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Five decades of balsam fir stand development after spruce budworm-related mortality

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ABSTRACT

We report on stand development of nine plots in northern New Brunswick, Canada from 1956 to 2012, including a severe spruce budworm (SBW; *Choristoneura fumiferana* [Clem.]) outbreak from 1951 to 1960 and a SBW outbreak moderated by insecticide protection from 1975 to 1988. Our objectives were to (1) determine how mortality caused by SBW defoliation altered self-thinning competition over the next 50 years; (2) compare stand development of SBW-impacted stands with that of long-term precommercial thinning trials in the same area; and (3) determine whether regeneration data and projected future stand composition supported the Baskerville hypothesis that the SBW–fir (*Abies*) forests of northwestern New Brunswick form a self-regulating cyclical successional system. The SBW outbreak caused 18–80% tree mortality, and this variable impact reduced relative density of host tree populations from a mean of 69% in 1956 to 22–66% by 1965. Stand development and competition-induced mortality over the next 50 years varied as a function of post-outbreak stocking. By 2012 (age 92 years), total softwood volume ranged widely from 150 to 342 m^3 ha^{-1}. Comparison with long-term published Green River Thinning Trial data indicated that both thinned and unthinned plots had higher volume at younger ages than those 'thinned' by SBW, and that lower stand-level production after the SBW outbreak resulted from understocked conditions. Prolific advance balsam fir regeneration was present in the plots in 2012; this and stand dynamics simulations supported the Baskerville self-regulating cyclical successional hypothesis. Results demonstrate how long-term stand development following a SBW outbreak is strongly influenced by outbreak severity and resulting stand structure.

1. Introduction

Spruce budworm (SBW, *Choristoneura fumiferana* [Clem.]) outbreaks in immature (age ~20–40 years) balsam fir (*Abies balsamea* (L.) Mill.) stands typically result in an average of 42% mortality based on a review of 26 stands from various studies (MacLean, 1980). Mortality levels in immature balsam fir stands vary widely as a function of the local severity of SBW defoliation, with about 40% of plots having 21–40% mortality, 15–20% of plots in each of the 0–20, 41–60 and 61–80% mortality classes, and 4% of plots with 81–100% mortality (MacLean, 1980). SBW outbreaks in immature fir stands therefore typically result in partial mortality, which reduces stand density and has been shown to increase subsequent stand growth (e.g., MacLean and Andersen, 2008).

Disturbance-mediated mortality dominates during severe insect outbreaks, but self-thinning processes resume after the disturbance subsides. Hence, if mortality during SBW outbreaks is variable and results in varying post-outbreak stand density, this should alter subsequent self-thinning processes and long-term stand development. Higher mortality during the SBW outbreak would lower stocking post-outbreak, and this should reduce subsequent self-thinning mortality in comparison to stands with lower SBW-caused mortality. Undisturbed balsam fir stands are often subject to intense self-thinning pressure due to their high density (e.g., McCarthy and Weetman, 2007), with self-thinning beginning at 16–24 years post-harvest at ~8000 stems $\cdot ha^{-1}$ in northwestern New Brunswick (Pitt and Lanteigne, 2008).

Baskerville (1975) hypothesized that stand dynamics are driven by the interdependency between SBW and balsam fir in northwestern New Brunswick. His conjecture was that mature or overmature balsam fir stands are periodically killed by SBW outbreaks and advance fir regeneration present then develops into dense pole-sized stands, which are subsequently 'thinned' by the next SBW outbreak about 35 years later. This second SBW outbreak sufficiently opens the canopy to permit seedling establishment and

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the subsequent development of a new understory of advance fir regeneration. Hence Baskerville (1975) termed SBW a 'super silviculturist'.

In immature stands the silvicultural treatment that comes closest to emulating SBW is precommercial thinning (Baskerville, 1975), but unlike precommercial thinning where optimal spacing is provided for selected individual trees, spatial variability associated with SBW defoliation typically results in a patchy distribution of surviving trees (Baskerville and MacLean, 1979). Precommercial thinning of young stands to reduce density that have developed from prolific natural regeneration is used operationally to increase product yield and reduce time to merchantability (Pitt and Lanteigne, 2008). Over 3 million hectares of young forest were precommercially thinned in eastern Canada from 1990 to 2014, and thinning continues at a rate of about 122,000 ha $year^{-1}$ (Canadian Council of Forest Ministers, 2015). However, the sequential mortality from SBW outbreaks has a spatially contagious distribution that tends to create 'holes' in stands, which become larger and larger due to defoliation-caused mortality and windthrow, leaving the surviving trees in an increasingly clumped configuration (Baskerville and MacLean 1979). In contrast, thinning aims to evenly space selected crop trees in order to maximize growth.

In this paper, we report a case study of stand development of nine plots in northern New Brunswick from 1956 to 2012, including a severe SBW outbreak from 1951 to 1960 and a SBW outbreak moderated by insecticide treatment from 1975 to 1988. This long-term data set allowed us the unique opportunity to examine stand development over five decades following a SBW outbreak, and by measuring current regeneration and using stand dynamics models, to infer future stand development. Objectives were to (1) determine the interactions of mortality caused by SBW defoliation and by self-thinning competition over 56 years; (2) compare stand development of SBW-impacted stands with long-term data from precommercial thinning trials in the same area (using results of Pitt and Lanteigne, 2008); (3) determine regeneration and project future stand composition; and 4) test the Baskerville (1975) hypothesis that the SBW–fir forests of northwestern New Brunswick form a self-regulating cyclical successional system. We predicted that 1) the timing and amount of self-thinning mortality over the five decades following the SBW outbreak would differ depending upon the amount of SBW-caused mortality, e.g. self-thinning mortality volume would be greater and occur earlier when low SBW-caused mortality occurred; (2) spatially contagious mortality caused by SBW would reduce stocking and result in lower volume production than in evenly spaced precommercially thinned stands; and (3) the 56 years of stand development data and regeneration information measured in the plots would support the Baskerville (1975) SBW-fir self-regulating successional system hypothesis.

2. Methods

2.1. Plot establishment and development

Details of stand history are presented in MacLean and Andersen (2008) and only a summary and description of the 2012 measurements are included here. The dataset comprised 10, 0.04-ha plots randomly established in 1956 in a single 8-ha, 35 year old, even-aged balsam fir stand (approximately 12 km northeast of Summit Depot, New Brunswick; 47°52′05.8″N 68°12′07.1″W). The stand originated from advance growth that was present under a mature stand killed in the SBW outbreak of 1913–1919 (Vincent 1962; Baskerville 1975). It was even-aged, dating from release in the early 1920s, and on an excellent site, well-drained upland silty clay loam. The stand was included in a 5400-ha tract of land that was set aside near the center of a SBW outbreak, and not sprayed with insecticide or logged, so that effects of an uncontrolled outbreak could be studied. One of the original 10 plots was cut between 1975 and 1980; data presented here are for the nine remaining plots.

From 1957 to 1961 annual assessments of SBW defoliation were conducted at the stand level along with tree-level assessments of mortality. No ground-based annual defoliation data were available after 1965, so annual aerial defoliation survey data collected by the Canadian Forest Service or New Brunswick Department of Natural Resources were used. Each tree in the plots was assessed every 5 years from 1965 to 1995 for dbh, height, species, and mortality, and then assessed again in 2012.

2.2. Outbreak and stand history

The stand originated from an early 1900s SBW outbreak (Tothill, 1923; Hughes, 1957; Vincent, 1962; Baskerville and MacLean, 1979). Growth reductions from SBW defoliation were detected in northwestern New Brunswick in 1913, however SBW populations were likely present as early as 1909 (Swaine and Craighead, 1924). By 1919 the outbreak had largely subsided (Tothill, 1923) with population levels being reduced such that no noticeable defoliation occurred by 1922 (Swaine and Craighead, 1924). Across New Brunswick, losses of up to 55 million m^3 of timber volume were estimated between 1910 and the early 1920s (Swaine and Craighead, 1924).

At plot establishment in 1956, total volume of the nine plots ranged from 157 m^3 ha^{-1} to 211 m^3 ha^{-1} (Table 1). Average stand-level current defoliation (mean % of current-year foliage removed) each year from 1948 to 1960 was 0, 0, 20, 45, 91, 98, 98, 34, 92, 48, 2, 2, and 2% (Morris, 1963).

2.3. 2012 plot re-measurement

In 2012, the plots were relocated and their centers recorded with a GPS. Trees were re-measured for dbh, height, tree status (live or dead), and crown class (dominant, co-dominant, intermediate, suppressed). Where tree tags could not be located, tag numbers were inferred based on tag sequence and tree condition in 1995 (i.e., species and dbh). New ingrowth trees with ≥5 cm dbh were measured and assigned tree numbers.

Regeneration was sampled to help infer future stand succession. Four 14 m transects were established on random compass bearings from plot center, with one transect located within each of the four 90° compass quadrants. Along each transect, three 2 m × 2 m quadrats were randomly located and all trees ≥2 m in height and <5 cm dbh were recorded by species and dbh. Within each 2 m × 2 m quadrat a 1 m × 1 m quadrat was established and regeneration 5–199.9 cm in height was recorded by species and seven height classes (5–15, 15.1–30, 30.1–45, 45.1–60, 60.1–100, 100.1–150, and 150–199.9 cm).

2.4. Plot data analyses

Following SBW-caused mortality from 1956 to 1965, the 1965 (age 45 years) basal area (BA) of the nine plots ranged from 14 to 42 m^2 ha^{-1} (Table 1). In the absence of plot-level defoliation data, post-outbreak BA was used to infer a measure of SBW outbreak severity, in order to evaluate the effect of outbreak severity on subsequent plot growth and mortality, species composition, and regeneration. Stand development measures included stand density, BA, volume, species composition, and changes in these through mortality, growth on surviving trees, and ingrowth (saplings). Five-year periodic volume increment (PI, m^3 ha^{-1}/5-years) was calculated as: