Competition, species interaction and ageing control tree mortality in boreal forests

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Summary

1. Tree mortality has important influences on forest structure and composition, but the mechanisms that cause tree mortality are not well understood. Asymmetric competition is known to be a dominant cause of plant mortality, but this idea has not received much attention in studies of long-lived trees.

2. We hypothesised that while tree mortality is dependent on size relative to neighbours as a result of asymmetric competition, tree mortality of shade-tolerant species varies little with size because of their physiological and morphological adaptations to shaded environments. Furthermore, we hypothesised that tree mortality is higher in more crowded stands because of higher average resource competition, in conspecific stands because of potential negative intra-specific interactions, and in older stands because of the physiological limitations and susceptibility to minor disturbances of large trees.

3. Using data from repeatedly measured permanent sampling plots that covered a wide range of tree sizes, stand developmental stages and stand compositions in boreal forests, we simultaneously tested, by boosted regression tree models, the effects of an individual's relative size, stand crowding, species interaction and ageing on mortality of *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*.

4. Mortality increased strongly with decreasing relative size for all study species, and the size-dependent mortality was stronger for shade-intolerant than for shade-tolerant species. With increasing stand basal area, mortality increased for *Pinus banksiana*, *Populus tremuloides* and *Picea mariana* but decreased for *Betula papyrifera*. Mortality was higher in stands with more conspecific neighbours for *Populus tremuloides*, *Betula papyrifera* and *Picea mariana,* but was slightly lower for *Pinus banksiana*. Mortality also increased with stand age for all species. Furthermore, the size-dependent mortality was generally stronger in more crowded stands.

5. *Synthesis.* Our findings show that tree mortality over a wide range of tree sizes, stand developmental stages and stand compositions in non-equilibrium boreal forests was strongly controlled by competition, but species interactions and ageing were also important mechanisms. Furthermore, the relative importance of these mechanisms to tree mortality differed with the shade tolerance of species.

Key-words: asymmetric competition, boosted regression trees, intra-specific interaction, non-equilibrium forests, plant–plant interactions, shade tolerance, size-dependent, species traits, stand crowding, tree ageing

Introduction

Tree mortality is a critical process in forest ecosystems, influencing forest structure, composition and biodiversity (Laurance *et al.* 2004; Lutz & Halpern 2006; Phillips *et al.* 2009; Comita *et al.* 2010). The direct causes of tree mortality are generally understood to be carbon starvation caused by the

respiratory losses larger than photosynthetic production (Guneralp & Gertner 2007), failure to allocate sufficient energy to defend against disturbance agents such as pests and herbivores (Loehle 1988), or mechanical damages such as breaking, uprooting or crushing (Lutz & Halpern 2006; Larson & Franklin 2010). A major challenge for ecologists is to predict tree mortality over a wide range of environmental conditions. While the metabolic ecology theory predicts that tree mortality is scaled to −1/4 of body mass or −2/3 tree diameter in

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equilibrium forest communities, where mortality rates nearly equal fecundity rates (Brown *et al.* 2004; Enquist, West & Brown 2009), in non-equilibrium boreal and temperate forests (Chen & Popadiouk 2002; Franklin *et al.* 2002), previous studies have focused on competition-driven mortality and typically have been restricted to a limited range of stand developmental stages (e.g. Lutz & Halpern 2006) or juvenile trees such as seedlings and saplings under forest canopy (e.g. Kobe *et al.* 1995; Wyckoff & Clark 2002). Few studies have considered a wide range of tree sizes, stand developmental stages and types of stand composition to identify how multiple mechanisms such as competition, species interaction, ageing and their interactions with minor disturbances (Franklin, Shugart & Harmon 1987; Peet & Christensen 1987) affect tree mortality.

Assuming that tree mortality is a result of carbon starvation or failure to tolerate the disturbance agents, and their interactions, regardless of stand development stages, trees with relatively small sizes are expected to experience size-asymmetric competition for light and other resources, and to be more susceptibility to mechanical damages, resulting in a higher mortality (Weiner 1990; Muller-Landau *et al.* 2006; Larson & Franklin 2010). This asymmetric relationship between mortality and size may differ with species' life-history traits that affect growth, allocation, resource uptake and resource utilisation in stressed environments (Schwinning & Weiner 1998). Tree species differ in their ability to survive under shaded environments (Kobe *et al.* 1995; Wyckoff & Clark 2002) because of their variations in morphological and physiological traits. For example, the lower leaf-mass ratios, lower whole-plant respiration rates, higher plasticity in crown architecture and lower light compensation points of shade-tolerant species allow them a net carbon gain in shaded environments (Niinemets & Valladares 2006); their thicker bark and higher wood densities make them more resistant to disturbance agents (Poorter *et al.* 2010), and their higher carbohydrate storage in roots and stems leads to a quicker recovery from damages (Canham *et al.* 1999). Consequently, we hypothesise that mortality is dependent on relative size, but shade-tolerant species present less sensitivity of relative-size-dependent mortality than shade-intolerant species.

Second, stand crowding influences resource uptake, available growing space and crown development of the individual within a stand (Canham, Lepage & Coates 2004; Coates, Canham & Lepage 2009), consequently affecting tree mortality. The higher resource competition in more crowded stands also has below-ground effects because root competition influences the performance of the focal individuals (Schnitzer, Kuzee & Bongers 2005; Kueffer *et al.* 2007). Therefore, we hypothesise that individuals within more crowded stands have higher rates of mortality.

Third, intra-specific competition may be stronger than inter-specific competition because individuals of the same species may occupy the same ecological niche, e.g. resource and space. Additionally, facilitation may occur among species (Callaway 1995) by ameliorating environmental variability, altering substrate characteristics or improving resource use efficiency through mycorrhizal networks. Furthermore, the Janzen–Connell hypothesis (Janzen 1970; Connell, Tracey & Webb 1984) predicts that nearby conspecific trees reduce the focal tree's performance (i.e. survival) in the presence of host-specific pests. For example, the negative plant–soil feedback mediated by soil biota such as soil-borne fungi, bacteria and fauna may be responsible for mortality (Mangan *et al.* 2010). The individuals' performances may also be reduced by insects associated with conspecific neighbours because they may act as either an attractant or a source of the herbivores. As a result, our third hypothesis is that tree mortality is higher in stands with more conspecific individuals.

Finally, as trees age and grow in size, their physiological functions such as photosynthesis rates decline, resulting in mortality from carbon starvation or minor disturbances (Lugo & Scatena 1996). Furthermore, larger trees may have a higher risk of mortality from limitations imposed by size on water and nutrient transport to their canopy (Domec *et al.* 2008). However, the ageing-related mortality of tree species has not been adequately studied because most studies covered a small range of ages for tree species, and age information of individual trees is hard to obtain (Peet & Christensen 1987). In boreal forests, most trees are established during the stand initiation stage, they form relatively even-aged stands (Greene *et al.* 1999) and the increasing mortality rates of large trees occur at the time of stand decline (Lugo & Scatena 1996). Consequently, we hypothesise that tree mortality increases with stand age (SA) in boreal forests.

In this article, we attempt to understand how the mechanisms of competition, species interaction and ageing influence the mortality in boreal forests for four tree species with increasing shade tolerance, i.e. *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *B. papyrifera* Marsh. and *Picea mariana* Mill. Specifically, we tested our four hypotheses by using data from the repeatedly measured permanent sampling plots (PSP) from the Ontario forest inventory programme, which covers a wide range of tree sizes, stand compositions and SAs. To simultaneously test these hypotheses, we used boosted regression tree (BRT) models to disentangle the influences of relative tree size within a stand (relative basal area, RBA), stand basal area (SBA), the ratio of focal species' basal area to stand basal area (rFSBA) and SA on tree mortality.

Materials and methods

STUDY AREA AND DATA COLLECTION

The study area is located in the eastern-central part of the Canadian Boreal Shield, near the town of Longlac, Ontario, Canada (49°24′–50°10′N, 85°93′–87°24′W). Elevation ranges from 290 to 411 m a.s.l. Mean annual precipitation in 1971–2000 was ~760 mm, of which ~214 mm was snow (Geraldton A meteorological station) (Environment Canada 2005). Mean annual temperature in 1971–2000 was ~0.3 °C. This area 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. The major stand-replacing disturbance in this area is fire with an estimated average fire return interval of ~100 years (Senici *et al.* 2010).

In addition to our study species, *Populus balsamifera* L., *Picea glauca* (Moench) Voss, *Abies balsamea* (L.) Mill. and *Thuja occidentalis* L. occur as minor components in stands.

A total of 123 plots originating from stand-replacing fire, each measuring 809 m² in area, were established from 1952 to 1965 by the Kimberly–Clark Canada. These plots were located on mesic sites, the most productive segment of the boreal forest; they were established in stands (> 1 ha in area) that were visually homogeneous in structure and composition and were at least 100 m from any openings to minimise edge effects. The plots, if not damaged by fire or cutting, were re-measured until 2000 at varying, but mostly 5-year intervals. Trees larger than 2 cm in diameter at breast height (d.b.h.) were identified by species, tagged and recorded as either dead or alive at each measurement. Diameter at breast height was measured for all live trees at each census. When a plot experienced a major disturbance from fire, windthrow, outbreak of insects or cutting since its establishment, it was abandoned from further measurement.

To eliminate the effect of different measurement lengths on mortality, sample plots with measurements occurring in 5-year intervals were used. In this study, analyses were limited to *P. banksiana*, *P. tremuloides*, *B. papyrifera* and *P. mariana* because sample sizes of other species were too small to conduct a meaningful analysis. Of a total of 123 plots, 109 plots, each with 2–5 measurements, were used. The total observations for *P. banksiana*, *P. tremuloides*, *B. papyrifera* and *P. mariana* were 20 157, 5743, 2924 and 31 413 with mortality cases being 1778, 716, 217 and 2724, respectively (Table 1). The numbers of plots involved were 91, 51, 48 and 98 for *P. banksiana*, *P. tremuloides*, *B. papyrifera* and *P. mariana*, respectively (see Appendix S1 in Supporting Information). The size distribution analyses following the method by Enquist, West & Brown (2009) indicated that these stands are non-equilibrium stands (see Appendix S2).

EXPLANATORY VARIABLES

All explanatory variables were calculated using the preceding measurements of each interval. Because the realised resource uptake for individuals depends not only on individual's uptake ability but also on resource availability for individuals, we used relative size and stand crowding as proxies for these two factors. We used relative size, rather than the absolute size (i.e. d.b.h.) used in studies in equilibrium forests (Brown *et al.* 2004; Muller-Landau *et al.* 2006), because our study covered a wide range of stand developmental stages, and relative size better reflects the competitiveness of individuals when encountering other individuals in the same forest community. For example, we observed that trees with 16-cm d.b.h. were the largest in some ~38-year-old plots but were smallest in some ~100-year-old plots. The correlation between d.b.h. and height indicated that the basal area can be utilised as approximate plant biomass. Thus, we used RBA, a ratio of a subject tree's basal area to the mean tree basal area at each measurement of the stand, to represent the relative size. To examine whether d.b.h. has additional explanatory power in addition to RBA, we added d.b.h. as an additional explanatory variable to our models, and the resulted models had the same or less predictive ability (see Appendix S3). Thus, d.b.h. was not included in the final models. Stand crowding determines the average resource availability for trees within a stand. The higher stand crowding suggests fewer resources available per individual. As in other empirical studies (e.g. Coomes & Allen 2007a), we used SBA as a surrogate for stand crowding.

To take into account the effect of species interactions on mortality, we used the ratio of focal species basal area to stand basal area (rFSBA). SA was derived from the plot establishment records (Table 1).

Table 1. Summary statistics (mean ± 1 SD and range in brackets) for explanatory variables: relative basal area (RBA), stand basal area (SBA, m² ha⁻¹), ratio of focal species basal area to stand basal area (rFSBA) and stand age (SA, years). The explanatory variables were calculated based on the previous census (5 years before the observed tree's status). Stand density (STD, stems ha⁻¹) is also presented to describe stand characteristics. The summary statistics for the stand-level variables (SBA, rFSBA, SA and STD) may be identical for live and dead trees because stands may include both live and dead trees

Explanatory variable	*Pinus banksiana* Live trees n = 18 379	Dead trees n = 1778	*Populus tremuloides* Live trees n = 5027	Dead trees n = 716	*Betula papyrifera* Live trees n = 2707	Dead trees n = 217	*Picea mariana* Live trees n = 28 689	Dead trees n = 2724
RBA	1.34 ± 0.71 (0.02–9.65)	0.66 ± 0.48 (0.05–6.01)	1.21 ± 0.76 (0.02–5.70)	0.50 ± 0.42 (0.03–3.72)	0.52 ± 0.45 (0.03–3.89)	0.30 ± 0.22 (0.04–1.06)	0.89 ± 0.57 (0.01–5.28)	0.52 ± 0.42 (0.02–2.72)
SBA	34.90 ± 6.02 (16.6–53.4)	34.75 ± 6.11 (16.6–52.6)	36.43 ± 6.25 (17.6–53.4)	35.21 ± 5.88 (17.6–52.6)	37.01 ± 5.25 (20.6–50.8)	37.34 ± 5.59 (23.9–49.9)	38.13 ± 6.72 (16.6–53.4)	38.97 ± 6.41 (17.6–53.4)
rFSBA	0.76 ± 0.24 (0.002–1.00)	0.78 ± 0.24 (0.003–1.00)	0.58 ± 0.36 (0.003–1.00)	0.60 ± 0.38 (0.009–1.00)	0.13 ± 0.12 (0.001–0.38)	0.15 ± 0.12 (0.001–0.38)	0.67 ± 0.28 (0.001–1.00)	0.71 ± 0.25 (0.005–1.00)
SA	75.86 ± 28.50 (34–154)	70.78 ± 30.16 (34–154)	66.50 ± 22.96 (34–120)	56.50 ± 21.00 (34–115)	73.53 ± 24.15 (34–154)	82.55 ± 24.60 (35–154)	93.92 ± 28.20 (34–155)	96.01 ± 27.99 (34–155)
STD	2515 ± 1325 (815–6461)	2867 ± 1476 (815–6461)	2236 ± 1125 (519–6462)	2690 ± 1159 (519–5201)	2258 ± 1195 (519–5226)	1981 ± 992 (581–5226)	2732 ± 945 (581–5226)	2777 ± 924 (741–5226)

We used BRT to model the relationships between explanatory variables and the response variable. BRT combines two simple algorithms, regression trees and boosting (Elith, Leathwick & Hastie 2008). Specifically, a large number of simple trees are produced using recursive binary splits based on the value of a single predictor variable at each node that results in the two most homogeneous subsets of the response variable. Each tree is built from a random subset of the data, which is known as bagging, and introduces stochasticity to the model. The terms are fitted in a stage-wise manner by building trees from the residuals of the prior collection of trees, thereby allowing the model to put more emphasis on the points that are more difficult to classify. The resulting BRT model can be viewed as an additive regression model in which every term is a tree. More information about BRT can be found in references (De'ath 2007; Elith, Leathwick & Hastie 2008; Hastie, Tibshirani & Friedman 2008).

Boosted regression tree model was chosen for our analyses because of the following advantages. First, with a 'Bernoulli' error structure (Ridgeway 2007), BRT can be employed to analyse discrete data like ours (i.e. live trees or dead trees) (Elith, Leathwick & Hastie 2008). Second, as a tree-based method, BRT automatically takes into account interactions among variables (i.e. every successive tree node constitutes a potential interaction) and the nonlinearity between the dependent variable and the predictors, without the need of data transformation. Third, BRT is able to deal with multi-dimensionality of predictors and disentangle the effect for each variable.

There are three input settings for BRT models: tree complexity, learning rate and bagging. Tree complexity consists of the number of nodes or variable interactions in each tree. The learning rate is shrinkage parameter, and it regulates the amount of learning possible in each tree. Typically, a low learning rate, used in conjunction with a large number of trees, enables BRT to generate highly complex response functions. A fast learning rate requires fewer trees but is subject to more noise induced by the bagging and a lack of smoothness in the response functions. Bagging fraction specifies the proportion of data to be randomly sampled without replacement for sequent fitting, to introduce stochasticity into BRT models.

For each species, BRTs with a range of values for tree complexity (2, 3 and 4), learning rate (0.01, 0.005 and 0.001) and a bagging fraction 0.5 or 0.75 were fitted. To prevent over-fitting the training data, a cross-validation method was used (Hastie, Tibshirani & Friedman 2008). We used default 10-fold cross-validation procedures described by Elith, Leathwick & Hastie (2008). The model with the smallest predictive error—which represents the unexplained variation by the model—for cross-validation was considered the best model. Finally, based on the overall trend of mortality probability against each predictor, the monotonic BRT models were also fitted, using BRT settings for the best model, to facilitate the interpretation of the relationship between response variable and each predictor. The predictive performances of the monotonic BRT models were also assessed. The BRTs were computed in R 2.10.1 (R Development Core team 2009) with the '*gbm*' package using a Bernoulli error structure (Ridgeway 2007), and with *brt.functions* written by Elith, Leathwick & Hastie (2008).

We interpreted the results by examining the relative influence of predictors from the best model, the predictive value plot of response to individual predictors and the main interactions in each model (De'ath 2007; Elith, Leathwick & Hastie 2008). The relative influence of each predictor in the model was measured based on the number of times a variable is selected for splitting, weighted by the squared improvement to the model as a result of each split and averaged over all trees (Friedman & Meulman 2003). Predictive value plot of a predictor quantifies the relationship between the predictor in the model and the response variable after accounting for the effects of other predictors. Finally, we conservatively reported top-ranked interactions among predictors in each monotonically fitted model, because, first, BRT provides the relative strength of interaction rather than the absolute value provided by traditional statistical methods (e.g. *P* value in logistic regression) and second, the accommodation of outliers in BRT might introduce more noise to a best model than to a monotonically fitted model. The strength of interaction was determined following De'ath (2007) and Elith, Leathwick & Hastie (2008). Essentially, predictions were simulated from BRT using a temporary data set, which contained involved pair variables representing combinations of values at fixed intervals along each of their range, as well as other variables of their respective means. Then, the predictions were related to the marginal predictors using a linear model and fitting the marginal predictors as factors. The residual variance in this linear model indicated the relative strength of the interactions fitted by BRT.

To determine the sensitivity of the size-dependent mortality among species, we compared the regression slopes of predicted mortality probability against RBA. A greater slope indicates more sensitivity between mortality and RBA. At equal intervals of RBA, we chose 1000 data points of predicted mortality probability against RBA from each best model. Then linear regression analyses were conducted with the RBA range from the smallest value up to the value at which the predicted mortality probability became consistent. We calculated 95% confidence intervals for slopes to facilitate the comparison among species. Because *P. banksiana* had an initial increase of the marginal effect size of RBA, we developed slopes both with and without the initial increase of marginal effect size.

Results

The predictive errors of the best models were 0.427, 0.529, 0.458 and 0.489 for *P. banksiana*, *P. tremuloides*, *B. papyrifera* and *P. mariana*, respectively (Table 2); these models predicted nearly half of the observed variation in mortality. These models also had high discriminate power as indicated by the area under receiver operating characteristic curve (AUC) ≥0.78 for crossing-validation data (Table 2). The monotonically fitted models were also able to explain nearly half observed variation of response variables and had high discriminate power (Table 2). But the monotonically fitted models slightly decreased the model predictive performances, indicated by a slight increase of predictive error and a decrease of AUC.

Relative basal area was the most important variable among predictors, accounting for 81.94%, 66.93%, 45.31% and 48.81% relative influence on mortality of *P. banksiana*, *P. tremuloides*, *B. papyrifera* and *P. mariana*, respectively (Fig. 1). For all species, the predicted value plots from the fitted model indicated that, when other predictors were held constant, individuals with small RBA generally had a higher probability of mortality (Fig. 2a–d). The RBA values at which the marginal effect sizes became constant were ~1.29, ~1.29, ~1.08 and ~1.88 for *P. banksiana*, *P. tremuloides*, *B. papyrifera* and

Table 2. Optimal settings and predictive performances of boosted regression trees (BRT) analyses for *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*. The best models (BM) were determined by smallest mean predictive error for crossing-validation data (PE). CV AUC is the area under receiver operating characteristic curve (ROC) for crossing-validation data. The MFM is monotonically fitted model, using BRT settings for best model of each species

Tree species	Learning rate	Tree complexity	Bag fraction	Number of trees		PE		CV AUC	
				BM	MFM	BM	MFM	BM	MFM
P. banksiana	0.01	4	0.75	1750	900	0.427	0.433	0.87	0.86
P. tremuloides	0.01	4	0.50	1350	750	0.529	0.544	0.87	0.86
B. papyrifera	0.01	4	0.50	1150	450	0.458	0.469	0.78	0.77
P. mariana	0.01	4	0.75	3050	1450	0.489	0.510	0.80	0.77
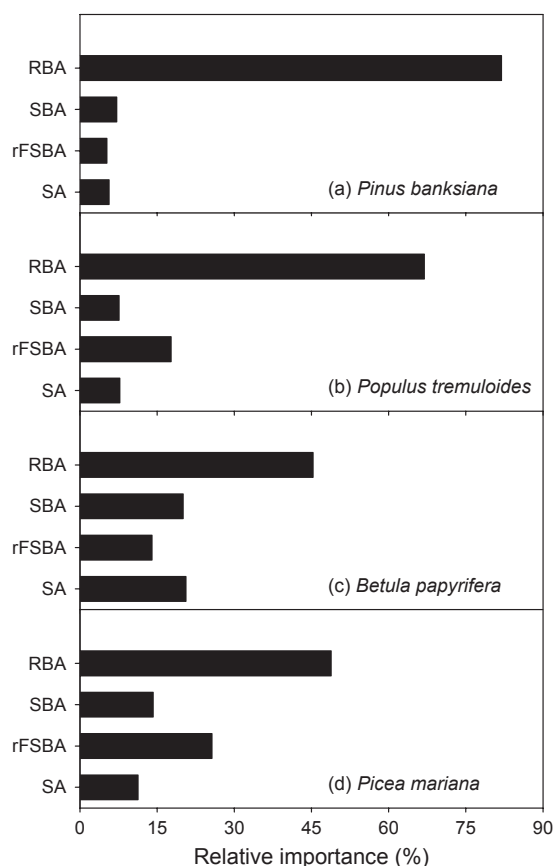
Fig. 1. The relative influence of relative basal area (RBA), stand basal area (SBA, m^2 ha^{-1}), ratio of focal species basal area to stand basal area (rFSBA) and stand age (SA, years) on mortality probability for (a) *Pinus banksiana*, (b) *Populus tremuloides*, (c) *Betula papyrifera* and (d) *Picea mariana*. The total values add to 100% for each model. In each model, predictors with larger values in relative influence have more explanatory power.

P. mariana, respectively. However, for *P. banksiana*, the mortality probability increased initially to ~0.18 of RBA (Fig. 2a).

Linear regressions fitted data very well as indicated by the high r^2 and narrow confidence interval (Table 3). The regression analyses between predicted mortality probability and RBA showed that, with or without the initial increase of predicted mortality probability for *P. banksiana*, the sensitivity of RBA-dependent mortality was the highest for two shade-intolerant species, *P. banksiana* and *P. tremuloides*. The sensitivity

of RBA-dependent mortality for *B. papyrifera* was medium, and that for *P. mariana* was the lowest. With 0.1 unit of increase in RBA, the decline of predicted mortality probability was about 0.417, 0.473, 0.453, 0.218 and 0.152 for *P. banksiana* (with initial increase), *P. banksiana* (without initial increase), *P. tremuloides*, *B. papyrifera* and *P. mariana*, respectively (Table 3). The 95% confidence intervals for slopes did not overlap among species except for two shade-intolerant species, *P. banksiana* and *P. tremuloides* (Table 3).

CROWDING-INDUCED MORTALITY

The relative influence of SBA on mortality was 7.15%, 7.6%, 20.08% and 14.22% for *P. banksiana*, *P. tremuloides*, *B. papyrifera* and *P. mariana*, respectively (Fig. 1a–d). Two general trends of mortality against SBA are shown in predicted value plots (Fig. 2e–h). For *P. banksiana*, *P. tremuloides* and *P. mariana*, mortality increased with SBA (Fig. 2e,f,h). The mortality of *P. banksiana* gradually increased with SBA and reached its plateau at ~46 m^2 ha^{-1} in SBA (Fig. 2e). The mortality of *P. tremuloides* and *P. mariana* dramatically increased at ~30 and ~24 m^2 ha^{-1} in SBA, respectively and remained at a higher level (Fig. 2f,h). Mortality of *B. papyrifera*, however, decreased with SBA (Fig. 2g).

SPECIFIC INTERACTIONS ON MORTALITY

The ratio of focal species' basal area to stand basal area had the weakest influence on mortality among the four predictors for *P. banksiana* and *B. papyrifera* with 5.24% and 14% in relative importance, respectively (Fig. 1a,c). The rFSBA ranked as the second strongest predictor in the models for *P. tremuloides* and *P. mariana*, accounting for 17.72% and 25.66% in relative importance, respectively (Fig. 1b,d). The predicted value plots indicated that the mortality of *P. banksiana* decreased, whereas those of *P. tremuloides* and *P. mariana* increased with increasing rFSBA (Fig. 2j–l). Even with a narrow range of rFSBA, *B. papyrifera* presented an increase of mortality with rFSBA (Fig. 2k).

AGE-RELATED MORTALITY

For *P. banksiana* and *P. tremuloides*, the relative influence of SA on mortality was weak as indicated by its small relative
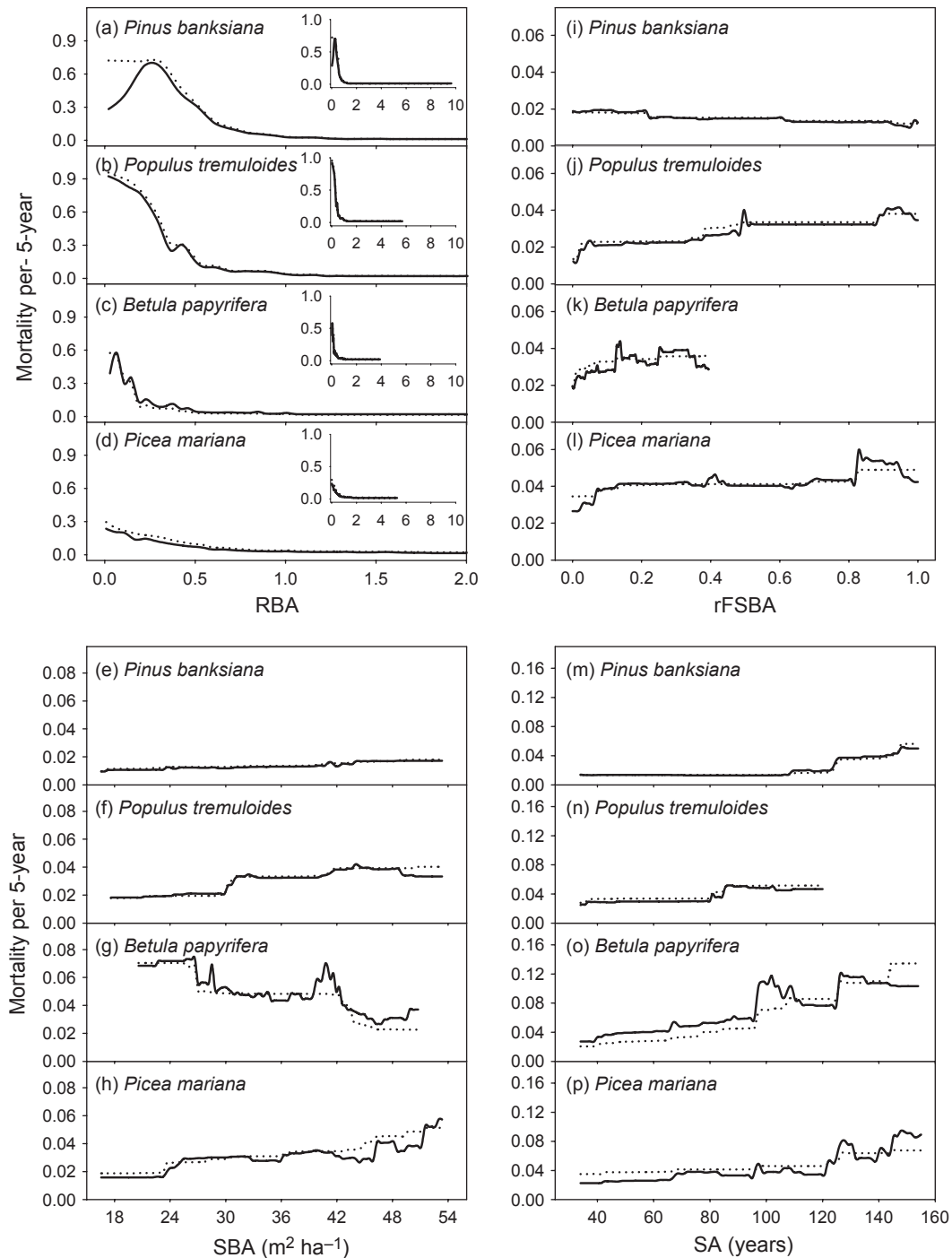
Fig. 2. Predicted mortality per 5 year in relation to relative basal area (RBA) (a–d), stand basal area (SBA) (e–h), ratio of focal species basal area to stand basal area (rFSBA) (i–l) and stand age (SA) (m–p) for *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*. The black lines indicate the predicted values from best models, and dotted lines indicate the predicted values from monotonically fitted models.

influence value (<8%) (Fig. 1a,b). For *B. papyrifera*, SA had the second strongest influence on mortality with 20.61% in relative influence (Fig. 1c). SA was the weakest variable in the model for *P. mariana* with 11.31% in relative influence (Fig. 1d). The predicted value plots showed that mortality increased with SA for all study species (Fig. 2m–p). The patterns, however, differed among the study species. For

P. banksiana, mortality increased in stands > 110 years of age with an apparent increase at ~120 in SA (Fig. 2m). For *P. tremuloides*, mortality had a steep increase between 80 and 90 years and then remained at the higher level with a few fluctuations (Fig. 2n). For *B. papyrifera*, mortality increased through the whole range of SA (Fig. 2o). For *P. mariana*, mortality began to increase at a SA of ~125 years (Fig. 2p).

Table 3. Sensitivity analysis of size-dependent mortality using linear regression between predicted mortality probability and relative basal area (RBA) for *Pinus banksiana*, *Populus tremuloides*, *Betula papyrifera* and *Picea mariana*. A steeper slope indicates higher sensitivity of size-dependent mortality

Species	Range of RBA	Slope	95% Confidence interval		r^2
			Lower	Upper	
P. banksiana (with initial increase)	0.02–1.29	−4.17	−4.40	−3.94	0.91
P. banksiana (without initial increase)	0.18–1.29	−4.73	−4.91	−4.56	0.96
P. tremuloides	0.02–1.29	−4.53	−4.73	−4.32	0.89
B. papyrifera	0.03–1.08	−2.18	−2.31	−2.05	0.81
P. mariana	0.01–1.88	−1.52	−1.58	−1.46	0.87

MAIN INTERACTIONS

In the monotonically fitted model, the interactions between RBA and SBA were found for all species (Fig. 3a–d). For *P. banksiana*, *P. tremuloides* and *P. mariana*, individuals with smaller RBA had a higher probability of mortality in stands with higher SBA (Fig. 3a,b,d), but *B. papyrifera* had a lower probability of mortality in the stands with higher SBA (Fig. 3c). Interaction was also found between RBA and rFSBA for *P. tremuloides* and *P. mariana*, i.e. the individuals with smaller RBA had a higher probability of mortality in stands with higher rFSBA (Fig. 3e,g). For *B. papyrifera*, mortality probability was higher for individuals in stands with a combination of less SBA and higher SA (Fig. 3f).

Discussion

SIZE-DEPENDENT MORTALITY

Our first hypothesis that tree mortality is dependent on relative size is strongly supported, i.e. smaller individuals have higher mortality, for all studied species across a wide range of SAs and forest compositions. Our results are in agreement with other studies reporting that higher mortality occurs at the lower end of size (Chen *et al.* 2008; Kunstler, Coomes & Canham 2009). The effect of relative size on mortality may be explained by the size-dependent resource uptake ability (Brown *et al.* 2004), resource availability (Weiner 1990; Muller-Landau *et al.* 2006), external-stress susceptibility (Loehle 1988) and their interactions. In our study area, forest tent caterpillar (*Malacosoma disstria* Hbn.), spruce budworm (*Choristoneura fumiferana* Clem.) and *Armillaria* root disease (*Armillaria* spp.) appear to be common agents. Browsing by mammals, such as moose (*Alces alces* L.), white-tailed deer (*Odocoileus virginianus* Zimmerman), porcupine (*Erethizon dorsatum* L.) and hares (*Lepus americanus* Erxleben) may also kill small trees.

Also, as we hypothesised, the sensitivity of size-dependent mortality generally decreased with increasing shade tolerance of the studied species. The differences of the size-dependent mortality sensitivity may reflect variations in species' responses to resource limitations and (or) disturbance agents among species. Overall, our findings support that shade-intolerant species require higher light availability to maintain carbon balance (Leverenz 1996). Alternatively, smaller carbon storage in roots and stems (Canham *et al.* 1999) and lower wood density (Poorter *et al.* 2010) make shade-intolerant species more susceptible to disturbance agents.

CROWDING-INDUCED MORTALITY

Our second hypothesis that tree mortality increases with SBA is supported by the findings for *P. banksiana*, *P. tremuloides* and *P. mariana*. Our results are consistent with those in temperate forests, i.e. crowding has a positive effect on tree mortality (Dwyer *et al.* 2010) and a negative effect on growth (Coates, Canham & Lepage 2009). The crowding-induced mortality may reflect competition for below-ground soil resources and above-ground light, and for space both below and above ground (Canham, Lepage & Coates 2004).

The interactions between the RBA of the subject tree with a stand and SBA in the models for *P. banksiana*, *P. tremuloides* and *P. mariana* suggest that small individuals tend to die because of stand-crowding competition. This finding may be understood as the small individuals receiving less resource in more crowded stands. Given that a tree's crown is scaled with its basal area and more crowded in a stand (Enquist & Niklas 2002), an individual in the understory is expected to receive less light under a denser canopy.

It is not clear why mortality of *B. papyrifera* decreased with increasing SBA. There are two possible explanations. In less crowded stands that are described by SBA of the tree layer, higher mortality of *B. papyrifera* trees was a result of competition with tall shrubs such as beaked hazel (*Corylus cornuta* Marsh.) and mountain maple (*Acer spicatum* Lam.), which are most commonly associated with *B. papyrifera* in North American boreal mixed-wood forests (Chen & Popadiouk 2002; Hart & Chen 2008). Alternatively, because moose and other mammals feed to a large extent on *Betula* spp. (Danell, Huss-Danell & Bergstrom 1985), higher mortality of small-sized *B. papyrifera* trees could be resulted from more intense browsing in less crowded stands because of better mobility and higher abundance of edible shrubs.

SPECIES INTERACTIONS AND MORTALITY

The lower mortality of *P. tremuloides*, *B. papyrifera* and *P. mariana* as their conspecific component decreases supports
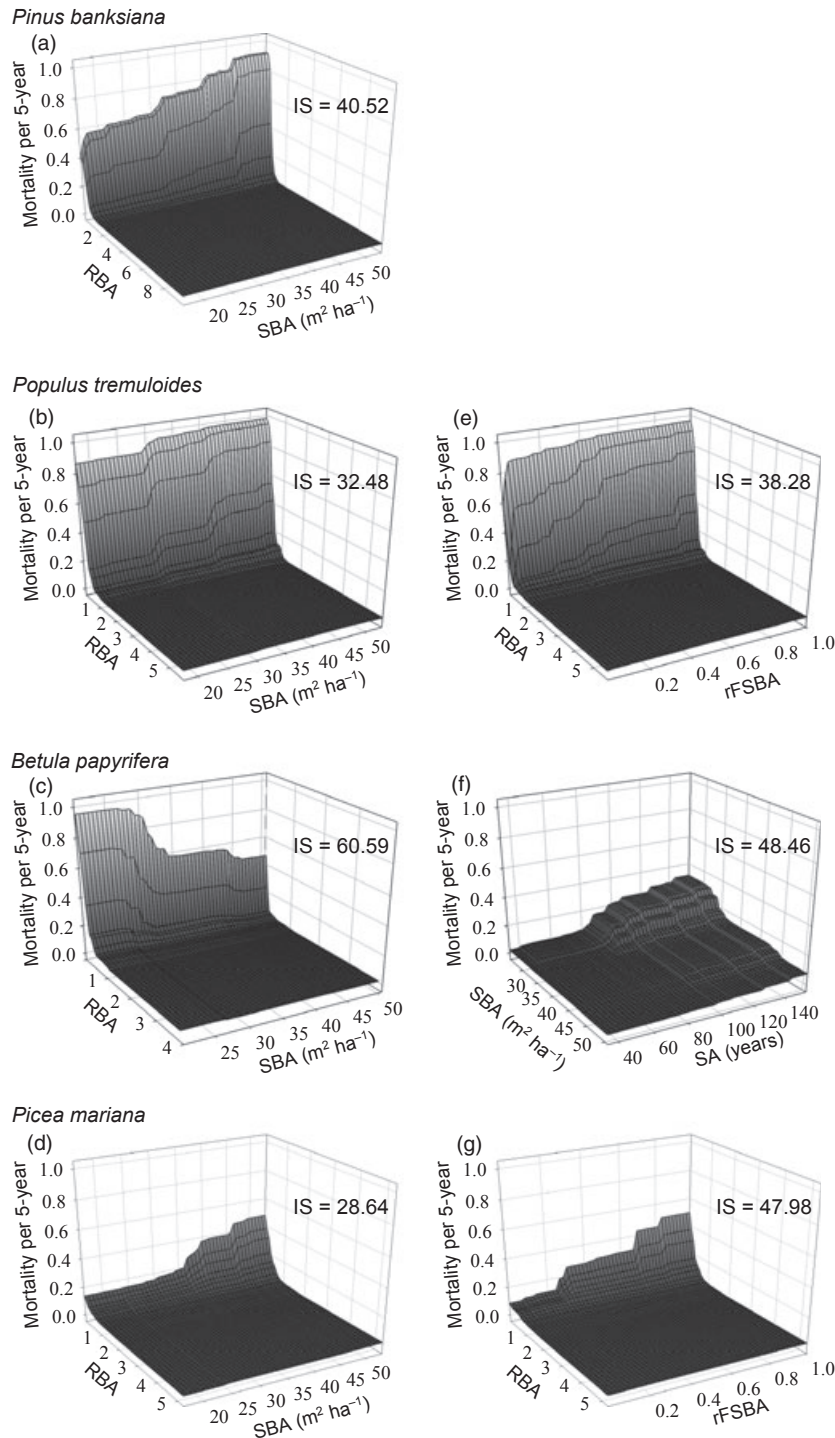
Fig. 3. Predicted mortality per 5 year showing the main interactions in the monotonically fitted BRT model for *Pinus banksiana* (the first row), *Populus tremuloides* (the second row), *Betula papyrifera* (the third row) and *Picea mariana* (the last row). RBA, SBA, rFSBA, and SA stand for relative basal area, stand basal area (m^2 ha^{-1}), ratio of focal species basal area to stand basal area, and stand age (years), respectively. IS is the interaction size, indicating relative interaction strength in the model.

our hypothesis that a negative conspecific interaction reduces tree mortality. The negative effects of conspecific neighbours on tree mortality are reported to be an important mechanism to promoting species coexistence and diversity in tropical forests (Janzen 1970; Connell, Tracey & Webb 1984; Comita *et al.* 2010). The mortality increase in stands with more conspecific

individuals may be explained by the following mechanisms. First, intra-specific competition may be stronger than inter-specific competition as a result of possible inter-specific niche separation, e.g. temporal niche separation may occur between *P. tremuloides* and *P. mariana* in that the former has leaves only in mid-summer and the latter tends to photosynthesize

for 6 months a year. Second, inter-specific facilitation may occur, e.g. the presence of *P. tremuloides* can improve the performance of *P. mariana* by delaying the paludification process and increasing surface soil concentrations of exchangeable cations (Fenton *et al.* 2005; Legare, Pare & Bergeron 2005). Third, Janzen–Connell effects may reduce the performance of individuals through negative plant–soil feedback and above-ground accumulation of species-specific enemies. Although few studies have reported the Janzen–Connell effects in boreal forests, studies conducted in tropical and temperate forests suggest that the below-ground plant–soil feedback is a key driver for coexistence (Comita *et al.* 2010; Mangan *et al.* 2010). Regardless of the specific mechanisms evolved, our study demonstrates that individuals in stands with more conspecific neighbours experience higher mortality.

In contrast with our hypothesis, *P. banksiana* presented a slight decrease of mortality with increasing ratios of its basal area to stand basal area. Lower mortality has also been found for other species when surrounded by more conspecific individuals (Das *et al.* 2008). A potential explanation is that faster-growing *P. tremuloides* over-shades highly shade-intolerant *P. banksiana*, leading to higher mortality of *P. banksiana*, because *P. banksiana* is mostly mixed with *P. tremuloides* when it is a minor component in our data.

While most studies focus on the negative intra-specific effect on trees at early stages, i.e. seedlings and saplings (Comita *et al.* 2010) and others indicate that such an effect occurs for all trees (Peters 2003; Gonzalez *et al.* 2010), our results suggest that these negative effects are stronger for smaller trees of *P. tremuloides* and *P. mariana*, indicated by interactions between RBA and the rFSBA. The results demonstrate that the individuals under stressed conditions have a higher probability of mortality as a result of the negative effects from conspecific neighbours. Our results, however, do not show this pattern for *B. papyrifera*, probably due to its narrow range of rFSBA (i.e. from ~0 to ~0.4).

AGE-RELATED MORTALITY

Our results support the fourth hypothesis that mortality increases with SA in boreal forests. It is intuitive that when stands age, larger trees die (Coomes & Allen 2007b), contributing to coarse woody debris (Brassard & Chen 2008) and facilitating canopy succession (Chen & Taylor 2011; Taylor & Chen 2011). Age-related mortality is determined by a species' genetics and its interaction with the environment. Because our sites are similar for all studied species, our results appear to reflect both a genetic-driven process and its interaction with disturbance. The increase in the onsets of mortality in these species appears to be consistent with their documented autecology (Burns & Honkala 1990). The presence of disturbance may be the reason for fluctuations of mortality probability against SA for *B. papyrifera* and *P. mariana*, because our data include plots with minor disturbances and these two species are susceptible to forest tent caterpillar and spruce budworm, respectively (Chen & Taylor 2011; Taylor & Chen 2011).

For shallow-rooted *B. papyrifera*, we found an interactive response of mortality to SA and SBA, i.e. trees in older stands with less SBA had a higher mortality rate. This result may be attributable to the windthrow-caused mortality of large individuals in less crowded stands, because windthrow risk is typically higher in less crowded stands (Thorpe, Thomas & Caspersen 2008).

Conclusion

Using a set of long-term repeated measurements, covering a wide range of tree sizes, stand developmental stages and stand compositions, we show that tree mortality of the four boreal tree species was strongly dependent on relative size, and the sensitivity of the size-dependent mortality differed among species with shade-intolerant species being more sensitively than shade-tolerant species. Second, mortality increased with stand crowding, supporting the notion that more crowded stands resulted in on average lower resource availability and consequently higher mortality. However, this negative effect was not true for *B. papyrifera*, which has higher mortality in less crowded stands, suggesting that competition from tall shrubs, coupled with browsing from large mammals, might be an alternative cause for mortality. Third, species interaction affects mortality either negatively or positively, depending on the traits of the species and its neighbours. Finally, mortality increases with SA because of tree ageing and its interactions with minor disturbances. In summary, our results indicate that asymmetric competition is a dominant cause for tree mortality in boreal forests, but the patterns of the asymmetric competition differed strongly with the species' shade tolerance trait. In addition, mortality is also regulated by stand crowding, species interactions and tree ageing process in non-equilibrium boreal forests.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Characteristics of study plots.

Appendix S2. d.b.h. distribution for study plots.

Appendix S3. An examination of independent influence of d.b.h. on tree mortality.

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