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Relative size and stand age determine *Pinus banksiana* mortality

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ABSTRACT

Tree mortality is a poorly understood process in the boreal forest. While large disturbances reset succession by killing all or most trees, background tree mortality was hypothesized to be affected by competition, ageing, and stand composition. We tested these hypotheses on jack pine (*Pinus banksiana* Lamb.) mortality using data from long-term repeatedly measured permanent sample plots collected between 1952 and 1989 in Ontario, Canada. The probability of mortality over a 5-year period was modeled using logistic regression with the maximum likelihood estimation employed for parameter estimation. Relative competitiveness measured as the ratio of individual tree diameter at breast height (DBH) to mean stand DBH explained more variation in mortality than stand age did. Mortality increased rapidly with decreasing DBH ratio. A U-shaped mortality pattern with stand age was found while stand composition had no effect on mortality. Developed by using a residual sequential regression approach, our final mixed-effects model with a 81% model correctness of mortality prediction conclusively demonstrated that relative competitiveness is the key determinant for jack pine mortality.

1. Introduction

Tree mortality is a critical, but poorly understood ecological process that affects stand composition, structure, and productivity through succession (Mencuccini et al., 2005; Lutz and Halpern, 2006; van Mantgem and Stephenson, 2007). The pattern and causes of tree mortality vary greatly at different spatial scales. Catastrophic wildfires and insect outbreaks reset forest succession at large spatial scales (Turner et al., 1997; Bouchard et al., 2006). In contrast, background tree mortality occurs at a small, local scale as a consequence of competition (Kenkel, 1988) or gap forming related to ageing, diseases, or small-scale wind or snow damage (Kneeshaw and Bergeron, 1998; Hill et al., 2005).

We hypothesize that there are three key factors controlling background tree mortality: relative competitiveness, longevity, and stand composition. First, we hypothesize that relative competitiveness of a tree determines its probability of mortality, as competitive ability of an individual for resources in a community determines its fitness in succession (Tilman, 1982). The direct causes of mortality may include frictional interaction and localized resource limitation (Newton, 2006). Relative competitiveness for resources can be measured as a ratio of the diameter of the subject tree to the average diameter of the stand. This ratio has been found to be a significant predictor for tree mortality (Monserud, 1976; Monserud and Sterba, 1999; Yang et al., 2003). Second, we hypothesize mortality increases with stand age because individual trees will eventually die due to longevity and increased susceptibility to non-stand replacing disturbances (Chen and Popadiouk, 2002; Busing, 2005). Third, given that different species may have different resource requirements (Callaway and Walker, 1997; Michalet et al., 2006), we hypothesize that mortality will be lowest in mixedwood stands because temporal niche separation between deciduous and evergreen species may produce a positive effect on tree survival of component species.

Jack pine (*Pinus banksiana* Lamb.) is one of the primary commercial tree species in the boreal forest of North America. Because of its importance, a long history of jack pine growth and yield modeling exists. Early work included normal yield tables (Kabzems and Kirby, 1956; Plonski, 1960), in which tree mortality rates are assumed to be consistent through stand development. Hegyi (1971) built the first jack pine stand simulation model, in which mortality was modeled by matching the assumed rate in the normal yield table and allocated to trees with the largest inter-tree competition indices (80%) and randomly (20%). Buchman et al. (1983) were the first to model jack pine mortality (survival, actually) using a formulation akin to a gamma function of survival with diameter and diameter growth rate as predictors. Currently, both the

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STEMS and TWIGS stand simulators used the Buchman et al. (1983) species-specific survival equations to model stand dynamics in the Lake States (Brand et al., 1988), as did the initial Lake States variant of the Forest Vegetation Simulator (FVS) (Bush and Brand, 1995). However, the current Lake States FVS variant instead uses the mortality formulation of Wykoff et al. (1982), which models background mortality as a logistic function of diameter and a density-dependent multiplier that is a function of relative height (height/top height). Lacerte et al. (2006) modeled survival for jack pine in Ontario as a function of diameter, diameter growth, and basal area in larger trees. Conversely, Woodall et al. (2005) used methods from medical survival analysis (Cox and Oakes, 1984) to estimate a hazard function for jack pine. They used diameter growth as a surrogate for time, and included crown ratio, stand basal area, basal area in larger trees, and crown class as covariates.

Our objectives for this study were (1) to improve understanding of the factors that control jack pine tree mortality process through testing above-mentioned hypotheses and (2) to develop a jack pine tree mortality model to compliment the need for developing individual tree-based yield and succession models. We used data from repeatedly measured permanent sample plots to help accomplish these objectives.

2. Materials and methods

2.1. The data

The data for this study came from a database of permanent sample plots, each 0.0578 ha (1/7 acres) in area, established from 1952 to 1965, and repeatedly measured on varying intervals by Kimberly Clark of Canada. These plots were near the town of Longlac, Ontario (49°47′N, 86°33′W). The study area is located in the eastern–central part of Canadian Boreal Shield. Mean annual temperature is 1.3 °C and mean annual precipitation 831 mm, of which 313 mm is snow (Environment Canada, 2005). This is a largely forested, glacial region, with little topographic relief, interspersed with lakes, rivers, marshes, and bogs. Forest soils originate from a variety of modes of glacial deposition, including tills, glaciofluvial, glaciolacustrine, and organic deposits. Dominant tree species with increasing shade tolerance include trembling aspen (*Populus tremuloides* Michx.), jack pine, balsam popular (*Populus balsamifera* L.), white birch (*Betula papyrifera* Britt.), black spruce (*Picea mariana* (Mill.) BSP), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), and eastern white cedar (*Thuja occidentalis* L.). Other infrequently occurring species include tamarack (*Larix laricina* (Du Roi) K. Koch) and willows (*Salix* spp.).

In this study, we used plots that had jack pine trees with measurements occurring in 5-year sequential intervals and at least five sequential remeasurements (25-year span) because longer (>10 years) sampling periods are preferred for a good representation of individual tree mortality (Monserud and Sterba, 1999; Eid and Tuhus, 2001). Consequently, 42 plots were selected from the database. All selected plots were allocated on relatively dry to fresh, upland sites. The data collected at each plot included: diameter at breast height (DBH at 1.3 m above ground) and age of stand (Table 1). All selected stands originated from wildfire with stand age ranging from 34 to 159 years since fire. Stand basal area averaged 33 m^2/ha, ranging from 17 to 48 m^2/ha. DBH averaged 16 cm for live trees, ranging from 2 to 36 cm, and 10 cm for dead trees, ranging from 2 to 30 cm (Table 1).

Table 1
Summary statistics for data used in model development

Variable	Live trees (n = 14797)			Dead trees (n = 1235)		
	Mean	Min.	Max.	Mean	Min.	Max.
Tree DBH (cm)	16.19	2	36	9.99	2	30
Stand DBH (cm)	13.07	7.65	20.79	11.67	7.65	20.56
DBH ratio (R_D)	1.29	0.20	3.49	0.88	0.18	2.44
Stand basal area (m^2/ha)	33.67	17.05	48.09	32.91	17.05	48.09
Stand Age (years)	79.71	34	159	72.43	34	154

All trees were tagged and recorded either dead or alive at each measurement. If a tree was observed to be dead at a given measurement, it would mean that death occurred during the 5-year interval. In total, live trees had 14797 counts and dead trees had 1235.

2.2. Exploratory variables

Selection of explanatory variables was based on our hypotheses that competition, senescence due to ageing and susceptibility to non-stand replacing disturbances, and species association are related to tree size, stand age, and stand type, respectively. Tree size is related to its competitiveness to resource availability, particularly light availability and growing space (Grace and Tilman, 1990; Chen et al., 1996; Newton, 2006). In this study, we used the ratio of subject tree's DBH to the mean DBH of the stand (R_D) as a measure of relative competitiveness. Similar to other studies (Monserud and Sterba, 1999; Yao et al., 2001; Yang et al., 2003), D, D^{-1}, D^2, R_D, $R_D{}^{-1}$, and $R_D{}^2$ were used as predictors to include possible curvilinear relationships between mortality and tree size for both relatively small and relatively large trees.

We expected that stand age (A) would explain additional variation in tree mortality, particularly longevity related senescence for jack pine. A second age variable was calculated (A^2) to account for possible curvilinear mortality response to increasing age. Stand composition was analyzed as percentage of jack pine as well as stand type. Both approaches produced the same results. We report the results using stand type. Stand type was classified into

Table 2
Selection and diagnostics for logistic regression models for jack pine mortality

Model	Model terms	l	k	AIC	ROC	R^2
[1] Null	Intercept only (β_0)	4352	1	8706	NA	NA
[2] Relative size	$R_D + R_D{}^2 + 1/R_D$	3300	4	6608	0.844	0.294
[3] Absolute size	$D + D^2$	3490	3	6986	0.811	0.244
[4] Tree size	$R_D + R_D{}^2 + 1/R_D + D'$	3236	5	6484	0.851	0.309
[5] Age	$A + A^2$	4263	3	8531	0.608	0.027
[6] Stand type	ST$	4350	3	8706	0.514	0.001
[7] Size and age	$R_D + R_D{}^2 + 1/R_D + D' + A'$	3225	6	6462	0.855	0.315
[8] Final[a]	$R_D + R_D{}^2 + 1/R_D + D' + A'$ + plot	3009	48	6116	0.881	0.368

Note: Abbreviations are l, the negative of the log-likelihood from maximum-likelihood estimation; k, the number of parameters estimated in the model; ROC, receiver operating characteristics; NA, not available. R_D – ratio of tree to stand average DBH, D – DBH (cm), A – stand age (years), ST$ – stand type (pure, mixed, or other), $D' = D - 4.1046 - 9.438 \times R_D$, $A' = A - 25.907 - 3.2839 \times D$.

[a] Standard deviation for plot = 1.94.

Table 3
Maximum-likelihood estimate and their standard errors for each term in model [8] (see Table 2)

Term	β	Standard error	ΔAIC
Intercept	8.556	0.936	
R_D	−13.662	0.959	131
$1/R_D$	−1.459	0.237	33
R_D^2	3.333	0.320	64
D'	0.158	0.049	8
A'	0.044	0.005	67
Random effect: plot	NA	NA	

Note: ΔAIC is the increase of AIC when each term is removed from the model [8].

three categories: pine dominant (P), mixed species (M), and other species dominant (O). Pine dominated stands are characterized by populations composed of 67–100% pine trees by basal area, mixed stands are composed of 34–66% pine trees, and other species dominated stands have 0–33% pine trees.

2.3. Analysis

We used logistic regression analysis to test a series of hypotheses for the independent influence by absolute tree size (measured by D), competition (measured by R_D), stand age (A), and stand type on tree mortality. The forward and backward stepwise selection procedures with the critical $\alpha = 0.05$ were used to determine the best model individually for tree size, stand age, and stand type. We considered that the best model had the highest R^2 while all selected variables were significant. To determine the best overall model that includes all significant predictors, we assessed the collinearity between tree size, stand age, and stand type. Given that there was a significant correlation between D and R_D ($r = 0.62$) and between D and A ($r = 0.56$), we used the residual and sequential approach (Graham, 2003) to disentangle shared contributions from R_D, D, and A by assuming functional importance is in a decreasing order of R_D, D, and A. This assumption was validated by their relative importance (Table 2), which was assessed by comparing the variation explained by each model using Akaike's Information Criterion (AIC) scores and Nagelkerke R^2 (Nagelkerke, 1991). Independence between transformed D' and R_D was achieved by transferring $D' = D - 4.1046 - 9.438 \times R_D$ and that between A' and D by transferring $A' = A - 25.907 - 3.2839 \times D$ (see Graham, 2003).

Because data are longitudinal, a mixed-effects model was developed by including a random effect to describe variation of the intercept for plot (Tables 2 and 3). Model goodness-of-fits were assessed by the area under the Receiver Operating Characteristic (ROC) curve (Hosmer and Lemeshow, 2000). A logistic model is considered excellent in discrimination when the area under ROC is ≥0.8 (Hosmer and Lemeshow, 2000). Because the model delivers a continuous probability of mortality for each tree, it was necessary to determine a probability threshold whereby a tree will either survive or die. For the purpose of classification, we determined an "optimal" choice for the cutpoint where the sensitivity and specificity curves crossed (Hosmer and Lemeshow, 2000). All statistical tests were performed with logit regression in SYSTAT 12 (SYSTAT, 2007).

3. Results

Jack pine mortality was affected significantly by relative tree size, absolute tree size, and stand age ($P < 0.001$) (Table 2). Among the three factors tested, tree size was the most significant variable in affecting tree mortality. Of the two measures of tree size, relative tree size (R_D) had a smaller AIC and bigger R^2 than absolute size (D)

Table 4
Deciles of risk for the observed and predicted dead and live trees by probability class predicted by model [8] in Table 3

Probability class	Dead		Live	
	Observed	Predicted	Observed	Predicted
<0.1	274	303	12428	12399
0.1–0.2	242	219	1307	1330
0.2–0.3	173	155	464	482
0.3–0.4	119	132	264	251
0.4–0.5	133	131	165	167
0.5–0.6	112	115	97	94
0.6–0.7	85	80	40	45
0.7–0.8	73	72	23	24
0.8–0.9	18	20	6	4
0.9–1.0	6	8	3	1

(Table 2). Mortality showed a negative exponential decline with R_D (Fig. 1A), which was accounted by R_D, R_D^2, and $1/R_D$ in model [2]. Absolute tree size (D) was also a significant predictor for mortality (model [3] in Table 2). In addition to the shared contributions with R_D, absolute size D′ decreased AIC by 124 in the tree size model [4] from model [2].

Stand age was a significant predictor ($P < 0.001$, model [5], Fig. 1B) while stand type had an insignificant effect on jack pine mortality ($P = 0.06$, model [6]). The change in AIC from the null

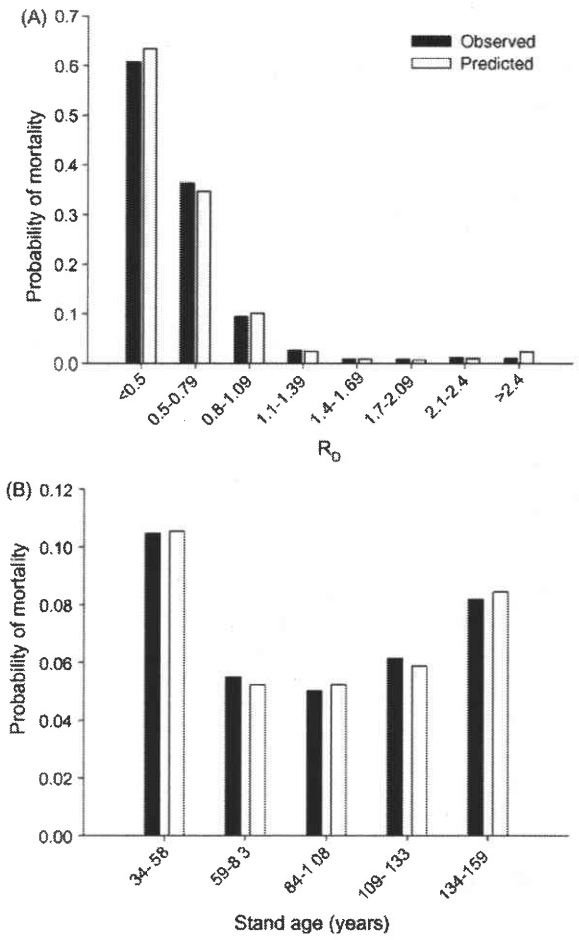

Fig. 1. Observed and predicted probability of jack pine 5-year mortality by (A) the ratio of tree to stand average DBH (R_D) and (B) stand age (years).

model was 175 for stand age and <1 for stand type (Table 2). Stand type was excluded using backward stepwise procedure, resulting in the fixed-effects model [7] and the final mixed-effects model [8].

In the final mixed-effects model [8] (Table 3), the three terms for R_D accounted for ΔAIC = 228. Apart from shared contributions, D' accounted for ΔAIC = 8 and A' accounted for ΔAIC = 67, both positively related to mortality, indicating increased mortality with absolute size and stand age (Fig. 1B).

All models except [5,6] had a ROC ≥0.8. Using model [8], we determined the "optimal" cutpoint for predicted probability of 5-year mortality to be 0.0855 where the sensitivity and specificity curves crossed at 0.811, i.e., 81.1% correctness in classifying both death and live trees. The correctness was constant through the range of R_D and stand ages (Fig. 1A and B). Deciles of risk analysis indicated that the model [8] provided similar correctness in each probability class and between live and dead trees (Table 4).

4. Discussion

Our competition hypothesis is supported by the significant contribution of relative tree size to tree mortality. Probability of mortality was very high when $R_D < 0.5$ and it declined sharply for trees bigger than the stand average ($R_D > 1$). The significant effect of relative diameter on the probability of mortality may reflect the shade intolerant nature of jack pine as survivorship of shade intolerant species is largely determined by light availability (Kenkel, 1988; Chen, 1997). The significant contributions of $1/R_D$ and R_D^2 confirm a curvilinear relationship between tree mortality and relative tree size. Similar findings have been reported on other tree species (Monserud and Sterba, 1999; Yao et al., 2001; Yang et al., 2003). Our finding on the effect of an individual's relative size on its competitiveness, and its eventual survivorship, is consistent with density-dependent mortality patterns as predicted by self-thinning theory (Newton, 2006).

The significant effects of stand age and absolute tree size support our hypothesis that mortality is higher on older stands due to senescence. The U-shaped pattern of mortality with stand age (Fig. 1B) indicates mortality was also high when stands were young. A similar pattern was found by Monserud and Sterba (1999) for *Picea abies* in Austria. However, many studies are unable to detect senescence of older trees (Eid and Tuhus, 2001), including Monserud and Sterba (1999) for the non-*Picea abies* species in Austria. One drawback to the dataset used in this study was that the youngest stand was 34 years old. Had younger stands been available, it is expected that mortality would have been even higher for the earliest age classes (Kenkel, 1988; Lutz and Halpern, 2006), which would exhibit more complete mortality behavior through the stem exclusion phase.

Our data do not support the hypothesis that the presence of other species reduces jack pine mortality. Yao et al. (2001) reported the survival of both trembling aspen and lodgepole pine (*Pinus contorta* Dougl. ex Loud) was greater in pure than in mixedwood stands while that of white spruce did not differ with stand type. These authors attributed the negative effects of mixtures on survival to potentially less favorable growing conditions in mixedwoods than respective pure stands. Interactive effects between tree species can vary greatly between species and their growing environment (Michalet et al., 2006; Hooper et al., 2005; Yachi and Loreau, 2007; Partel et al., 2007). Many high-latitude studies have not found positive mixture effects on respective tree species or overall stand productivity (e.g., Chen and Klinka, 2003; Chen et al., 2003; Brassard et al., 2008). The insignificant effect of stand type on jack pine tree mortality may suggest a trade-off between shading over top from faster-growing aspen trees (a negative effect) and temporal niche separation and nutrient facilitation of aspen litters on soil (positive effects).

In comparison with previous tree mortality models, this study attempted to explicitly test the effects of competition, stand aging, and stand type on tree mortality. We conclude, for the range of data in our study, relative competitiveness is the most important factor in determining the fate of a tree while stand age becomes an important factor influencing mortality when stands are >133 years of age. This methodology, including the mixed-model approach, is proved to be successful, as can be seen from the high level of correctness in mortality predictions (Table 4).

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