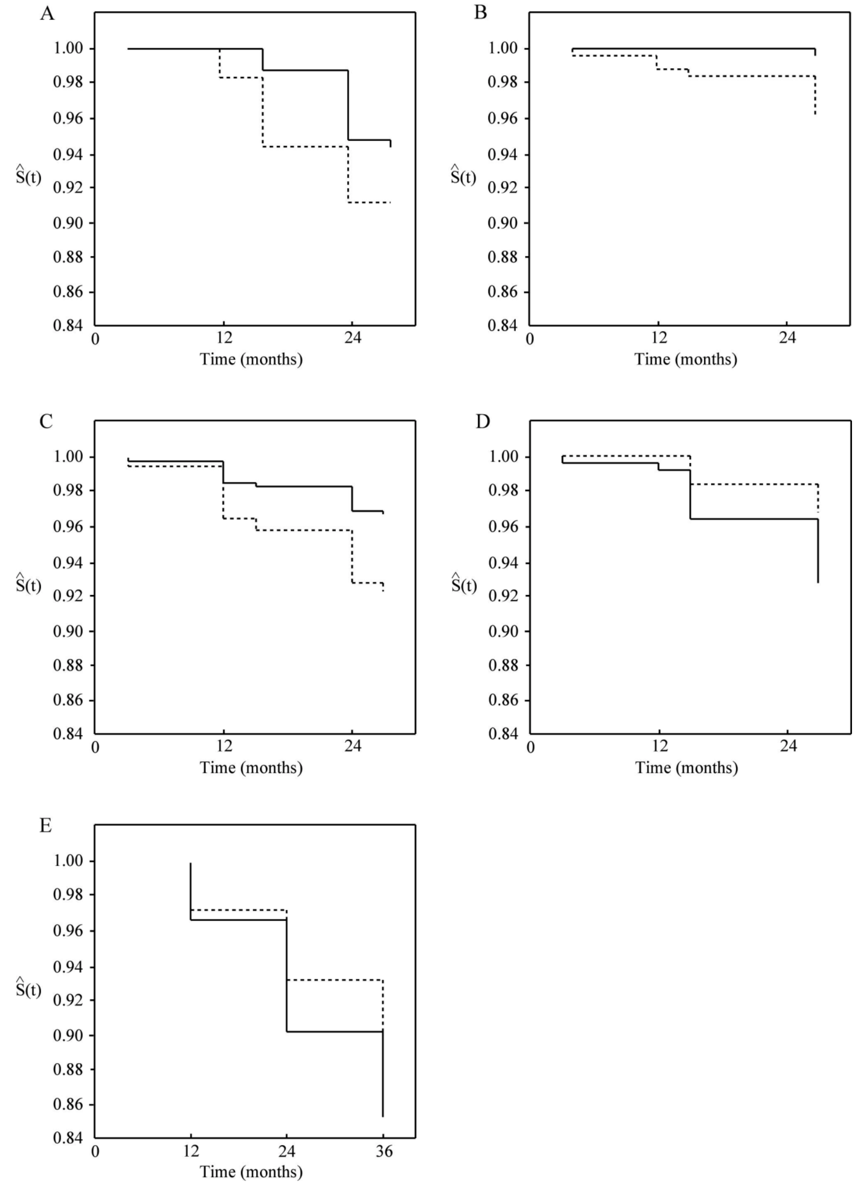

Figure 7. KM estimated survival curves for advance regeneration of balsam fir. Separate survival functions are shown for open (broken line) and closed (solid line) canopy conditions for EMEND (A), Duck Mountains (B), Duparquet (C), Forêt Montmorency (D), and Chicoutimi (E). Log-Rank statistical tests of functions for open versus closed canopy are significant for Duck Mountains (Log-Rank statistic=7.52; P=0.0061, Duparquet (Log-Rank statistic=10.02; P=0.0016), and Forêt Montmorency (Log-Rank statistic=4.07; P=0.0436).

Relative height growth (RHG)

RHG is relatively consistent across regions, with a few exceptions. White spruce growth in open sites is higher in Duck Mountains than in other regions; black spruce growth in open sites is higher in the Ashuapmushuan reserve than in other regions; and balsam fir growth in open sites is higher in Forêt Montmorency than in other regions. All of these sites exhibit extremely high mean %PAR relative to other open sites of a given species, explaining the high

RHG observed. The extensive spruce budworm gaps at the Forêt Montmorency sites indicate inter-regional differences in light environments for balsam fir regeneration. However, differences in light availability and corresponding RHG between regions for white and black spruce are a reflection of variation in site conditions, but not overall differences among regions.

All species exhibit elevated relative growth rates in open canopy regimes (Tables 8-11), with the exception of balsam fir, which demonstrated greater RHG in canopy gaps than under closed canopy only for Forêt Montmorency sites. This suggests that sapling RHG varies between different light environments only if the light environments are substantially different from one another. The difference in RHG between open and closed canopy regimes is more dramatic for black spruce than for white spruce (Tables 8,9). Again this reflects the larger variation between high and low light treatments for black spruce than white spruce. The average light availability under the mixed-conifer canopy where white spruce was monitored is generally higher than that under black spruce canopy where black spruce regeneration was monitored.

Table 7. Cox PH regression models for balsam fir advance regeneration growing under either open (post-harvest) or closed canopy conditions, for each region of the study. The exponent of the variable coefficient *B* is the predicted change in hazard for a unit increase in the predictor variable. Values less than 1 correspond to a decrease in hazard, or increase in predicted survival time, with increasing values of the predictor variable. The 95% confidence interval for exp(*B*) for all variables excludes 1.0, therefore there is a 95% chance that the hazard ratio for the population varies across different values of predictor variables. Variables were entered into models using a forward likelihood ratio test at the 0.05 significance level. All models have significant X^2 test statistics, which measure the change in -2Loglikelihood between two successive models, where each successive model has an additional predictor variable, and significant Wald test statistics (shown).

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
		%PAR 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
Duparquet, 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	-	-	-	-	-	-	-	-	-

*Saplings growing under closed canopy in EMEND sites are the only ones for which the causal factor %PAR is a good predictor of mortality.

Crown morphology

Mean L:B ratios are >1 in open canopy environments for the two spruce species, particularly black spruce. The spruces exhibit stronger apical dominance in disturbed and post-harvest sites, and weaker apical dominance under closed canopies. There is a notable difference in balsam fir L:B ratio between gaps and closed canopy conditions only in cases where there is a large difference in light conditions between the two regimes. These results 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).

Live crown ratio is significantly greater in high than low light regimes for most regions for all species. 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.

Light availability at the individual-level as a predictor of advance regeneration growth

Apart from a few exceptions the coefficients of determination are generally very low for linear regression models predicting RHG by light (Table 12). One likely explanation for the poor predictive ability of light 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.

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. Light does predict live crown ratio consistently among regions for aspen regeneration in open sites, but nonetheless there remains much residual variation for these models.

Table 8. Summary statistics for RHG, %PAR, 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. P values are shown in brackets for t-test comparisons made between canopy regimes for sapling response in growth and crown morphology, and for %PAR availability. Significant differences are highlighted.

Region	Canopy	n	RHG (cm/year)		%PAR leader		Initial live crown ratio		Initial L:B ratio**		Initial height (cm)		Initial diameter (cm)	
			mean	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**
EMEND, AB	Open	250	**0.08**	0.04	**41.95**	17.01	0.71	0.15	**1.06**	0.34	71.13	20.05	1.27	0.53
	Closed	250	**0.07**	0.04	**14.45**	7.89	0.71	0.18	**0.92**	0.32	45.36	17.61	0.92	0.31
			(0.0002)		***(<0.0001)***		*(0.8500)*		***(<0.0001)***					
Lac La Biche, AB	Open	250	**0.12**	0.05	**48.96**	18.94	**0.86**	0.08	**1.15**	0.30	63.68	20.59	1.31	0.50
	Closed	245	**0.06**	0.03	**21.13**	12.66	**0.76**	0.12	**0.96**	0.29	65.68	20.55	1.10	0.40
			(<0.0001)		***(<0.0001)***		***(<0.0001)***		***(<0.0001)***					
Duck Mountains, MB	Open	264	**0.17**	0.05	**67.19**	15.90	**0.87**	0.09	**1.47**	0.67	54.98	26.45	1.36	0.64
	Closed	266	**0.10**	0.06	**10.22**	6.56	**0.68**	0.18	**1.07**	0.09	47.21	30.53	0.86	0.55
			(<0.0001)		***(<0.0001)***		***(<0.0001)***		***(<0.0001)***					
Duparquet, QC*	Open	331	**0.07**	0.07	**87.80**	18.22	**0.83**	0.17	0.93	0.85	41.74	25.18	1.10	0.44
	Closed	270	**0.05**	0.07	**4.65**	2.38	**0.73**	0.16	0.90	1.27	43.68	20.04	0.79	0.35
			(0.0014)		***(<0.0001)***		***(<0.0001)***		*(0.7886)*					

*Sample sizes for %PAR measurements for Duparquet sites are n=195 for open sites, and n=204 for closed sites.

**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 sites respectively, for Duck Mountains, n=250 and 223 for open and closed sites respectively, and for Duparquet, n=280 and 193 for open and closed sites respectively.

Table 9. Summary statistics for RHG, %PAR, 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. P values are shown in brackets for t-test comparisons made between canopy regimes for sapling response in growth and crown morphology, and for %PAR availability. Significant differences are highlighted.

Region	Canopy	n	RHG (cm/year)		%PAR leader		Initial live crown ratio		Initial L:B ratio		Initial height (cm)		Initial diameter (cm)	
			mean	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**	**mean**	**sd**
Manitoba shield, MB	Open	295	**0.12**	0.04	**37.64**	10.53	**0.88**	0.08	**1.48**	0.58	60.61	20.62	1.03	0.47
	Closed	274	**0.04**	0.02	**9.79**	4.74	**0.69**	0.17	**0.97***	0.41	52.92	21.55	0.94	0.45
			(<0.0001)		***(<0.0001)***		***(<0.0001)***		***(<0.0001)***					
Iroquois Falls, ON	Open	288	**0.12**	0.04	**46.50**	19.32	0.77	0.14	**1.35***	0.48	49.32	26.58	0.88	0.55
	Closed	275	**0.04**	0.02	**10.84**	4.58	0.76	0.15	**0.98***	0.44	42.79	30.24	0.69	0.66
			(<0.0001)		***(<0.0001)***		*(0.3319)*		***(<0.0001)***					
Ashuapmushuan Reserve, QC	Open	246	**0.18**	0.09	**82.55**	17.22	**0.89**	0.16	**1.68**	0.65	59.62	27.34	1.23	0.01
	Closed	237	**0.04**	0.02	**12.29**	4.16	**0.67**	0.21	**1.00**	0.61	45.22	25.97	0.64	0.42
			(<0.0001)		***(<0.0001)***		***(<0.0001)***		***(<0.0001)***					

*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 sites are based on 270 measurements. L:B ratios in Ontario sites are based on 287 and 269 measurements for open and closed sites respectively.

Table 10. Summary statistics for RHG, RDG, %PAR, initial live crown ratio, height and 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. P values are shown in brackets for t-test comparisons made between canopy regimes for sapling response in growth and crown morphology, and for %PAR availability. Significant differences are highlighted.

Region	Canopy	n	RHG (cm/year)		%PAR leader		Initial live crown ratio		Initial L:B ratio†		Initial height (cm)		Initial diameter (cm)	
			mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
EMEND, AB	Open	228	0.05	0.03	**23.93**	12.57	**0.84**	0.14	1.02	2.73	60.96	20.50	1.35	0.50
	Closed	236	0.05	0.03	**10.61**	4.99	**0.80**	0.17	0.79	1.48	57.52	19.69	1.20	0.44
			(0.9318)		***(<0.0001)***		***(0.0075)***		*(0.3049)*					
Lac La Biche, AB	Open	250	**0.09**	0.05	**14.32**	8.77	**0.82**	0.12	0.87	1.25	59.69	19.82	1.20	0.42
	Closed	248	**0.08**	0.04	**8.88**	4.75	**0.74**	0.15	0.74	0.62	55.42	17.80	1.01	0.41
			(<0.0001)		***(<0.0001)***		***(<0.0001)***		*(0.2122)*					
Duck Mountains, MB	Open	260	0.07	0.06	**19.29**	7.97	0.71	0.13	1.05	0.50	77.79	30.92	1.45	0.73
	Closed	269	0.06	0.05	**12.63**	5.04	0.68	0.15	0.99	0.76	68.37	26.95	1.27	0.50
			(0.1833)		***(<0.0001)***		*(0.0572)*		*(0.3658)*					
Duparquet, QC*	Open	578	0.05	0.12	**13.03**	10.22	**0.61**	0.22	0.99	2.16	56.83	29.84	1.00	0.45
	Closed	477	0.04	0.14	**10.39**	4.95	**0.67**	0.21	0.87	1.96	46.71	24.55	0.90	0.41
			(0.5432)		***(<0.0001)***		***(<0.0001)***		*(0.5357)*					
Forêt Montmorency, QC	Open	240	**0.16**	0.08	**40.67**	20.34	0.84††	0.15	**1.15**	0.43	56.75	27.89	0.81	0.44
	Closed	230	**0.04**	0.03	**18.44**	10.56	0.61††	0.23	**0.47**	0.49	43.89	31.32	0.65	0.50
			(<0.0001)		***(<0.0001)***				***(<0.0001)***					
Chicoutimi, QC**	Open	65	**0.04**	0.04	**30.77**	9.30	-	-	-	-	60.53	31.26	0.85	0.52
	Closed	159	**0.07**	0.05	**8.82**	3.23	-	-	-	-	21.08	19.55	0.32	0.38
			(<0.0001)		***(<0.0001)***									

*Sample sizes for %PAR measurements for Duparquet sites are n=179 for open sites, and n=368 for closed sites.

**No measures of crown morphology available for Chicoutimi sites.

†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=156 and 189 for open and closed sites respectively, for Lac La Biche, n=231 for open sites, for Duck Mountains, n=229 and 242 for open and closed sites respectively, for Duparquet, n=254 and 245 for open and closed sites respectively, and for Forêt Montmorency, n=218 for closed sites.

††Live crown ratio values for Forêt Montmorency sites are from 2002, whereas for other sites values of live crown ratio are from the first year of the study.

Table 11. Summary statistics for RHG, RDG, %PAR, initial live crown ratio, height and basal diameter of trembling aspen for each canopy regime and region. Summary values were derived from all saplings which were alive at the end of the study period. P values are shown in brackets for t-test comparisons made between canopy regimes for sapling response in growth and crown morphology, and for %PAR availability. Significant differences are highlighted.

Region	Canopy	n	RHG (cm/year)		RDG (cm/year)		%PAR leader		Initial live crown ratio		Initial height (cm)		Initial diameter (cm)	
			mean	sd	mean	sd	mean	sd	mean	sd	mean	sd	mean	sd
EMEND, AB*	Open	238	**0.19**	0.12	-	-	**68.81**	8.52	**0.73**	0.13	90.19	25.80	1.19	0.31
	Closed	156	**0.15**	0.13	-	-	**34.03**	10.92	**0.62**	0.14	67.98	19.91	0.09	0.28
			(0.0002)				***(<0.0001)***		***(<0.0001)***					
Lac La Biche, AB*	Open	220	**0.13**	0.11	-	-	**71.91**	19.86	**0.60**	0.14	131.09	37.05	1.66	0.58
	Closed	202	**0.05**	0.12	-	-	**26.76**	9.62	**0.47**	0.16	140.19	37.69	1.71	0.54
			(<0.0001)				***(<0.0001)***		***(<0.0001)***					
Duck Mountains, MB	Open	208	**0.12**	0.11	0.06	0.08	**69.66**	30.13	0.50	0.15	150.73	36.57	1.43	0.44
	Closed	216	**0.04**	0.19	0.004	0.08	**15.44**	5.64	0.50	0.18	132.01	54.25	1.28	0.54
			(<0.0001)		*(<0.0001)*		***(<0.0001)***		*(0.7919)*					
Manitoba shield, MB	Open	71	0.12	0.06	0.11†	0.06	**32.21**	9.72	0.51**	0.15	136.17	28.60	1.33	0.34
	Closed	20	0.14	0.13	0.13	0.06	**2.82**	2.18	0.56**	0.22	81.11	18.47	0.79	0.22
			(0.3658)		*(0.2982)*		***(<0.0001)***		*(0.2550)*					
Duparquet, QC	Open	134	**0.09**	0.18	0.06	0.17	**71.95†**	21.49	0.59	0.20	143.77	50.70	1.56	0.66
	Closed	223	**0.00**	0.21	0.03	0.16	**43.96†**	22.57	0.57	0.17	148.27	58.31	1.25	0.51
			(<0.0001)		*(0.1430)*		***(<0.0001)***		*(0.2360)*					

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

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

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

Table 12. Coefficients of determination and significance levels for simple linear regressions of RHG, RDG, live crown ratio, and L:B ratio against %PAR 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.

Species	Region	Canopy	n	RHG		RDG		Live crown ratio		L:B ratio	
				r^2	P	r^2	P	r^2	P	r^2	P
White spruce	EMEND, AB	open	248	**2.7**	**0.009**	-	-	**3.7**	**0.0022**	**3.3**	**0.0049**
		closed	246	**12.5**	**<0.0001**	-	-	**5.2**	**0.0003**	**3.1**	**0.0069**
	Lac La Biche, AB	open	248	0	0.7406	-	-	0.3	0.3921	**2.3**	**0.0233**
		closed	245	1.1	0.0939	-	-	0.3	0.4093	**6.5**	**<0.0001**
	Duck Mountains, MB	open	264	0.1	0.5311	-	-	**11.9**	**<0.0001**	0.2	0.4462
		closed	261	**14.0**	**<0.0001**	-	-	**5.3**	**0.0002**	0.7	0.2092
	Duparquet, QC	open	185	**21.3**	**<0.0001**	-	-	**4.0**	**0.0065**	0	0.9190
		closed	160	1.7	0.0989	-	-	**10.0**	**<0.0001**	1.5	0.1588
Black spruce	Manitoba shield, MB	open	295	**1.9**	**0.0169**	-	-	1.0	0.0931	0.2	0.4153
		closed	274	**1.7**	**0.0331**	-	-	0	0.8197	**6.3**	**<0.0001**
	Iroquois Falls, ON	open	288	**7.0**	**<0.0001**	-	-	0.9	0.1087	0	0.9900
		closed	281	0.1	0.5900	-	-	0.1	0.6715	0	0.9913
	Ashuapmushuan Reserve, QC	open	246	0.6	0.2344	-	-	0.3	0.3846	**3.8**	**0.0020**
		closed	236	1.5	0.0610	-	-	0	0.7671	0.3	0.3911
Balsam fir	EMEND, AB	open	227	0.0	0.9739	-	-	0.8	0.1859	0.4	0.4069
		closed	236	**16.6**	**<0.0001**	-	-	**9.2**	**<0.0001**	**4.8**	**0.0024**
	Lac La Biche, AB	open	250	**5.1**	**0.0003**	-	-	**1.8**	**0.0320**	0	0.9488
		closed	248	**28.9**	**<0.0001**	-	-	**5.2**	**0.0003**	**8.0**	**<0.0001**
	Duck Mountains, MB	open	245	**9.7**	**<0.0001**	-	-	**15.7**	**<0.0001**	**12.5**	**<0.0001**
		closed	241	**4.1**	**0.0015**	-	-	**10.5**	**<0.0001**	**3.5**	**0.0047**
	Duparquet, QC	open	146	**7.1**	**0.0011**	-	-	**20.6**	**<0.0001**	1.1	0.26
		closed	261	**4.5**	**0.0005**	-	-	**16.1**	**<0.0001**	**5.2**	**0.0033**
	Forêt Montmorency, QC	open	240	1.5	0.0580	-	-	**3.4**	**0.0049**	1.4	0.0674
		closed	230	0.1	0.5724	-	-	0.6	0.2749	0.1	0.5775
	Chicoutimi, QC	open	11	34.3	0.0585	-	-	-	-	-	-
		closed	91	**8.4**	**0.0053**	-	-	-	-	-	-
Trembling aspen	EMEND, AB	open	225	**1.8**	**0.0469**	-	-	**13.1**	**<0.0001**	-	-
		closed	133	0.4	0.4642	-	-	**5.8**	**0.0051**	-	-
	Lac La Biche, AB	open	203	**18.3**	**<0.0001**	-	-	**12.5**	**<0.0001**	-	-
		closed	166	0.4	0.4358	-	-	2.0	0.072	-	-
	Duck Mountains, MB	open	179	**39.4**	**<0.0001**	2.0	0.0593	**30.8**	**<0.0001**	-	-
		closed	153	0.1	0.6404	0.3	0.5264	1.6	0.1216	-	-
	Manitoba shield, MB	open	70	**6.9**	**0.0277**	0	0.9446	**7.4**	**0.0230**	-	-
		closed	17	**43.9**	**0.0037**	**29.4**	**0.0246**	16.4	0.2033	-	-
	Duparquet, QC	open	78	0.9	0.4054	4.4	0.0639	0.1	0.8074	-	-
		closed	51	4.1	0.1553	0.8	0.5409	0.5	0.6704	-	-

Mean light availability and other site-level factors as predictors of advance regeneration growth

For all four species, percent light availability is a good predictor of growth when mean values of RHG and %PAR for each site (including both open and closed canopy treatments) are regressed against one another (Figure 8). Open and closed canopy treatments form distinct groups in each linear regression model. Additional site-level variables of slope, aspect, %coarse particles (>2mm) in soil, total canopy basal area, and mean canopy height were included as potential variables in stepwise multiple linear regression, but the only model that improved upon the addition of site-level factors is the white spruce model. Here, site estimates of % coarse particles in the soil increased the coefficient of determination marginally, from 42.7% to 54.6% (excluding Duparquet sites for which % coarse material data was not available).

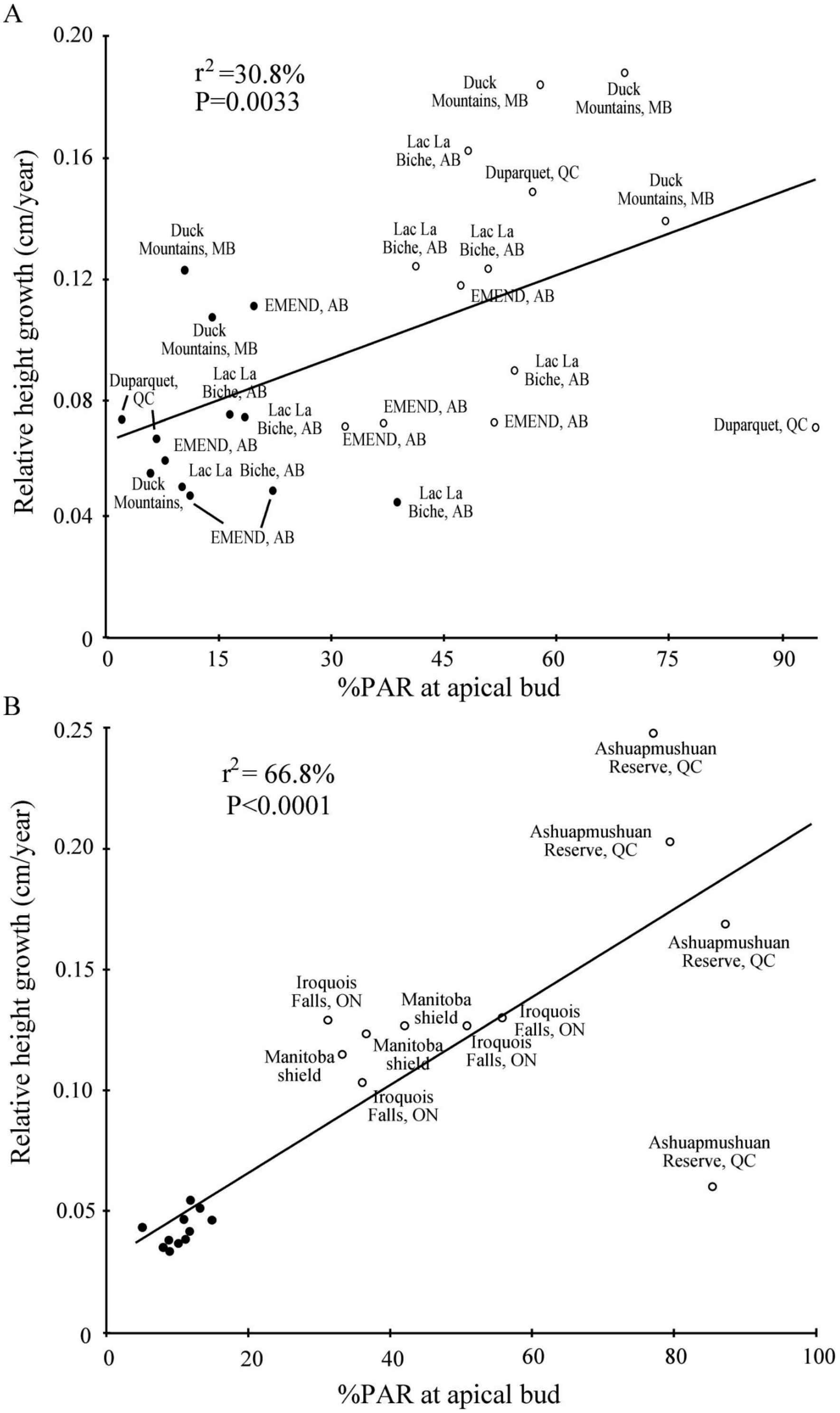

Figure 8. Simple linear regression models of RHG predicted by %PAR, for white spruce (A), black spruce (B), balsam fir (C), and trembling aspen (D). Individual points in the regression model represent site replicates for each canopy regime and region. The RHG and corresponding %PAR for saplings in a given site replicate were averaged to give a single measure of growth and light availability. Open circles represent high light, open canopy sites and shaded circles represent low light, closed canopy sites. Individual points are labeled when large variation within a light regime (open or closed) is present. Note differences in y and x-axis scales for each species.

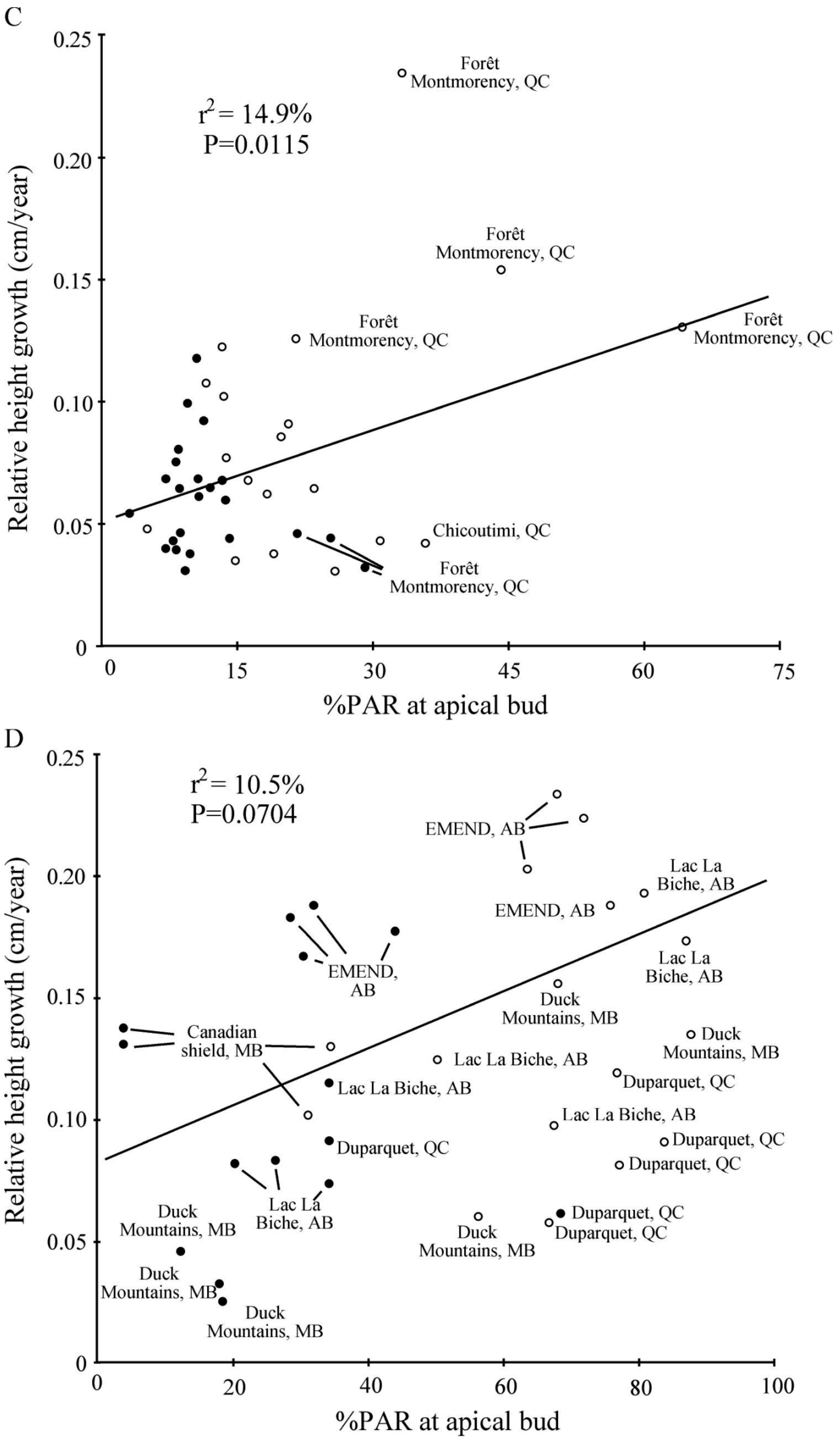

Figure 8 (continued).

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 aspen suckers browsed each year in a given canopy regime is relatively low for Duparquet sites as compared to Alberta and Manitoba sites (Table 13). There may also be a difference in the importance of browsing species across sites or regions. Ungulate herbivores typically browse the leader and upper branches of both fir and 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 fir browsed appears to be higher for Lac La Biche and Duck Mountain sites than for either EMEND or Québec sites. The dominant browse agent of 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.

Table 13. Summary of percentage of live saplings of trembling aspen and balsam fir browsed each year. Values are means across the 3 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 Duparquet, therefore there is no estimated annual variation.

Species	Region	Canopy regime	Average % browse	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 site replicates of aspen regeneration in Duparquet.

DISCUSSION

Inter-regional variation in growth and mortality

Our research indicates that most of the variation in sapling growth and mortality noted among regions is the result of differences in site-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. Similar to our study, 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.

Our results suggest that some of the variation in sapling growth and mortality among study locations may occur on a larger scale at the regional-level, in particular for balsam fir. 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 regions in Québec where fir was monitored under vast spruce budworm-caused canopy gaps, the difference in growth, crown morphology, and mortality between open and closed canopy sites is more dramatic than for other regions. Because of the integral role of spruce budworm in eastern forests, there exists regional-level differences in the growing conditions for balsam fir advance regeneration under canopy gaps. Our study shows that the response of fir to large spruce budworm-caused canopy openings is different than that which occurs under smaller canopy gaps. Therefore, differential growth and mortality of balsam fir advance regeneration may occur on a large scale, reflective of regional differences in disturbance regimes.

Differential growth and mortality among species in relation to shade-tolerance

Interspecific differences in sapling mortality have been shown to be critical in determining forest composition during secondary succession (Pacala et al. 1994; Kobe et al. 1995; Kobe and Coates 1997). Of the four species examined in this study, aspen demonstrates higher mortality rates under low light conditions, and higher growth rates under high light conditions, than the coniferous species. 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). However, our results suggest that this relationship is not as clear between the extremely shade-tolerant balsam fir and the somewhat less shade-tolerant spruces. Fir demonstrated higher mortality under low light conditions than did white spruce. This is most likely attributable to factors other than light and shade-tolerance. Specifically, factors such as herbivory, and density of the regenerating stand, compromise growth and increase mortality of balsam fir under closed canopy conditions.

In general, differential growth and mortality between aspen and the coniferous species examined in our study are attributable mainly to differences in their relative shade-tolerance. However, within the more narrow range of shade-tolerance among coniferous species, interspecific differences are attributable to factors other than light (e.g. herbivory, regeneration density) which differ for fir and spruces.

The season of mortality

More saplings of both fir and aspen generally die over the winter months for regions exhibiting high mortality, as is shown in KM survival functions. 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.

Our results indicate that aspen mortality may be greater over the growing season when seasonal mortality rates are adjusted to unit time. Although seasonal differences in aspen mortality were noted only in the two of the study locations (Manitoba shield and Duparquet), these regions exhibited the highest mortality rates. Therefore as mortality increases over time for other study locations, a similar pattern of higher summer mortality may become evident.

Differential growth, crown morphology, and mortality between open and closed canopy environments

Differences in mortality between open and closed canopy conditions were not consistent across regions, for either aspen or fir. However, the causes of mortality may differ between canopy regimes and among regions, and this may obscure any overall differences in the occurrence of mortality between light regimes. Factors other than light may be important determinants of mortality for balsam fir advance regeneration. Canham et al. (1999) examined survival of two-year old hardwood seedlings under each of four canopy conditions: closed canopy, small gap, large gap, and recent clearcut. They found that 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. Our results indicate that factors other than degree of canopy opening affect growth and survival of larger juveniles.

Our results demonstrate that all species generally exhibit elevated relative growth rates in open canopy regimes. It has been shown that growth rates and survival of juvenile trees generally increase with increasing light availability (Pacala et al. 1994, Walters and Reich 2000). Studies examining post-harvest growth response of advance regeneration have shown an increase in height growth following canopy removal (Kneeshaw et al. 1998; Kneeshaw et al. 2002). Our results also indicate elevated growth rates in disturbed, high-light environments. For shade-intolerant aspen, low height growth under shaded conditions is attributable to insufficient resource supply. By contrast, reduced height growth in shade-tolerant coniferous species under shaded conditions reflects 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 or herbivore defense favours long-term survival in the understory, but precludes the allocation of photosynthate to rapid growth. In trees, interspecific differences in light-dependent growth and mortality (shade-tolerance) can be explained by differences in carbohydrate allocation among species (Kobe 1997).

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 is 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 generally greater in high light environments for all three coniferous species examined. 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). Live crown ratio of aspen saplings differed significantly between light environments for only the Alberta sites, but not consistently among regions.

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. Apparent variation in morphological plasticity observed among coniferous species in our study mainly reflect differences in their respective light treatments.

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

The probability of survival for aspen regeneration increases with light availability, height, and especially with live crown ratio. The survival time of fir is also best predicted by live crown ratio. The inability of %PAR to predict fir survival under shaded conditions suggests that factors other than light availability govern 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 is a strong predictor of mortality, light remains an important factor. It should be noted that Cox PH regression models for fir were based on relatively low levels of mortality for each region. A larger sample size of dead fir saplings (which should be available in a few years time) will help clarify the relationship between light availability and mortality in fir. Overall, our results corroborate previous evidence that height and live crown ratio are good indicators of mortality (Ruel et al. 1995).

Light as a predictor of growth at the individual sapling level

The ability of light to predict growth and crown morphology at the individual sapling level (i.e. within a defined light treatment) is inconsistent among regions. Light availability is best able to predict growth for conifers growing in low light environments, 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 experienced by the saplings examined. For conifer saplings in open canopy treatments, light is not a limiting factor except perhaps for fir regeneration in small canopy gaps (Alberta, Manitoba). Conversely, light is a significant predictor of aspen growth in open canopy conditions, suggesting that light is a limiting factor for dense stands of aspen regeneration. 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, and for some regions light proved a good predictor of sapling growth. Although variation in light availability for closed canopy sites of balsam fir regeneration is similar to that for black spruce, it is possible that the growth of shade-tolerant fir may be more sensitive to small changes in light.

In all cases, much of the variation in growth and crown morphology within a defined canopy treatment is unexplained by light. 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 levels by increasing their height 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 years). Pacala et al. (1994) also 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. 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.

Factors predicting variation in growth at the site-level

Although variation in light availability was found to be low within a defined canopy regime, it was sufficiently high between canopy light regimes to predict a substantial amount of variation in average growth rates among sites for all species. Kneeshaw and Bergeron (1996) used site-level measures of abiotic and biotic factors to predict the abundance of advance regeneration for a number of species, including the four examined in our study. Our abiotic and biotic site variables (slope, aspect, percent gravel, canopy basal area and height) are generally poor predictors of site-level variation in growth. Kneeshaw and Bergeron (1996) found that abiotic site-variables were relatively poor at predicting abundance of regeneration, but that stand basal area was a relatively good predictor. Greater basal area corresponds greater seed availability, which in turn increases the abundance of coniferous regeneration. However, stand basal area is not an important predictor of sapling growth once light availability is taken into account.

MANAGEMENT APPLICATIONS

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; 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 (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; Pothier 2000). 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). Therefore, careful logging should also be explored as a silvicultural tool in western boreal regions. For example, a combination of careful and partial harvesting is a more sustainable strategy for logging western boreal riparian ecosystems than is clear-cutting (Timoney and Peterson 1996).

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, and protecting advance regeneration from damage during harvesting (Greene et al. 1999; Ruel et al. 2000). 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).

Our study supports previous findings that shade-tolerant coniferous advance regeneration demonstrates a "plastic" crown morphology which allows it to respond positively to overstory removal provided that proper management strategies are employed to minimize stress during and after harvesting. 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 (Orlander 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). Thus 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. Light availability, together with stand basal area and forest floor characteristics, play a role in determining 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 in hardwood stands, and strong competition from shade-intolerant species in large gaps of coniferous stands, limits the utility of advance regeneration strategies in these stands. An additional consideration is season of harvest: winter harvesting affords greater protection to advance regeneration (eg. Pothier 2000).

Empirical growth and mortality rates for white spruce, black spruce, balsam fir, and trembling aspen, 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 determining 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 plays an important role in the future development of these forests. High mortality of aspen suckers in the understory suggests an alternative strategy for canopy replacement: a continuous turnover of short-lived aspen suckers occurs, thus ensuring a constant supply of advance regeneration. Conifer survival and aspen turnover are high enough, and growth responses are plastic enough, to reasonably presume that some of these saplings will respond positively to canopy gap formation and shape the future composition of the forest.

Our study has also addressed the potential for geographic variation across the Canadian boreal forest. With few exceptions, our results indicate that mean relative growth rates and mortality rates are fairly consistent across regions. This result suggests that empirically derived growth rates may be good overall estimates of height growth under different environmental conditions. Our results can therefore be used directly in growth and yield models, and in forest simulation models used in the development and testing of alternative management strategies.

The mortality rates, survival probabilities and survival times presented can be used to predict mortality of advance regeneration at both the site and individual levels. In addition to abundance of regeneration, interspecific differences in mortality should be considered when assessing the potential of a site for careful harvesting. For example, advance regeneration of balsam fir is often more abundant than spruce, but our results indicate that fir has consistently higher mortality rates than spruce.

Specific field criteria for assessing growth and survival of advance regeneration following overstory removal

To ensure adequate stocking of harvested stands, preserved advance regeneration must be maintained in a healthy state. In addition, 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. However, they also suggested that additional indicators may be required, and that specific threshold values may need to be developed for different regions. From our study, survival analysis has provided estimates of the instantaneous potential of an individual sapling to die in a given season, given that it has survived up to the time at which the observation is made. Threshold values of %PAR and initial height for aspen, and live crown ratio for fir, can be determined for acceptable probabilities of mortality (within a three year time frame) under low light conditions, for each of the regions studied. It is therefore recommended that our results be used to develop a suite of indicators that can be used in the field to predict the survival time of saplings growing under different light environments. Ruel et al. (1995) demonstrated that sapling suppression prior to release, and logging damage during harvest, are required to assess mortality immediately following release. 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.

Growth and mortality compared in high and low light conditions

In exploring strategies for the management of advance regeneration in boreal forests, an understand of the ecology of regeneration in the shaded understory is required (Messier et al. 1999). Our study has characterized certain aspects of growth and mortality of advance regeneration in shaded conditions. In addition, our study has provided comparisons of growth and mortality between shaded (intact forest) and open environments (natural or human-caused disturbance). Open and closed canopy sites were chosen adjacent to one another in an attempt to control for intersite variation. Observed differences in growth, crown morphology, and mortality between adjacent open and closed canopy sites may reflect potential differences in regeneration vigour between pre- and post-harvest conditions. Aspen mortality was relatively consistent between open and closed canopy conditions, but the causes of mortality differed. Fir mortality was higher in low light conditions than high-light spruce budworm gaps (Quebec), but was higher in small gaps than closed forest in western regions (Manitoba, Alberta). The "plastic" crown morphology of conifer saplings in the advance regeneration layer allows them to adapt quickly to changes in light conditions following harvesting (Kneeshaw et al. 1998, 2002).

As with black spruce, aspen regeneration was monitored in post-harvest sites, which permitted a direct examination of post-harvest growth. A wide range in relative height growth is exhibited in dense post-harvest sites of aspen regeneration. These stands exhibit high mortality rates as a result of rapid self-thinning. However, with moderation of self-thinning over time mortality rates will necessarily decline. Aspen suckers exhibiting highest RHG are likely to overtop neighbours and reach canopy size. It is suggested that a hands-off management policy for densely regenerated naturally self-thinning aspen stands following clearcutting will ensure that the most ecologically fit aspen suckers are successful in reaching canopy size. If post-harvest sites are encroached upon by non-desirable shade-intolerant competitors such as beaked hazelnut, the different growth strategies of the competing plants, and their proportional abundance, should be examined prior to any vegetation control intervention (Mallik et al. 1997).

CONCLUSIONS

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 consistent among regions. The growth and mortality rates presented are 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. Mortality is highest for aspen regeneration, followed by balsam fir, then black spruce, and white spruce. 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. Our study demonstrates that light is a reasonably good predictor of growth and mortality only if it is a limited resource, and only if there is sufficient variation in light availability among the saplings examined. Mortality, growth and crown morphology differ significantly across light environments encompassing a broad range of light availability. Management strategies that preserve advance regeneration should continue to be explored as low-cost alternatives to planting, and for improving the preservation of natural forest structure and composition. Careful logging takes advantage of the inherent plasticity that coniferous advance regeneration exhibits in response to light variation and should be considered in both clearcut and partial cut situations. The growth and mortality rates presented here can be used in forest simulators to derive and test alternative management strategies. Furthermore, from our results threshold values can be derived for in field assessments of survival of advance regeneration.

REFERENCES

Bergeron, Y., and Archambault, S. 1993. Decreasing fire frequency of forest fires in the southern boreal forest. Ecology, 81:1500-1516.

Bergeron, Y., Harvey, B., Leduc, A., and Gauthier, S. 1999. Forest management guidelines based on natural disturbance dynamics: stand-and forest-level considerations. For. Chron. 75: 49-54.

Brand, D. G., Weetman, G. F., and P. Rehsler. 1987. Growth analysis of perennial plants: the relative production rate and its yield components. Ann. Bot. 59:45-53.

Burton, P.J., Kneeshaw, D.D., and Coates, K.D. 1999. Managing forest harvesting to maintain old growth in boreal and suboreal forests. For. Chron. 75:623-631.

Canham, C.D., Kobe, R.K., Latty, E.F., and Chazdon, R.L. 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia 121:1-11.

Chen, H.Y., and Popadiouk, R.V. 2002. Dynamics of North American boreal mixedwoods. Environ. Rev. 10: 137-166.

Claveau, Y., Messier, C., Comeau, P. G., and Coates, K.D. 2002. Growth and crown morphological responses of boreal conifer seedlings and saplings with contrasting shade tolerance to a gradient of light and height. Can. J. For. Res. 32:458-468.

Drobyshev, I., and Nihlgard, B. 2000. Growth response of spruce saplings in relation to climatic conditions along a gradient of gap size. Can. J. For. Res. 30:930-938.

Greene, D.F., Zasada, J.C., Sirois, L., Kneeshaw, D., Morin, H., Charron, I., and M.J. Simard. 1999. A review of the regeneration dynamics of North American boreal forest tree species. Can. J. For. Res. 29:824-839.

Harvey, B.D., Leduc, A., Gauthier, S., and Bergeron, Y. 2002. Stand-landscape integration in natural disturbance-based management of the southern boreal forest. For. Ecol. Manage. 155: 369-385.

Kleinbaum, D.G. 1996. Survival analysis. Springer-Verlag, New York, Inc. 323 p.

Klinka, K., Wang, Q., Kayahara, G.J., Carter, R.E., and Blackwell, B.A. 1992. Light growth response relationships in Pacific silver fir (*Abies amabilis*) and subalpine fir (*Abies lascocarpa*). Can. J. Bot. 70:1919-1930.

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

Kneeshaw. D., Bergeron, Y., and DeGrandpré, L. 1998. Early response of *Abies balsamea* seedlings to artificially created openings. J. Veg. Sci. 9: 543-550.

Kneeshaw, D., Williams, H., Nikinmaa, E., and Messier, C. 2002. Patterns of above- and below-ground response of understory conifer release after partial cutting. Can. J. For. Res. 32:255-265.

Kobe, R. K. 1996. Intraspecific variation in sapling mortality and growth predicts geographic variation in forest composition. Ecol. Mon. 66:181-201.

Kobe, R.K. 1997. Carbohydrate allocation to storage as a basis of interspecific variation in sapling survivorship and growth. Oikos 80:226-223.

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

Kobe, R. K., Pacala, S. W., and Silander, J. A. Jr. 1995. Juvenile tree survivorship as a component of shade-tolerance. Ecol. App. 5: 517-532.

Krebs, C.J. 1999. Ecological Methodology. Addison Wesley Longman, Inc., California. 620 p.

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

Lieffers, V.J., Messier, C., Gendron, F., Stadt, K.J., and Comeau, P. 1999. Predicting and managing light in the understory of boreal forests. Can. J. For. Res. 29:796-811.

Mallik, A.U., Bell, F.W., and Gong, Y. 1997. Regeneration behavior of competing plants after clear cutting: implications for vegetation management. For. Ecol. Manage. 95:1-10.

Messier,C., Doucet, R., Ruel, J.C., Claveau, Y., Kelly, C., and M.J. Lechowicz. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. 29:812-823.

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

Orlander, G., and Karlsson, C. 2000. Influence of Shelterwood density on survival and height increment of Picea abies advance growth. Scand. J. For. Res. 15:20-29.

Pacala, S.W., Canham, C.D., Silander, J.A., Jr., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. 24: 2172-2183.

Parmar, M., K., B., and Machin, D. 1995. Survival analysis: a practical approach. John Wiley and Sons, Chichester. 255 p.

Pothier, D. 2000. Ten-year results of strip clear-cutting in Quebec black spruce stands. Can. J. For. Res. 30:59-66.

Ruel, J-C., Doucet, R., and Boily, J. 1995. Mortality of balsam fir and black spruce advance growth 3 years after clear-cutting. Can. J. For. Res. 25:1528-1237.

Ruel, J-C., Messier, C., Doucet, R., Claveau, Y., and Comeau, P. 2000. Morphological indicators of growth response of coniferous advance regeneration to overstory removal in the boreal forest. For. Chron. 76: 633-642.

Timoney, K.P., and Peterson, G. 1996. Failure of natural regeneration after clearcut logging in Wood Buffalo National Park, Canada. For. Ecol. Manage. 87:89-105.

Walters, M. B., and Reich, P.B. 1996. Are shade-tolerance, survival, and growth linked? Low light and nitrogen effects on hardwood seedlings. Ecology 77:841-853.

Walters, M. B., and. Reich, P. B. 2000. Seed size, nitrogen supply, and growth rate affect tree seedling survival in deep shade. Ecology, 81:1887-1901.

Weir, J.M.H., Johnson, E.A., and Miyanishi, K. 2000. Fire frequency and the spatial age mosaic of the mixed-wood boreal forest in western Canada. Ecol. Appl. 10: 1162-1177.

Williams, H., Messier, C., and D. D. Kneeshaw. 1999. Effects of light availability and sapling size on the growth and crown morphology of understory Douglas-fir and lodgepole pine. Can. J. For. Res. 29:222-231.