

Article

# Deterministic Models of Growth and Mortality for Jack Pine in Boreal Forests of Western Canada

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**Abstract:** We developed individual tree deterministic growth and mortality models for jack pine (*Pinus banksiana* Lamb.) using data from permanent sample plots in Alberta, Saskatchewan and Manitoba, Canada. Height and diameter increment equations were fitted using nonlinear mixed effects models. Logistic mixed models were used to estimate jack pine survival probability based on tree and stand characteristics. The resulting models showed that (1) jack pine growth is significantly influenced by competition; (2) competitive effects differ between species groups; and (3) survival probability is affected by tree size and growth, stand composition, and stand density. The estimated coefficients of selected growth and mortality functions were implemented into the Mixedwood Growth Model (MGM) and the simulated predictions were evaluated against independently measured data. The validation showed that the MGM can effectively model jack pine trees and stands, providing support for its use in management planning.

**Keywords:** *Pinus banksiana*; boreal forest; mortality; forest growth; Mixedwood Growth Model

## 1. Introduction

Jack pine (*Pinus banksiana* Lamb.) is the most widely distributed pine species in Canada's boreal forest, with a geographical distribution from Alberta to Nova Scotia. Together with other pine species, it accounts for  $2.67 \times 10^9$  m<sup>3</sup> of growing stock, more than 11% of the Canadian boreal tree volume [1]. Commercially, it is an important source of round timber, construction lumber and pulpwood [2].

Numerous factors influence the growth and mortality of jack pine. The establishment of natural regeneration is best on bare mineral soil, present often after stand replacing disturbances such as fire or harvesting [2]. Water availability, adequate temperatures and herbaceous competition strongly influence initial survival [3–6]. Early growth is slow, but increases rapidly after the third year, with trees reaching 1.4 m height in 5 to 8 years. For trees in later stages, intra and interspecific competition becomes more influential in determining the condition of a tree, primarily due to jack's pine strong shade intolerance [7]. On average sites (site index (SI) of 14 to 17 m at age 50), maximum mean annual increment is achieved at around 50 to 60 years with 1.6 to 3.2 m<sup>3</sup>/ha in Manitoba, 2.0 m<sup>3</sup>/ha in Saskatchewan and 2.7 m<sup>3</sup>/ha in Ontario [2]. Soil type can affect regeneration indirectly [8] and influence growth responses to climate [9] or control the mixing with aspen [10]. High intensity fires can hinder regeneration [11], but medium intensity fires increase tree diversity and delay replacement by other species [12]. Pre-commercial thinning and fertilization improves tree growth [13,14], with the largest effect being observed for young trees [15] and represent potentially viable silvicultural investments [16]. Considering the ecological and economic importance of this species in the boreal forest, there is a need for improved knowledge on growth, yield and mortality of jack pine. This knowledge has to be translated into practical tools, such as validated growth models that can be used by forest managers.

A number of forest growth models are available for the Canadian boreal forest, but are used in different jurisdictions, ecological areas or have different uses: Tree and Stand Simulator (TASS) [17,18] and PrognosisBC [19,20] in British Columbia, process based models such as Triplex (based on Physiological Processes Predicting Growth model) [21] in northern Ontario, Capsis (CroBas-PipeQual) [22] in Quebec or some novel approaches that use neural networks in Nova Scotia [23]. For boreal jack pine, few empirical models are available: Forest Vegetation Simulator (FVS)-Ontario in Ontario [24,25], Growth and Yield Projection System (GYPSY) [26] a stand based model used by the province of Alberta or Subedi and Sharma [27] who developed diameter growth models for jack pine plantations in northern Ontario. However, tree level models calibrated for jack pine are not currently available for western Canada.

The Mixedwood Growth Model (MGM) [28] is a distance-independent, individual tree based stand growth model. It was created to help forest managers and decision makers develop yield tables and yield curves needed for management planning [29,30]. The MGM was originally constructed for pure and mixed stands of white spruce (*Picea glauca* (Moench) Voss), aspen (*Populus tremuloides* Michx.), lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and black spruce (*Picea mariana* (Mill.) B.S.P.) using Alberta's permanent sample plot (PSP) data. Other species use the growth and mortality of a similar species (e.g., jack pine uses functions developed for lodgepole pine). This can be problematic, as the two species may be very different in terms of the ecoregions where they occur, the sites they occupy, their growth rates, crown characteristics and overall allometry.

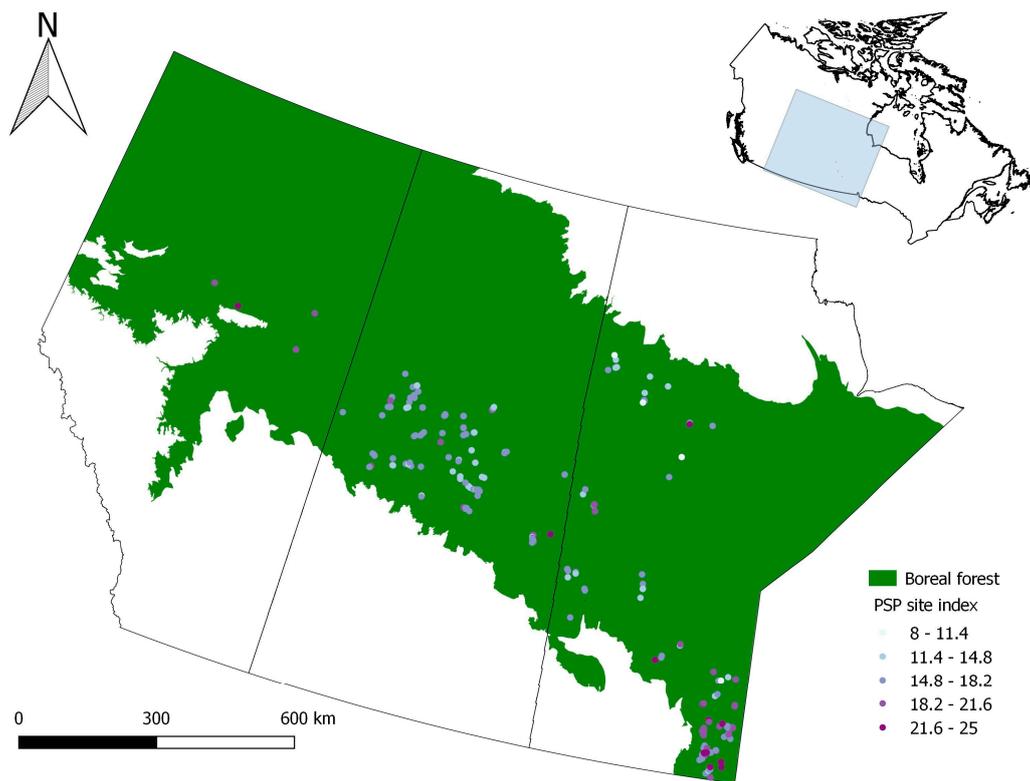
The purpose of this study was to evaluate the effects of competition on the growth and mortality of jack pine in the boreal forest of Western Canada. For this purpose, we use data from 422 remeasured PSPs to build (1) models of height and diameter growth; and (2) models of survival probability. Model predictions are validated against independent data as part of a system of equations implemented in the MGM in order to assess the ecological viability, accuracy and precision of MGM predictions.

## 2. Materials and Methods

### 2.1. Study Area and Description of Datasets

The data used for this study covered a large area across the western Canadian boreal forest (Figure 1), with 422 permanent sample plots located in the provinces of Alberta, Saskatchewan and Manitoba. The mean annual temperature at the plot locations ranged from  $-3.2$  °C to  $2.1$  °C and mean annual precipitation from 410 to 537 mm/year (ClimateNA: <http://tinyurl.com/ClimateNA> accessed on 25 February 2015). Plot size varied from  $27.8$  m<sup>2</sup> to  $1500$  m<sup>2</sup>, depending on source and year of measurement. PSP data was provided by Alberta Agriculture and Forestry (AAF), Saskatchewan Ministry of Environment and Manitoba Provincial Government. Information on plot design, measurement protocols, and plot history can be found in Alberta Environment and Sustainable Resource Development (AESRD) [31] and AESRD [32] for the plots in Alberta, in Teco Natural Resource Group Limited [33] for the plots in Saskatchewan, and in Vyvere [34] for the plots in Manitoba.

The data from the three sources were combined into a single dataset and plots were carefully reviewed to determine their suitability. In order to be selected for analysis, a plot had to be measured at least twice and include jack pine trees. Selected plots include a variety of stand types (structure and species mixtures) and various stand ages (juvenile, mid-rotation and mature) (Table 1).



**Figure 1.** Permanent sample plot location by jack pine site index in the Canadian provinces of Alberta, Saskatchewan and Manitoba.

**Table 1.** Summary of data used in the study with tree and stand variables.

Variable	Units	Mean	Std. Dev.	Minimum	Maximum
Jack pine diameter at breast height (DBH)	cm	10.67	6.14	0.20	58.50
Jack pine height	m	10.65	5.17	1.30	31.60
Jack Pine DBH increment	cm/year	0.14	0.14	−0.2	1.16
Jack Pine height increment	m/year	0.19	0.19	−0.4	1.2
Measurement interval	years	6.33	3.37	2.00	36.00
Jack Pine Mortality	% trees dead/plot	14%	17.8%	0.8%	100%
Number of plot remeasurements		1.78	0.93	1.00	5.00
Site Index	m	16.53	2.78	7.73	25.69
Stand age	years	54.17	24.84	6.00	154.00
Coniferous density	tph	2587.58	5098.28	12.36	75,184.96
Deciduous density	tph	230.86	679.44	0.00	12,230.00
Coniferous Avg DBH	cm	13.30	5.35	0.63	35.50
Deciduous Avg DBH	cm	5.99	7.42	0.00	37.80
Coniferous Avg Height	m	12.52	4.31	1.50	23.49
Deciduous Avg Height	m	6.15	7.01	0.00	27.30
Coniferous basal area	m <sup>2</sup> /ha	21.22	9.66	0.10	47.44
Deciduous basal area	m <sup>2</sup> /ha	2.06	5.26	0.00	38.35
Stand Quadratic Mean Diameter (QMD)	cm	13.59	5.17	0.71	32.11
Stand volume	m <sup>3</sup> /ha	148.98	88.13	0.54	450.14
Stand Basal area	m <sup>2</sup> /ha	23.28	9.50	0.55	48.63
Stand Density	tph	2783.42	5155.72	125.00	76,584.68

Diameter at breast height (DBH) was used as the response variable for the diameter growth model. For the height growth model, only trees with measured heights were used, excluding any trees with estimated or interpolated heights. All trees were included in the calculation of stand level variables. There were 7785 tree mortality events recorded in our dataset.

Prior to model building, 10% of the available plots were randomly removed from the dataset to provide independent data for model validation. Prior to selection of this validation dataset, the data

were stratified by age class (younger than 40 years, between 40 and 80 years and older than 80 years) and stand composition (jack pine basal area more than 80% of stand basal area and less than 80% of stand basal area). The independent validation plots were randomly selected from within each of the resulting six groups.

## 2.2. Diameter Growth Model

To develop the diameter growth model, we used the potential-modifier approach [35,36], in which the potential diameter growth was first estimated and then adjusted by a reduction factor to estimate growth. We used this approach as it is a common method used in growth modelling and in order to remain consistent with previous modelling of other species in the MGM. The potential DBH increment of the stand was calculated as the average DBH increment of the thickest 100 trees/ha. The reduction factor was expressed as a negative exponential function with a competition index represented as the sum of the DBHs of the trees with a larger DBH than the subject tree (DG). In order to account for different species competition effects on growth, the competition index was calculated separately for three species groups: deciduous (DDG), pine (PDG) and spruce/fir (SDG). Annual DBH increment was calculated as the diameter difference between two points in time divided by the period length.

The final form of the DBH growth equation was:

$$DI_{ijk} = Pot DI_{ik} * e^{-(d+d_i+d_{i,j})*DDG/10^5 - (p+p_i+p_{i,j})*PDG/10^5 - (s+s_i+s_{i,j})*SDG/10^5} + \varepsilon_{ijk} \quad (1)$$

where  $DI_{ijk}$  is the DBH increment in the  $i$ th plot, of the  $j$ th tree for the  $k$ th measurement;  $Pot DI_{ik}$  is the potential DBH increment; DDG, PDG and SDG are competition indices;  $d, p, s$  are the fixed effects associated with  $d_i, p_i, s_i$  as the plot level random effects assumed to be independent for different  $i$  and  $d_{i,j}, p_{i,j}, s_{i,j}$ , as the tree level random effects are assumed to be independent for different  $i$  and  $j$ ; and  $\varepsilon_{ijk}$  is the residual error and are assumed to be independent for  $i, j$  and  $k$ , and independent of random effects. The random effects were assumed to be normally distributed with  $d_i, p_i, s_i \sim N(0, \Psi_1)$  and  $d_{i,j}, p_{i,j}, s_{i,j} \sim N(0, \Psi_2)$ , where  $\Psi_1$  and  $\Psi_2$  are the variance–covariance matrices associated with the plot level random effect and tree level random effect, respectively.

## 2.3. Height Growth Model

The height increment model was also built using the potential modifier approach. The potential height increment of the stand was calculated as the average height increment of the thickest 100 trees/ha. The competition-based reduction factor used the sum of DBH greater than the subject tree for deciduous (DDG), pine (PDG) and spruce/fir (SDG). Annual height increment was calculated as the height difference between two points in time divided by the period length.

The final form for the height growth equation was:

$$HI_{ijk} = Pot HI_{ik} * e^{-(d+d_j)*DDG/10^5 - (p+p_j)*PDG/10^5 - (s+s_j)*SDG/10^5} + \varepsilon_{jk} \quad (2)$$

where  $HI_{ijk}$  is the height increment in the  $i$ th plot, of the  $j$ th tree for the  $k$ th measurement;  $Pot HI_{ik}$  is the height increment; DDG, PDG and SDG are competition indices;  $d, p, s$  are the fixed effects associated with  $d_j, p_j, s_j$  as the tree level random effects assumed to be independent for different  $j$ ; and  $\varepsilon_{jk}$  is the residual error and is assumed to be independent for  $j$  and  $k$ , and independent of random effects. The random effects were assumed to be normally distributed as  $d_i, p_i, s_i \sim N(0, \Psi_1)$  where  $\Psi_1$  is the variance–covariance matrix associated with the tree level random effect.

## 2.4. Statistical Fitting of Growth Models

We used a non-linear mixed modelling approach to fit the growth equations as the data had a hierarchical (trees within plots) and correlated (repeated measure of the same tree) error structure. For diameter increment, both tree and plot were considered as random effects, meaning that the

competition indices had a fixed component and a random component at both plot and tree level. For HI, only the tree level was used as a random effect as convergence could not be achieved with random effects at both tree and plot level. A diagonal variance–covariance structure was associated with the plot and tree random effects, which assumed independence among different grouping levels. In addition, an error correlation structure (compound symmetry) was used in the development of both models, considering the fact that measurements were taken repeatedly, at equal and unequal intervals. Structure search was based on the minimum Akaike Information Criterion (AIC) [37]. We used the *nlme* package version 3.1–108 [38] of the R statistical platform software [39] in order to fit, modify and assess the growth models.

## 2.5. Mortality Model

### 2.5.1. Variable Selection

In order to obtain a biologically meaningful model, we considered both tree- and stand-based variables as potential predictor variables for survival probability. Tree-based variables included in the final model were DBH [40] and DBH increment, both being variables commonly used in other mortality studies [41]. Furthermore, we used  $DBH^2$  to account for U-shape mortality pattern which is high in juvenile and old trees, but low in adult trees [40].

At the stand level, chosen explanatory variables were the sum of basal area of the thicker trees (BAGr) as a measure of competition;  $DBH^2$ /stand basal area/ha (StBA) as a measure for tree social status in the stand; and jack pine relative composition (JPRC) as a measure of intraspecific interaction, defined as

$$JPRC = \frac{BA_{JP}}{StBA} \quad (3)$$

where  $BA_{JP}$  was defined as the total basal area per hectare for jack pine.

The last variable in the model,  $L$ , represents the length of the growth interval and was calculated as the difference between measurement years. These selected variables were assessed for significance using the likelihood ratio test [42], so that the model significance represents a combined understanding of biological processes and a statistical assessment.

### 2.5.2. Mortality Model Specification

We used logistic regression to model mortality. To account for the unequal time intervals present in our data, interval length was included in the model resulting in a generalized logistic model [43], an approach successfully applied in other studies, e.g., Yang [44], Yao [41]. However,  $L$  was included as a covariate, in order to allow for mixed effects modelling.

A generalized mixed model was used to estimate the coefficients, in order to account for the hierarchical data structure. The final form of the mortality function was:

$$Prob\ survival_{ijk} = \left[ \frac{\exp(\beta_0 + b_i + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DI + \beta_4 * JPRC + \beta_5 * \frac{DBH^2}{StBA} + \beta_6 * BA\ Gr + \beta_7 * L + \epsilon_{ij})}{1 + \exp(\beta_0 + b_i + \beta_1 * DBH + \beta_2 * DBH^2 + \beta_3 * DI + \beta_4 * JPRC + \beta_5 * \frac{DBH^2}{StBA} + \beta_6 * BA\ Gr + \beta_7 * L + \epsilon_{ij})} \right] \quad (4)$$

where  $Prob\ survival_{ijk}$  is the probability of survival of the  $j$ th tree at  $k$ th measurement in the  $i$ th plot;  $\beta_0, \beta_1, \beta_2, \beta_3, \beta_4, \beta_5, \beta_6, \beta_7$  are the fixed effects coefficients;  $b_i$  is the plot level random effect and  $\epsilon_{ij}$  is the residual error. The random effects were assumed to be normally distributed as  $b_i \sim N(0, \Psi_1)$ , where  $\Psi_1$  is the variance-covariance matrix associated with the tree level random effect.

The coefficients for the intercept were considered mixed, with both a fixed and a random component. The significance of the random effects was assessed using the likelihood ratio test, by comparing the Bayesian Information Criterion (BIC) values and analyzing the ratio between the estimated random-effect standard deviation and the associated estimate of the fixed effect [37]. Package *lme4* version 1.0–4 [45] in R was used in order to fit, modify and evaluate the mortality model.

The commonly used Hosmer–Lemeshow test for evaluating the goodness of fit of a logistic regression was not suitable for our data as it contained over 25,000 observations (Paul, Pennell, and Lemeshow, 2013). Instead, we used the Receiver Operating Curve (ROC), which plots the proportion of true positives (events predicted to be events) versus the proportion of false positives (nonevents predicted to be events). The area under the curve is given by the  $c$  statistic, with any value greater than 0.5 showing a better than random discrimination. We applied the  $c$  statistic as a goodness of fit measure, using the R package *hmeasure* version 1.0 [46].

## 2.6. Validation Methods and Metrics

The fixed effects component of the developed growth and mortality models was implemented in the MGM. Using the independent validation dataset, we initialized the MGM with the first plot measurement and then projected the tree-list to the final re-measurement. The average projection interval was 18.2 years (min 5 years/maximum 36 years). The observed stand conditions were then evaluated against the MGM predictions. In order to determine potential height and DBH increment, the MGM uses SI as an input variable that measures site productivity [28]. In Alberta, SI was calculated according to Huang [47] and in Saskatchewan and Manitoba according to Cieszewski [48].

The models were validated at both tree and stand level. At the tree level, jack pine tree height (m) and DBH (cm) were used for validation, while at the stand level the model was validated for the following outputs: DBH increment (cm/year), height increment (m/year), stand volume ( $\text{m}^3\text{ha}^{-1}$ ), basal area ( $\text{m}^2\text{ha}^{-1}$ ), average DBH (cm), average height (m), top and height (m). Stand density ( $\text{trees ha}^{-1}$ ) was also examined as a basis for evaluating stand mortality. Top height was defined as the average height of the thickest 100 trees  $\text{ha}^{-1}$  of each species group. There were no removals over the projection periods and ingrowth was not included.

To assess the validity of the predictions, both graphical methods (plots of the observed ( $Y$ ) versus predicted ( $\hat{Y}$ )) and statistical metrics were used. As statistical measures, we calculated average model bias (AMB), relative model bias in percentage (RMB) and efficiency (EF) [49]. Average model bias represents the average of the residual errors and was computed using the following formula:

$$AMB = \frac{1}{n} \sum (Y_i - \hat{Y}_i) \quad (5)$$

where  $Y_i$ ,  $\hat{Y}_i$  are defined above, and  $n$  is the total number of observations.

The relative model bias (RMB) relates AMB to the observed mean estimator and is expressed as a percentage value, providing an indication of the magnitude of the AMB. It is calculated using the following formula:

$$RMB = \left( \frac{1}{n} \sum (Y_i - \hat{Y}_i) / \bar{Y} \right) \times 100 \quad (6)$$

where  $\bar{Y}$  is the average of the observed values.

Efficiency is a dimensionless statistic that relates the model predictions to the observed data in a manner similar to that of the coefficient of determination ( $R^2$ ), and is described by:

$$EF = 1 - \frac{\sum (Y_i - \hat{Y}_i)^2}{\sum (Y_i - \bar{Y}_i)^2} \quad (7)$$

where the variables are as defined in formulas [5,6]. The efficiency statistic has a theoretical upper bound of 1 indicating a perfect model fit, with a value of 0 indicating the model is no better than the mean.

### 3. Results

#### 3.1. DBH and Height Increment

Parameter estimates and asymptotic standard errors were obtained for both DBH and height increment models (Table 2). In the final DBH increment model, all fixed effects for the competition indices of the three species groups (deciduous, pine, spruce-fir) were highly significant ( $p < 0.01$ ) according to the conditional  $t$ -test.

**Table 2.** Estimated fixed effects coefficients and standard error for DBH and height increment models (with and without a specified correlation structure). The variables are represented by the sum of the DBHs of the deciduous trees (DDG), pine trees (PDG) and spruce-fir trees (SDG) with a larger DBH than the subject tree.

	Variable	Parameter (Degrees of Freedom)	No Correlation Structure		Correlation Structure	
			Estimate	SE	Estimate	SE
Diameter at breast height (DBH) increment		Rho	Not used		0.1554	
	DDG	d (42817)	6.2791	10.800	6.1838	10.900
	PDG	p (42817)	4.9404	0.1640	5.0129	0.16500
	SDG	s (42817)	36.324	4.2700	35.929	4.2400
Height increment		Rho	Not used		−0.06087	
	DDG	d (40404)	7.4728	0.40100	7.5410	0.39500
	PDG	p (40404)	3.0850	0.018900	3.0890	0.018600
	SDG	s (40404)	5.1236	0.43300	4.8842	0.42000

All random effects were retained in the DBH increment model, as the ratio of the random effect standard deviation (Table 3) to the associated fixed effect estimate was relatively high, indicating their importance in the model [37]. This was further supported by the likelihood ratio test, which indicated that the random effects for deciduous, pine and spruce-fir competition indices were significant.

**Table 3.** Estimated random effects standard deviation for the DBH (Diameter at breast height) increment model (plot and tree level) and for the height increment model (tree level).

	Variable	Random Effect	Standard Deviation
DBH increment	<b>Plot level</b>		
	DDG (deciduous trees)	$\sigma_1$	6.59
	PDG (pine trees)	$\sigma_1$	1.42
	SDG (spruce-fir trees)	$\sigma_1$	5.68
	<b>Tree level</b>		
	DDG	$\sigma_2$	122
	PDG	$\sigma_2$	2.63
	SDG	$\sigma_2$	40.8
		Residual	6850
Height increment	<b>Tree level</b>		
	DDG	$\sigma$	5.49
	PDG	$\sigma$	1.25
	SDG	$\sigma$	3.23
		Residual	1480

In the case of height increment, the fixed effects of the three competition indices were found to be significant, as indicated by the  $p$ -values of the conditional  $t$ -test ( $<0.05$ ). Random effects were

also significant and included in the model as their standard deviation was large in comparison to the associated fixed effects (Table 3).

Based on the AIC and BIC comparisons, the best correlation structure was compound symmetry (Table 2). Both growth models were tested for significant difference between the model with correlation structure and without correlation structure using a chi-square test. In both cases, the models were significantly different, with lower AIC and BIC for models with a specified correlation structure. The analysis of increment residuals in relation to maximum increment showed even spread for both models.

### 3.2. Mortality

Using the maximum likelihood method, we obtained parameter estimates and associated standard errors for all selected variables in the mortality model, as described in the methods section (Table 4). All variables listed in Table 4 were found to be significant at a 95% confidence interval using the likelihood ratio test.

**Table 4.** Parameter estimates and standard errors (SE) for the mortality model.

Variable	Estimate	SE
Intercept	−3.39488	0.649369
DBH (Diameter at breast height)	0.525338	0.016738
DBH <sup>2</sup>	−0.01791	0.000783
DBH increment	7.899263	0.280795
StComp	3.700769	0.632396
DBH <sup>2</sup> /StBA	0.044852	0.015472
BA greater	−0.00547	0.000235
L	−0.08825	0.009757

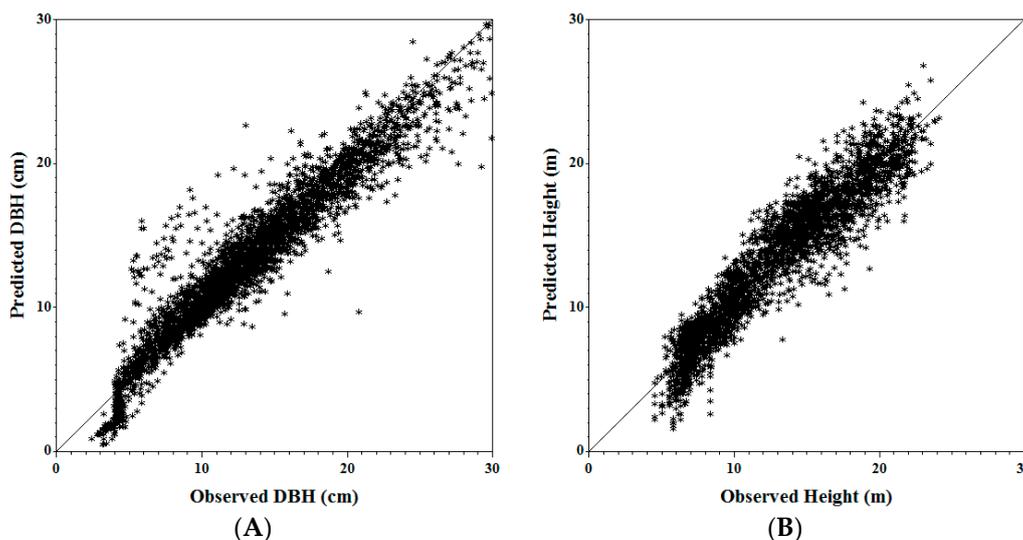
The final mortality model was built having mixed coefficients for the intercept, with a random coefficient  $b_i$  for within-plot variance. The large ratio of the random effect standard deviation (2.578) to the associated estimate of the fixed effects (−3.395) and the improved model fit (lower BIC) indicates the importance of the random effect. Adding random effects at the tree level did not produce a significantly different model and did not improve the BIC and therefore these were not included in the final model.

For this model formulation and selected predictor variables, the c-statistic was found to be 0.787, which can be translated into acceptable discrimination according to Hosmer and Lemeshow [42].

### 3.3. Validation of MGM

A total of 34 plots were randomly selected for the independent validation dataset. At tree level, the summary of validation metrics for the jack pine trees is shown in Table 5. A graphical representation of predicted vs. actual DBHs and heights is presented in Figure 2. Both tree DBH and tree height are under-predicted ( $AMB > 0$ ), but the median RMB is relatively small ( $<10\%$ ). One plot has a RMB% of 42% due to a large presence of white birch. Birch is modelled in the MGM as an aspen, as the closest surrogate species; however, the two species are very different in their growth and competitive nature which results in poor model performance. DBH efficiency is relatively high (0.83), with values ranging from 0.02 to 0.98. Height efficiency is lower, with a higher spread of the data.

Figure 3 shows the predicted vs. actual plot for the DBH increment and height increment at stand level, together with the validation metrics. The RMB is under 10% for both increments and the efficiencies have lower values (0.46 for DBH and 0.38 for height).



**Figure 2.** Observed vs. predicted tree DBH (A) and tree height (B) for jack pine using validation data in the Mixedwood Growth Model (MGM).

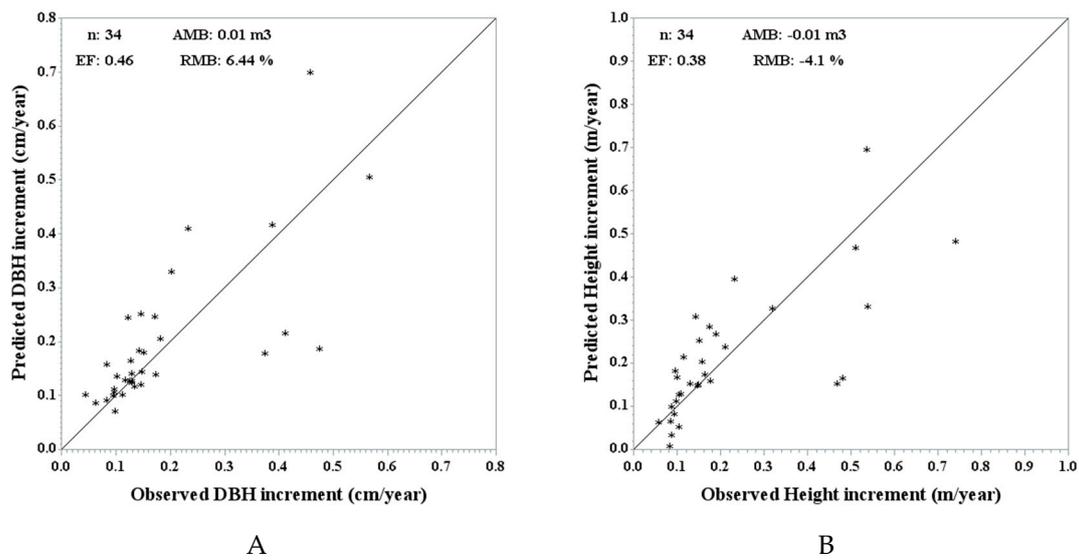
**Table 5.** Summary of the validation statistics (AMB = average mean bias in original units, RMB = relative mean bias in %, EF = efficiency) for DBH and height at the individual tree level based on the validation plot values.

		Mean	Median	Std. Dev.	Min	Max
DBH (Diameter at breast height)	AMB	0.07	0.06	1.22	−2.46	5.07
	RMB %	0.95%	0.34%	9.38%	−12.58%	42.55%
	EF	0.7	0.81	0.38	−1.15	0.98
Height	AMB	0.31	0.14	1.06	−1.94	2.73
	RMB %	1.65%	1.33%	7.86%	−21.98%	18.49%
	EF	0.05	0.25	0.7	−2.23	0.82

At stand level, Table 6 shows the actual, predicted and residual values of the analyzed variables for the entire plot, as well as for the coniferous and deciduous components. In Figure 4, predicted vs. actual stand volume/ha, average height, average DBH and density for the coniferous trees are displayed graphically. Graphs for the entire set of variables for both coniferous and deciduous trees are provided in the Supplementary material.

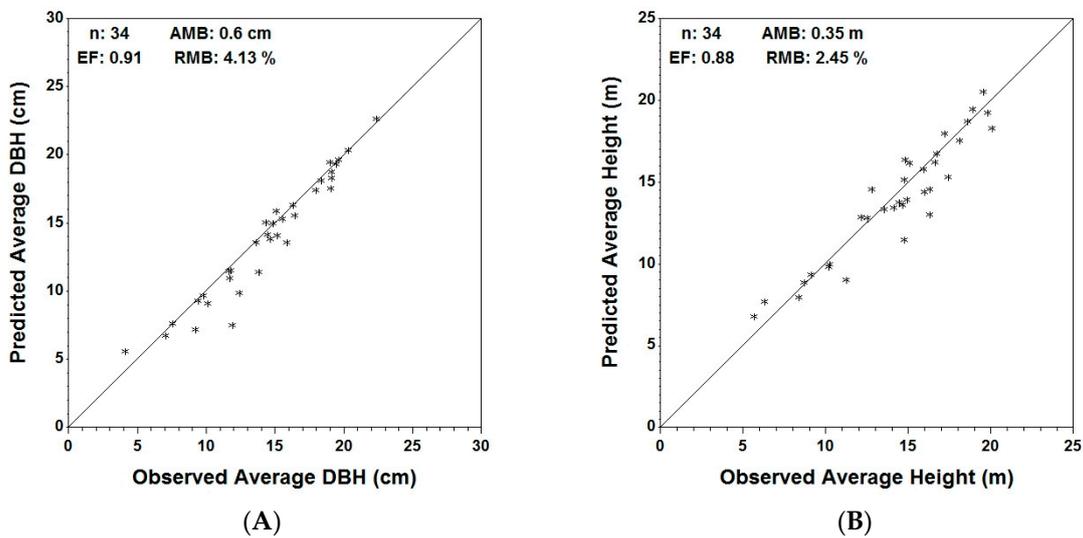
**Table 6.** Summary of actual, predicted and residual descriptive statistics for volume (m<sup>3</sup>/ha), basal area (m<sup>2</sup>/ha), average DBH (cm), average height (m), top height (m) at component level, density (tph), DBH increment (cm/year) and height increment (m/year) for the whole stand, and for coniferous and deciduous components.

		Observed				Predicted				Residuals			
		Mean	Min	Max	Std. Dev.	Mean	Min	Max	Std. Dev.	Mean	Min	Max	Std. Dev.
Stand	Volume	178.83	7.69	371.15	90.41	174.12	11.15	378.04	100.12	4.71	−102.22	76.10	35.32
	BA	25.94	1.67	42.14	9.03	25.45	2.66	42.98	10.54	0.48	−12.59	14.84	5.15
	Avg DBH	14.22	4.14	22.36	4.55	13.73	5.58	22.63	4.65	0.50	−1.44	3.57	1.11
	Avg Ht	14.16	5.80	20.10	3.92	13.85	6.83	20.18	3.75	0.30	−2.40	3.31	1.34
	Density	2161.69	333.33	17,068.39	2827.84	2122.35	389.43	13,416.97	2269.25	39.35	−1833.48	3651.42	911.00
	DBH increment	0.20	0.07	0.70	0.13	0.18	0.04	0.57	0.13	0.01	−0.29	0.24	0.10
	Height increment	0.20	0	0.70	0.15	0.20	0.05	0.74	0.17	−0.01	−0.32	0.17	0.12
Coniferous	Volume	175.26	7.69	371.15	91.40	169.42	11.15	378.04	102.00	5.84	−102.22	77.96	35.81
	BA	25.21	1.67	42.02	9.20	24.49	2.66	42.98	11.03	0.72	−12.59	15.90	5.29
	Avg DBH	14.46	4.11	22.36	4.30	13.87	5.58	22.63	4.49	0.60	−1.46	4.39	1.13
	Avg Ht	14.30	5.69	20.10	3.80	13.95	6.81	20.49	3.67	0.35	−1.79	3.31	1.27
	Density	1943.19	333.33	15,449.49	2516.60	1927.69	389.43	12,167.26	2070.99	15.51	−1833.48	3282.24	741.63
	TopHt	16.58	8.38	23.09	3.81	16.12	9.50	22.86	3.69	0.47	−1.64	3.17	1.08
	Height increment	0.19	0.07	0.54	0.11	0.18	0.02	0.57	0.14	0.01	−0.42	0.22	0.11
Deciduous	Volume	8.09	0.41	31.99	8.62	10.00	1.44	34.81	9.84	−2.41	−8.83	2.89	3.13
	BA	1.64	0.09	7.46	1.91	2.05	0.26	7.68	2.25	−0.51	−3.29	0.41	0.87
	Avg DBH	11.18	3.70	20.42	5.55	13.05	5.35	20.51	5.12	−1.39	−5.35	2.60	1.93
	Avg Ht	11.67	5.64	19.33	4.38	13.21	6.14	18.65	4.02	−1.34	−4.60	1.25	1.91
	Density	218.50	0.00	3720.64	696.25	194.66	0.00	2284.73	533.85	50.66	−1325.38	1799.68	583.38
	TopHt	12.76	8.02	19.33	3.61	13.80	7.27	18.65	3.26	−0.87	−4.60	2.17	2.13
	Height increment	0.06	0	0.73	0.25	0.12	0.00	0.54	0.16	−0.02	−0.23	0.24	0.09

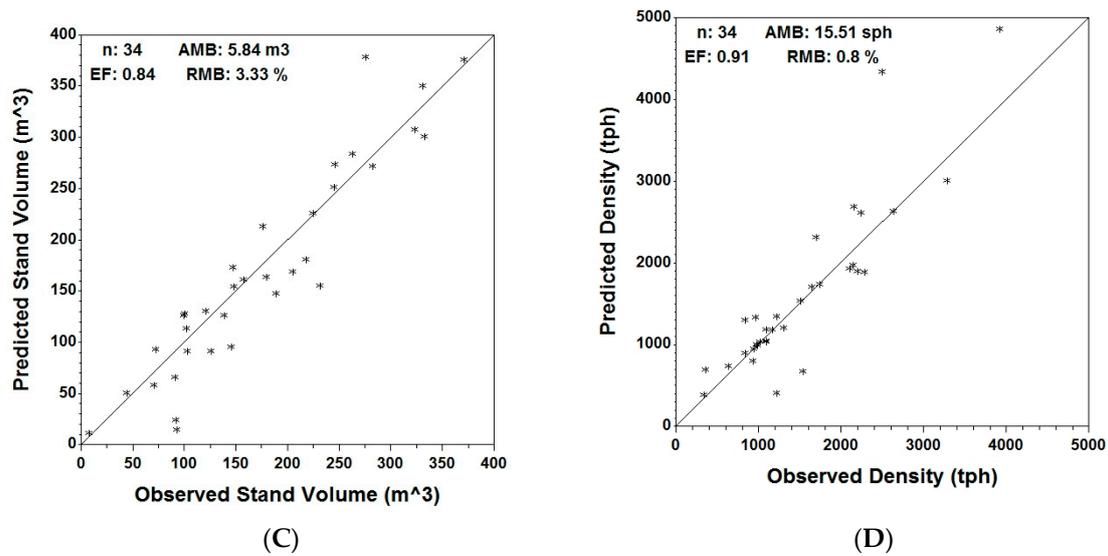


**Figure 3.** Observed vs. predicted DBH increment (A) and height increment (B) using the independent validation data and MGM stand predictions ( $n = 34$ ) with respective validation metrics: average mean bias (AMB), relative mean bias (RMB) and efficiency (EF).

Validation statistics for coniferous trees (Table 7) indicate an under-prediction ( $AMB > 0$ ) for all six variables, with the highest being average DBH ( $RMB = 4.13\%$ ) and the smallest being density ( $RMB = 0.8\%$ ). Efficiency for the coniferous component ranges between 0.66 for basal area/ha and a maximum of 0.91 for average DBH and density.



**Figure 4.** Cont.



**Figure 4.** Observed vs. predicted independent validation data ( $n = 34$ ) using MGM stand predictions for average DBH (A); average height (B); stand volume (C) and stand density (D) with respective validation metrics: average mean bias (AMB), relative mean bias (RMB) and efficiency (EF).

**Table 7.** Validation statistics (AMB = average mean bias in original units, RMB = relative mean bias in %, EF = efficiency) for the mean stand volume ( $\text{m}^3/\text{ha}$ ), stand basal area ( $\text{m}^2/\text{ha}$ ), average height (m), top height (m) average DBH (cm), density (tph), DBH increment (cm/year) and height increment (m/year) by species group component (coniferous and deciduous).

	Coniferous			Deciduous		
	AMB	RMB (%)	EF	AMB	RMB (%)	EF
Stand volume ( $\text{m}^3/\text{ha}$ )	5.84	3.33	0.84	−2.41	−29.8	0.78
Stand basal area ( $\text{m}^2/\text{ha}$ )	0.72	2.86	0.66	−0.51	31.23	0.71
Average height (m)	0.35	2.45	0.88	−1.34	−11.49	0.71
Top height (m)	0.47	2.81	0.90	−0.87	−6.84	0.59
Average DBH (cm)	0.6	4.13	0.91	−1.39	−12.42	0.81
Density (tph)	15.51	0.8	0.91	50.66	23.19	0.68
DBH increment (cm/year)	0.02	9.69	0.41	−0.04	−78.16	0.80
Height increment (m/year)	0.01	0.65	0.43	−0.02	−35.14	0.84

Unlike the prediction for conifers, there was an over-prediction of stand variables for the deciduous component, with a higher number of points lying above the 1:1 line. This was confirmed by the corresponding validation statistics, with most of the variables having a small negative AMB. Density was the only exception, which has a positive AMB of 50.66 tph for the deciduous component. In terms of efficiency, the highest value was obtained for average DBH (0.81), the lowest for top height (0.59).

## 4. Discussion

### 4.1. Ecological Significance

Jack pine is an early successional species; its strong pioneer character is mirrored in the ability to quickly regenerate on mineral soils after disturbances such as fire or management interventions. With fast early growth in the first 20 years of life [2], this species makes full use of the available light resources. As a result, jack pine is a highly shade-intolerant species. In our model, we have incorporated potential growth and competition measures that consider this silvicultural characteristic of jack pine.

The effect of inter- and intraspecific competition was incorporated in our growth models in the form of a distance-independent competition index, which has been used effectively in describing growth–competition relationships in boreal forests [36,50]. For Jack pine, Mugasha [51] showed that the distance-independent Lorimer’s index, calculated using only taller trees, was better than many other distance-dependent indices for characterizing variation in stem volume growth. In this study, we chose the sum of DBH of trees with a larger DBH than the subject tree as the competition index since it has been used successfully for other pioneer species [36]. We also tested the sum of basal area of trees larger than the subject tree, another commonly used competition index [36]. However, we rejected this index following exploratory analysis, as the AIC indicated a better fit for the DBH-based index. The sum of larger-DBH competition index is one sided and reflects only the dominant influence of light as a growth limiting factor. Nevertheless, for lodgepole pine Coates [7] stated that growth reduction is more likely to be influenced by shading rather than crowding, which should also apply to jack pine.

In the final DBH increment model, competition from the three species groups (deciduous, pine and spruce–fir) had a negative effect on pine growth, as indicated by the positive coefficients (Table 2). However, the three groups of competitors had different effect strengths, with deciduous (mainly aspen) competitors having the strongest effect and intraspecific competition having the lowest impact. Similar species-dependent competition effects were reported for lodgepole pine [7,52] and for eastern white pine [53]. This effect is likely related to species shade tolerance and stand development, with faster initial growth of aspen leading to the overtopping of the pine. As pine is a shade-intolerant species [2], the lack of light has a stronger effect on DBH growth. Spruce competition has a smaller effect on pine growth, due to its slower initial growth and with spruce remaining shorter than the pine until the stand reaches an advanced age. Results from the height growth model were similar to the DBH model, with the negative influence of competition being highest from the deciduous species group and weakest from the pine species group.

The DBH and height models have an inverse exponential form. Peak increment is achieved when a tree is competition free and decreases nonlinearly as the competition index increases. The response of predicted increment to species-specific competition is similar to the overall response, with increment decreasing in an inverse exponential way as competition increases for both growth models. Only in the case of deciduous competition, there is a short range of high competition where increment is increasing, but this is an artefact of the data, as the maximum increments are also higher. The analysis of increment residuals in relation to potential increment showed an even spread for both models.

In building the model, potential growth (measured by the increment of the thickest 100 trees/ha) was used as a measure of site productivity. In the MGM, potential growth is determined by SI, a variable that integrates many of the environmental factors that control growth. SI represents a widely accepted method for assessing site productivity [54,55] due to the ease of estimation from field observations and efficiency in growth and yield prediction. SI also has some limitations and can change with climate [55,56].

Tree mortality is a complicated process that is affected by a variety of environmental, pathological and physiological factors, as well as random events. However, tree mortality can frequently be explained by measures of tree size and growth rate, individual competition and stand density [57]. The variables selected to predict the probability of survival were DBH,  $DBH^2$ , DBH increment, jack pine relative stand composition,  $DBH^2$  divided by stand basal area, basal area greater and the time interval length. The positive coefficients for DBH and negative coefficients for  $DBH^2$  (Table 4) indicate a U-shaped mortality pattern: when trees are small (and young), they usually have relatively high mortality [58]. At this stage, DBH dominates the trend due to its higher coefficient compared with  $DBH^2$ . As trees increase in DBH, survival probability increases and becomes stable over the middle of the size range. At older stages and larger tree sizes, survival probability decreases again with  $DBH^2$  becoming dominant over DBH. This widely reported trend of increasing mortality in larger (older) trees (e.g., Cortini [59] for boreal jack pine) is caused by several factors. Old trees lose vigor due to physiological aging, increasing hydraulic resistance, decreasing leaf area, and leading to higher

maintenance respiration costs [60]. This leads to a decline in vitality and a reduced ability to survive insect attacks, diseases or climate extremes [41].

DBH increment was included in the mortality model as it is an indicator of tree vigor. The positive coefficients (Table 4) show that trees with a higher DBH increment also have a lower chance of mortality. This observation is consistent with other studies (e.g., [61]) that show diameter increment is strongly related to survival probability.

According to our model, the mortality of jack pine is lower in pure pine stands compared to mixed species stands, as indicated by the positive coefficient of relative pine stand composition (Table 4). This is likely related to the shade intolerance of pines in general, with Yao [41] reporting similar results for lodgepole pine. In mixed species stands, pine is overtopped by fast growing aspen resulting in a higher mortality.

Basal area greater (BA greater) and  $DBH^2$  divided by the stand basal area/ha ( $DBH^2/StBA$ ) are variables that measure the social status of a tree in the stand. The negative coefficient for BA greater indicates an increase in mortality as the number of trees larger than the subject tree increases. On the other hand, the probability of survival increases if the tree is situated in an upper size class (as indicated by  $DBH^2/StBA$ ). In addition,  $DBH^2/StBA$  provides a measure of the contribution of the tree to stand basal area. The last variable in the model, length of time interval (L), was used to account for unequal measurement intervals. The analysis showed that the probability of survival decreases with every year for which the tree is modelled; as the time interval increases, so does the risk of biotic or abiotic damage and the risk of mortality.

#### 4.2. Application in Forest Management

The developed growth and mortality models were successfully implemented in the MGM. At tree level, the model tends to slightly under-predict, with AMB being positive, but the bias is limited. Small dimension trees are under-predicted probably due to large variations in growth for saplings [62]. The height growth model has lower efficiency, probably due to lower precision of height measurements, as well as greater variation in height growth. There was no bias in relation to stand density or stand age. At stand level, DBH and height increment also showed a small bias, but lower efficiencies due to errors at higher increments. The model performed well for all stand variables and validation indicates that the MGM predicts stand volume/ha, stand density, average DBH and average height with a low bias. This supports the use of the MGM by forest managers in yield forecasting and management planning for pure and mixed jack pine stands in Western Canada.

### 5. Conclusions

Accurate forecasts of yield and forest stand composition over time are important for management planning, allowable cut determination and maintaining a balance of species mixture over the landscape. This study was aimed at developing deterministic growth and mortality models for jack pine using data from a large number of remeasured PSPs.

The development of the growth models was achieved using nonlinear mixed modelling to relate potential growth and competition. The mortality model was developed using a mixed logistic regression and having stand and tree level as explanatory variables. Both growth and mortality models make sense ecologically and are based on the silvicultural characteristics of jack pine, which can be used to interpret the model's estimated coefficients.

The resulting models were implemented into the MGM as part of the overall system of equations, and validated against an independent dataset. The good performance of the model predictions showed that now the MGM is able to predict with low bias variables such as stand volume, density, average DBH, and average height for stands that contain jack pine. Further refinements that can improve the MGM and expand its use in forest management in the western boreal region will likely be achieved by including climate effects in the growth and mortality functions and by refining the site index curves, with the inclusion of climate.

**Supplementary Materials:** The following are available online at [www.mdpi.com/1999-4907/8/11/410/s1](http://www.mdpi.com/1999-4907/8/11/410/s1), Figure S1: Observed vs predicted independent validation data ( $n = 34$ ) using MGM stand predictions with respective validation metrics: average mean bias (AMB), relative mean bias (RMB) and efficiency (EF).

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