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Survival probability of white spruce and trembling aspen in boreal pure and mixed stands experiencing self-thinning

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ABSTRACT

Tree mortality due to competition is one of the key drivers of forest succession in Canadian boreal mixedwood forests. We analyzed survival probability of trembling aspen (*Populus tremuloides* Michx.) and white spruce (*Picea glauca* (Moench) Voss.) trees and saplings, growing in pure and mixed stands experiencing self-thinning, in the Boreal Forest Natural Region of Alberta, Canada. Generalized logistic regression models were utilized to evaluate the effects of tree and stand characteristics on the survival probability of both species. Absolute size of the individuals, characterized by diameter at breast height, had a positive effect on the survival of both aspen and spruce. Aspen experienced decreasing survival with size, which is most likely linked to age rather than competition. Significant effects of basal area of trees larger than the subject tree indicated that one-sided inter- and intra-specific competition, rather than two-sided, is the primary driving force of competition-related mortality for both aspen and spruce. Periodic annual increment in diameter was a better predictor of survival than basal area of larger trees, indicating that growth rate is the most important individual characteristic that defines survival of both aspen and spruce in these self-thinning stands.

1. Introduction

Tree mortality has long term effects on stand composition, structure, productivity, and dynamics (Caspersen and Kobe, 2001; Mencuccini et al., 2005; Chen et al., 2008). Whereas large scale disturbances, such as wildfires and insect outbreaks, may act largely as whole stand replacing events (Turner et al., 1997), mortality of individual trees results from competition and carbon starvation and other local events (such as root or stem diseases, insects, or snow or wind damage) (Kneeshaw and Bergeron, 1998). Mortality due to these other events has also been called background mortality (Kenkel, 1998). In general, mechanical damage and the inability of trees to defend themselves against diseases are among the most important factors that cause background mortality of trees in forest stands (Luo and Chen, 2011). While the main causes of mortality might be known, it remains poorly understood and is not well quantified as a component of growth and yield estimation models (Yang et al., 2003). Nevertheless, a number of studies have shown that reliable estimates and predictions of the probability of mortality (or survival) of individual trees in forest stands are possible based on individual tree characteristics and stand level attributes (Hamilton, 1986; Yang et al., 2003; Chen et al., 2008).

In the specific case of density-dependent mortality in single species stands, which is thought to be mainly caused by the inability of trees to maintain a positive carbon balance causing them to die as a consequence of carbon starvation (Weiner, 1990; Guneralp and Gertner, 2007), it is widely assumed that the relative size of an individual tree as related to its neighbors has a substantial influence on the probability of a tree survival (Westoby, 1984; Weiner, 1990). The smallest trees in the stand are the most affected by asymmetric competition (i.e. larger individuals affect the ability of smaller individuals to acquire resources), thus variation in tree mortality can be better explained with measures of tree size, stand density, indicators of competition, and tree growth rate (Hamilton, 1986; Chen et al., 2008; Yang and Huang, 2013). With a limited supply of resources, the smallest size classes are usually the most affected and higher mortality rates of smaller and slow-growing individuals is anticipated (Westoby, 1984; Weiner, 1990). The relative competitiveness of the trees (i.e. degree of intraspecific competition), stand composition, tree longevity, and other factors influence the occurrence of this type of mortality (Chen et al.,

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2008; Yang and Huang, 2013). Since mortality of trees is strongly influenced by annual tree growth (Kozlowski et al., 1991), several studies that have analyzed survival probability based on recent growth rates have suggested a strong link between annual tree growth and survival of trees (Hamilton, 1986; Kobe and Coates, 1997; Yang et al., 2003; Bigler and Bugmann, 2004a,b; Chen et al., 2008; Yang and Huang, 2013). If individual annual diameter increment decreases below a certain absolute or relative limit, the tree is expected to be under high stress and will experience an increase in the risk of mortality (Wunder et al., 2006).

In mixed species stands where species with differences in morphology and physiological characteristics, as well as ecological requirements (such as differences in shade tolerance) are growing together, mortality is more difficult to understand and predict than in even-aged mono-specific stands (Westoby, 1984; Yang et al., 2003). The capacity of some species to live and photosynthesize in a shaded environment can provide them with certain advantages against competition. For example, in boreal mixedwoods aspen usually quickly re-occupy mixedwood sites after disturbance and remain dominant for extended periods; while, there is generally enough light reaching the understory to allow shade tolerant species such as white spruce to survive and grow under the canopy of the shade intolerant trembling aspen (Lieffers and Stadt, 1994; Chen and Popadiouk, 2002).

The logistic function has been the standard approach for modeling the probability of mortality or survival for a number of tree species (Monserud, 1976; Hamilton, 1986; Monserud and Sterba, 1999; Yang et al., 2003), and it represents perhaps the best approach for modelling tree mortality behavior (Yang et al., 2003; Feng et al., 2006; Groom et al., 2012). Standard logistic regression analysis works well with data collected in permanent sample plots in which the time interval between consecutive measurements is frequently homogenous (i.e. equal number of years between consecutive measurements). When the time interval is not equal among measurements, adjustments to the traditional logistic model may have to be made and a generalized logistic regression model should be used (Monserud, 1976).

Models for predicting the probability of either mortality or survival for individual trees have been developed for boreal tree species in western Canada including white spruce, trembling aspen, and jack pine (Yao et al., 2001; Yang et al., 2003; Yang and Huang, 2013). In the case of trembling aspen and white spruce in boreal forests of Alberta, Yang et al. (2003) found that a number of stand attributes are powerful predictors of individual tree mortality, including total stand basal area, diameter increment, relative size, and basal area of larger deciduous and conifer trees. However, these studies did not evaluate whether the probability of survival or mortality of individual trees is affected by stand composition in pure and mixed stands of these two species experiencing self-thinning; rather, these previous models were developed for predicting probability of mortality in a more general context, and although the effects of two-sided and one-sided competition were analyzed, these analyses did not focus on stands experiencing only density-dependent mortality.

The general objective of this study was to examine factors influencing the probability of survival of trembling aspen and white spruce trees growing in pure and mixed stands in Alberta boreal forests, which were previously identified as experiencing density-dependent mortality (Reyes-Hernandez et al., 2013). It is important to note that it is not the purpose of this research to generate new and/or more powerful models to predict individual tree survival or mortality of the above mentioned species in a more general context, since these models have already been generated and validated (Yang et al., 2003; Yang and Huang, 2013); rather, our main objective is to evaluate some of the stand and individual tree characteristics, including stand composition, that might be affecting and defining mortality that is occurring exclusively in self-thinning stands.

We hypothesize that the probability of survival of individual trees in boreal pure and mixed self-thinning stands comprised by trembling aspen and white spruce, can be modeled and predicted with measures of density and relative density (such as Reineke's Stand Density Index or SDI), stand structure and stand composition. We also hypothesize that stand composition (percentage of basal area in deciduous species) has an important effect and influences the probability of survival of individual trees in these stands, because the species of interest have differences in ecological requirements (i.e. there is niche separation between these two species). We attempt to elucidate whether species, size, relative size, and competitiveness are important in defining which trees survive and which trees die in self-thinning boreal pure and mixed stands of these two species. Also, these analyses will allow for further testing of stand characteristics to determine whether or not one-sided and not two-sided competition, is one of the key drivers of tree mortality in these stands. One-sided competition is defined as competition resulting exclusively from individuals larger than the subject tree, whereas two-sided competition results from all individuals larger, equal, and smaller than the subject tree (Cannell et al., 1984).

2. Methods

2.1. Study sites and data

This study was completed using long-term data from permanent sample plots (PSPs) established in pure and mixed stands of trembling aspen and white spruce, located in the Boreal Forest Natural Region of Alberta, Canada. The region ranges in elevation from 150 m in the Northern Mixedwood Natural Subregion to over 1100 m in the Upper Boreal Highlands Natural Subregion, with level to undulating plains with extensive wetlands, high elevation plateaus and dune fields (Forest Management Branch, 2005). The overall climate is characterized by long, cold, dry winters and short, warm, and moist summers, with between 50 and 100 frost-free days per year, mean annual temperature of about −0.2 °C, and an average annual precipitation of 470 mm (Natural Regions Committee, 2006). Our study included PSPs located mainly in the Central Mixedwood, the Dry Mixedwood, and the Northern mixedwood Ecological Subregions (Beckingham and Archibald, 1996). The PSPs are located in stands that originated following fire and that have been maintained free of any management activity (Forest Management Branch, 2005). Establishment and re-measurement of these PSPs were made following rigorous standards, albeit their size, establishment date, and re-measurement intervals are variable (Forest Management Branch, 2005). Most of these PSPs are 0.10 ha in size with all trees taller than 1.3 m or larger than 2.5 cm in diameter at breast height tagged and measured at time intervals ranging between 3 and 10 years.

For this analysis we used only stands that were previously identified as experiencing density-dependent mortality (Reyes-Hernandez et al., 2013). Identification of self-thinning stands was performed by developing maximum size–density relationships at the individual stand level, also called 'dynamic self-thinning lines' (Weller, 1987, 1990; VanderSchaaf and Burkhart, 2007b), with the use of a mixed model approach. We refer the readers to Hann et al. (2003), Poage et al. (2007), VanderSchaaf and Burkhart (2007a), VanderSchaaf and Burkhart (2007b), and VanderSchaaf (2010), for a more detailed description of the methodology and criteria used to separate self-thinning from non-self-thinning stands. A total of 179 plots were available for our study, with 653 observations at the stand level. A minimum