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Salvage logging during spruce budworm outbreaks increases defoliation of black spruce regeneration

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ABSTRACT

Although advance regeneration abundance and vigor are critical factors determining future forest composition and productivity, very few studies have focused on how they are affected by spruce budworm (SBW) outbreaks even though they affect millions of hectares of boreal forest on a cyclical basis. Post-SBW salvage logging is often used to reduce economic losses but could interact with the outbreak to affect advance regeneration. This study aims to determine the impact of SBW outbreaks and post-outbreak salvage logging on the defoliation of advance regeneration in mixed coniferous stands of northeastern Canada. Specifically, we assessed the effect of regeneration height and species (balsam fir or black spruce), as well as canopy composition, on the defoliation of advance regeneration. We then evaluated the effect of salvage logging on defoliation sustained by advance regeneration and compared it to the one observed in stands only affected by the SBW. Regeneration height and species, canopy composition and salvage logging all significantly affected defoliation and showed multiple interactions. Taller balsam fir seedlings were three times as defoliated as smaller ones, whereas it was 2.3 times for black spruce. Balsam fir seedlings were 15% more defoliated than black spruce. Seedlings of both species located beneath a balsam fir canopy were also more defoliated (> 50% defoliation) than seedlings found under black spruce trees (about 26% defoliation). Salvage logging in black spruce-dominated stands resulted in a ~25% increase in defoliation of tall (2.5 m) black spruce regeneration when compared to non-harvested sites. We speculate that this could increase the fir component in spruce-dominated stands, leading to forests that are more susceptible to future SBW outbreaks. To protect spruce advance regeneration from increased defoliation, salvage harvesting of spruce-dominated stands may thus be delayed until the outbreak has subsided. Long-term studies are needed to determine whether a compositional change occurs or not, particularly in spruce-dominated stands. As a precautionary measure, changes in salvage logging practices may be implemented immediately to avoid potential problems such as decreased black spruce abundance and increased susceptibility to future SBW outbreaks.

1. Introduction

In temperate and boreal biomes, recurrent insect outbreaks are an important component of forest ecosystems, influencing biogeochemical cycles, vegetation dynamics, and resource availability (Hunter, 2001; Martin et al., 2006; Edburg et al., 2012). This co-evolution of forest-insect systems induced a long-term biological resilience of forests to native insect outbreaks, *i.e.* their ability to absorb change and return to their original state (Drever et al., 2006; Thompson et al., 2009). For instance, in almost all outbreak-forming insect taxa (mostly defoliators and bark beetles), the insects primarily attack mature trees, which allows small understory trees, called advance regeneration, to grow and form the next stand (Mattson and Addy, 1975; Morin and Laprise, 1997; Greene et al., 1999; Astrup et al., 2008; Boggs et al., 2008; Kayes and Tinker, 2012). A typical example for this resilience pattern is that of the spruce budworm (SBW; *Choristoneura fumiferana*), a Lepidopteran defoliator native to the North American boreal forest. Baskerville (1975) labeled the SBW a super silviculturist, as it kills the overstory layer of forests thus releasing the understory regeneration. Since spruce budworm outbreaks last several years, during which establishment by seeds is low (Batzer and Popp, 1985; Astrup et al., 2008; Man and Rice, 2010; Moulinier et al., 2011), pre-established regeneration is the primary

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mechanism of stand replacement. However, it has also been reported that defoliation of regeneration occurs at high SBW densities, when mature trees are completely defoliated and larvae spin down on silk threads in search of food (Nealis and Régnière, 2004; Cooke et al., 2007). Given that advance regeneration abundance and quality are critical for post-disturbance stand recovery, *i.e.* their resilience, an evaluation of the conditions under which advance regeneration is defoliated will help understand when future dynamics will be affected.

Salvage logging to recover mature trees killed by insects could affect advance regeneration and lead to a compositional shift following outbreaks if it increases the vulnerability of one species over another (Burton et al., 2015). Similarly, future productivity could be reduced if the overall number of stems of advance regeneration is reduced (but see Griffin et al., 2013). A closer look into how salvage logging influences the defoliation of advance regeneration will thus inform us as to the future resilience of these forests to the combined effect of both SBW and salvage logging disturbances.

Using the boreal forest of eastern Canada, the general objective of this study was to acquire insight into the regeneration process of stands affected by a SBW outbreak, and how salvage logging influences it. At least three factors could affect the defoliation of advance regeneration. First, larger understory trees should be more defoliated than smaller ones because larvae have a greater probability of falling onto large stems than onto small ones, as observed by Nie et al. (2018). Second, the different species (balsam fir [*Abies balsamea* (L.) Mill] vs. black spruce [*Picea mariana* (Mill.) B.S.P]) of advance regeneration could experience differential defoliation levels because of the timing of their budburst, which occurs sooner in balsam fir, explaining its greater vulnerability than black spruce, as observed in the canopy (Nealis and Régnière, 2004). However, differential defoliation among host species in the understory might be different from that observed in the canopy depending on the moment of the spinning down of larvae. Third, stands with a higher percentage of balsam fir in the canopy should have higher SBW populations than in black spruce-dominated stands, increasing the probability of larvae falling onto advance regeneration in fir-dominated stands.

Salvage logging could either protect advance regeneration or increase its risk of being defoliated. Salvage logging could reduce the defoliation of advance regeneration because removal of the overstory would reduce the abundance of larvae spinning down and feeding on saplings and seedlings. Alternatively, salvage logging could increase defoliation of advance regeneration because the remaining saplings and seedlings would be the only egg-laying sites for SBW moths and subsequently the only food available for the larvae.

In this study, we specifically aimed (1) to determine the effects of height and species of advance regeneration and of canopy composition on the severity of the defoliation sustained by advance regeneration and (2) to determine the effects of salvage logging on the defoliation of advance regeneration. For the first objective, we hypothesized that (1) taller individuals would be more defoliated than smaller ones, that balsam fir regeneration would sustain more defoliation than black spruce regeneration, and that advance regeneration in balsam fir-dominated stands would experience more defoliation than in mixed or spruce-dominated stands. For the second objective, we considered two alternative hypotheses, *i.e.*, that advance regeneration located in salvage logged stands would either sustain less or more defoliation than that located in non-harvested stands.

2. Methods

2.1. Study area

A SBW outbreak which started in 2006 in the eastern boreal forest of Quebec (Canada), along with ongoing salvage logging operations in that area, provided the perfect opportunity to address these questions (Fig. 1). The study area is located on the North Shore of the St. Lawrence River and east of the Saguenay fjord in Quebec. The sub-arctic and sub-humid climate is characterized by a mean annual temperature of 1.7 °C (mean January temperature: −14.3 °C and mean July temperature: 15.6 °C), and mean annual precipitation of 1040.5 mm, 33% of which falls as snow (Environment Canada, 2016). The landscape is characterized by tall hills that rarely exceed 500 m, some rock cliffs and many valleys, while the metamorphic bedrock is covered mainly by thin tills. Forests are characterized by a mixture of balsam fir and black spruce, the latter increasing in abundance northward and inland (Robitaille and Saucier, 1998; De Grandpré et al., 2009).

2.2. Site selection

Eight sites, hereafter referred to as “natural sites”, were selected in old uneven-aged stands (120+ years) defoliated by the SBW but not harvested, representing a composition gradient ranging from balsam fir-dominated to black spruce-dominated stands. Six sites, hereafter referred to as “harvested sites”, were selected in stands that were salvage logged in 2011 (one stand), in 2012 (four stands), or in 2013 (one stand). In all sites, salvage harvest was carried out using careful logging standards (Cutting with protection of regeneration and soils or CPRS), which is the main type of logging in Quebec’s forests. This type of harvesting removes the overstory trees but leaves the naturally established regeneration. Prior to harvesting, these stands were similar to the natural sites (*i.e.*, old uneven-aged stands growing on till deposits) and their composition was selected to have a codominance of balsam fir and black spruce. All sites were at least 25 m from a road and showed no sign of other disturbances. To verify that there were no differences between the defoliation history in the natural and harvested sites, we used annual aerial detection survey data to compute cumulative defoliation in each stand (MFFP, 2015). Starting in 2006 (the first year of the outbreak), we added the defoliation values (1 = low, 2 = moderate, and 3 = severe) to obtain a defoliation severity index (Simard and Lajeunesse, 2015) representing cumulative defoliation since the beginning of the outbreak. Stand defoliation history was variable but comparable between the natural and harvested sites, except for one of the natural sites (site N3) that was more defoliated than the others (Fig. 2). Thus, any differences between the defoliation of advance regeneration in natural sites versus harvested sites should not be a result of differences in defoliation history.

2.3. Sampling

2.3.1. Advance regeneration

During the summer of 2015, one (in natural sites) or two (in harvested sites) 100-m long transects were sampled at each site to evaluate the abundance, composition and defoliation of advance regeneration. Natural sites were installed in 2013 whereas harvested sites were installed in 2015. Two transects were installed in the harvested sites to account for spatial heterogeneity due to skid trails and unsalvaged patches. At each site, 60 live balsam fir and 60 live black spruce regenerating stems were randomly selected along the transects, in each of the five following height classes (total of 300 stems per species): 8 to 14.9 cm, 15 to 49.5 cm, 50 cm to 1.29 m, 1.3 to 2.29 m, and > 2.3 m but with a dbh < 5 cm (diameter at breast height; 1.3 m above the ground). We tagged and mapped each stem, and noted their status (live or dead; all stems were alive in 2013 in natural sites and in 2015 in harvested sites) and cumulative defoliation caused by the SBW according to the following categories: 0 to 5%, 6 to 25%, 26 to 50%, 51 to 75%, 76 to 95%, and 96 to 100%.

At each site, more precise measurements were made of a subsample of 10 regenerating stems of each species and of each height class, for a