Forest Ecology and Management 432 (2019) 446–454

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Release response of black spruce and white spruce following overstory lodgepole pine mortality due to mountain pine beetle attack

Felix O. Oboite*, Philip G. Comeau

Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, AB T6G 2H1, Canada

ARTICLE INFO

Keywords:
Mountain pine beetle
White spruce
Black spruce
Growth response
Advance regeneration
Lodgepole pine

ABSTRACT

Advanced regeneration of black spruce and white spruce are common in lodgepole pine dominated stands of Alberta. These economically important species have the potential to replace lodgepole pine trees that are killed by mountain pine beetle (MPB). The growth responses of both species of spruce after overstory lodepole pine mortality were examined using data collected from seven sites in the lower foothills of western Alberta, Canada. We sampled understory black and white spruce (> 1.3 m in height) and characterize competitive effect of surrounding trees on growth response. Diameter and height growth responses of both species were affected positively by overstory pine mortality with white spruce having a shorter delay in release response than black spruce. While higher mean growth responses were observed for white spruce, both species of spruce increased in growth as initial tree size and understory light increases. Spruce/fir competition around the focal trees resulted in increased height growth and a reduction in diameter growth of both spruces. Overall, our results demonstrate that advance regeneration of both species of spruce can increase in growth and potentially replace pine in the canopy that have been lost to MPB.

1. Introduction

Mountain pine beetle, MPB (*Dendroctonus ponderosae* Hopkins) is an important natural disturbance agent in western North America. Its distribution is influenced by climate and forest type (Taylor et al., 2006). Following MPB outbreaks, there is a need to regenerate affected stands (McIntosh and Macdonald, 2013). In the absence of fire or anthropogenic disturbance, natural regeneration of lodgepole pine is usually poor (Teste et al., 2011) due to cone serotiny and lack of favourable seedbed conditions (McIntosh and Macdonald, 2013). Silvicultural interventions including salvage harvesting, mechanical site preparation, and planting seedlings, may be necessary to regenerate these stands, but this is expensive (Dhar and Hawkins, 2011).

Natural disturbances like MPB are seen by many ecologists as an important ecological process rather than as an ecological disaster requiring human restoration (Lindenmayer et al., 2004) and these disturbances have been linked to maintenance of biodiversity and productivity (Bradstock et al., 2002). Since MPB induced mortality emulates thinning from above, it should allow surviving trees to take advantage of increased resources (water, nutrient, light) (Hawkins et al., 2013). In the Canadian province of Alberta, the Alberta government has short-term and long-term pine strategies for managing forest areas affected by MPB (ASRD, 2007). The purpose of the long-term strategy is to increase the diversity of age classes and stand types in the landscape and to reduce the number of highly susceptible stands. Advance regeneration in affected stands can form a continuous new canopy and contribute significantly to recovery of stands affected by MPB outbreaks (Campbell and Antos, 2015) by causing changes in forest composition and structure over time of the forest (Dhar and Hawkins, 2011). Resulting forest with advance regeneration will decrease susceptibility to future MPB outbreak at stand and landscape levels (Schoennagel et al., 2012). Advance regeneration in lodgepole pine stands is generally dominated by shade tolerant species such as Engelmann spruce (*Picea engelmannii* Parry), white spruce (*Picea glauca* [Moench] Voss), hybrid (interior) spruce (*Picea glauca* [Moench] Voss x *engelmannii* Parry ex Engelm.), black spruce (*Picea mariana* (Mill.) B.S.P.), and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.), which are capable of surviving under low light levels common in the understory of lodgepole pine stands (Hawkins et al., 2012). While advance regeneration is typically destroyed when areas are salvaged, unsalvaged stands could potentially recover naturally (Mitchell, 2005). Consequently, understanding and quantifying the growth of residual trees in affected stands is important for predicting the long-term potential of these stands and for selecting stands which require silvicultural interventions to improve growth and yield (Dhar and Hawkins, 2011).

Previous studies have shown that release response of spruce is

* Corresponding author.
E-mail address: oboite@ualberta.ca (F.O. Oboite).

https://doi.org/10.1016/j.foreco.2018.09.029
Received 2 June 2018; Received in revised form 25 August 2018; Accepted 17 September 2018
0378-1127/

influenced by site productivity, size of trees at release, condition of trees (and damage) following release, and overtopping trees (DeRose and Long, 2010). As a result, strong release responses (i.e., large growth increases) have been observed for shade-tolerant species, such as spruce and subalpine fir, following canopy opening (Hawkins et al., 2013) and even after prolonged suppression (Antos et al., 2000). While some studies indicate that release responses were dependent on tree size (Webb and Scanga, 2001; Claveau et al., 2002), or age (Helms and Standiford, 1985; Hawkins et al., 2013), at least one study (Puttonen and Vyse, 1998) reports that age or size did not influence release. Other commonly reported indicators of growth response of advance regeneration are pre-release height growth, live-crown ratio, and stem height/ diameter ratio (Ruel et al., 2000). Understanding factors that contribute to variation in release responses for black and white spruce could be useful to improve our ability to predict stand growth for these conditions.

Following MPB outbreak, stands will develop complex structure with varying levels of standing dead trees and residual live trees (Coates and Hall, 2005) which can influence the distribution of light levels within the stand. Light is a major requirement for growth and regeneration in MPB affected stands (Dhar et al., 2016; Coates and Hall, 2005) and it is important to understand how changes in understory light levels will influence advance growth. Due to the magnitude of MPB outbreak in Alberta, a large portion of the landscape might be left unmanaged (Mitchell, 2005) and as such information of regeneration and stand development in unmanaged MPB affected stand is critical. The broad objective of this study was to examine the release response of white spruce and black spruce advance regeneration in post MPB attack stands. Specific objectives were to: (1) quantify changes in diameter and height growth of advance regeneration in stands where portions of the main canopy have died due to MPB; (2) examine whether diameter and height growth responses of advance spruce regeneration are related to understory light, initial tree sizes, age, and competition from surrounding trees.

2. Materials and methods

2.1. Study area

The study area was located in the Lower Foothills natural subregion of Alberta (Fig. 1). The lower foothills have a mean annual temperature (MAT), growing season precipitation (GSP) and a mean annual precipitation (MAP) of 1.8 °C, 430 mm and 588 mm respectively, with an average elevation of 950 m. The soils in this subregion are primarily orthic gray luvisols and brunisolic gray luvisols while the forest includes both pure or mixed stands of aspen, lodgepole pine, white spruce, black spruce and balsam fir (Natural Regions Committee, 2006). In the summer season of 2015 and 2016, we selected seven lodgepole pine dominated permanent sample plots (PSPs) (ASRD, 2005) having black and white spruce advance regeneration that were attacked by MPB in 2007 but left unharvested. Five of these stands located south of Grand Prairie (GP) had high pine mortality with a range of 31.75–40.64 m^2/ha of dead tree basal area, and two stands located near Whitecourt (WC) had low pine mortality with a range of 3.98–5.66 m^2/ha of dead tree basal area (Table 1).

2.2. Data collection

In each of the five plots with high pine mortality (> 67% reduction in basal area; Table 1), 24 black spruce and 24 white spruce understory trees were selected while in the low mortality plots (< 15% reduction in basal area; Table 1), 20 black spruce and 20 white spruce understory trees were selected. Preliminary assessment of the plots revealed that the low mortality plots had fewer understory spruce than the high mortality plots; hence less understory spruce trees were sampled. Understory trees were selected to represent the range of variation in understory spruce densities and height (above 1.3 m in height) within each stand. Maximum and minimum DBH and height values of sampled understory trees are presented in Table 2.

In a 5.64 m radius plot, centered on the sample tree, diameter at breast height (DBH) and height of all trees taller than 1.3 m were measured as well as their distances from the sample tree. The measured trees were regarded as the competing trees and their status (dead or alive) and species type were recorded.

Each sample tree was harvested and height increments for each of the preceding 15 years were determined using budscars and branch whorls. Stem diameter was also recorded at 30 cm and 130 cm height and disks were also taken from 30 cm and 130 cm height for measurement of radial increment. These collected disks were measured for diameter outside bark and then air dried and sanded. Ring widths from pith to bark were measured in the lab to a precision of 0.001 mm along 4 radii separated by 90° using the WinDendro computer program and a calibrated scanner (Regent Instruments Canada Inc, 2009). We measured the light levels resulting from surrounding trees after the sampled trees were felled in order to avoid the influence of the sample tree crown in the photographs. Hemispherical photograph was taken using a Nikon D90 camera fitted with a Sigma 4.5 mm circular fisheye lens at 1.0 m height above the ground. Photos were taken either early in the morning or late in the evening when the sun was not visible above the horizon. Photos were processed using SLIM (Spot Light Interception Model) software (Comeau et al., 2003) to estimate the influence of the surrounding stand on light levels (fractional transmittance) at the sampled tree. Estimates of percent (%) transmittance from SLIM were used in this study.

2.3. Data analysis

2.3.1. Release response of spruce over time

Diameter and height increments measured over three years prior to release (Pre-release growth rate; 2004–2006) and over seven years after release (Post-release growth rate; 2008–2014) were selected for comparison. A mixed model analysis of variance (ANOVA) was used to test the hypothesis that there was no difference between pre and post-release growth rates across the selected years. Tukey's honestly significant difference (HSD) test was used to compare differences among years by comparing least square means (lsmeans) (Lenth, 2016). Diagnostic plots of residuals versus fitted values were used to ascertain model fit. Random effects were included to account for variation among plots. Only the high mortality plots were used in this analysis because of the declining growth associated with one of the low mortality plots (Plot WC2) which is likely due to increases in soil water after MPB (Fig. 2). Analysis was done separately for white spruce and black spruce. The statistical model is:

$$Y_{ijk} = \mu + \text{Year}_k + \text{Plot}_i + \text{Tree}_{j(i)} + \varepsilon_{ijk} \quad (1)$$

where Y_{ijk} is diameter and height increment, Year_k is the fixed effect for years, Plot_i is the random effect for plots, $\text{Tree}_{j(i)}$ is the random effect for tree nested within plot and ε_{ijk} is the random experimental error.

2.3.2. Effect of initial tree size, competition, understory light and age on growth responses of spruce following MPB outbreak

Basal area per hectare is used as a measure of competition (Contreras et al., 2011; Huang et al., 2013) and it is reported to be more accurate than using number of stems per hectare since it captures both the number of trees in a stand and their sizes (Zeide, 2005). Initial testing showed that distance dependent competition indices were better than distance independent competition indices, and consequently, basal area distance ratio (Eq. (2)), which is a modification of the diameter distance ratio (Cortini and Comeau, 2008), was used. Basal area distance ratio (m/ha) was estimated using the following formula: