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Original article

The influence of natural disturbances on developmental patterns in Acadian mixedwood forests from 1946 to 2008

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A B S T R A C T

We used dendrochronological analyses to identify periods of natural disturbance and resulting growth responses in 32 mixed species stands in the Acadian forest. Stands represented five different development patterns, based upon 1946 softwood (SW) content (70–80%, termed SW versus 30–60%, termed mixedwood (MW)) and change in SW content from 1946 to 2006: SW-stable, SW-declining, MW-fluctuating, MW-stable, and MW-declining. Standardized growth chronologies were developed from 1163 increment cores sampled from balsam fir (*Abies balsamea*), red spruce (*Picea rubens*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*). Growth chronologies clearly identified three spruce budworm (*Choristoneura fumiferana*) outbreaks from 1914 to 1921, 1954 to 1961, and 1975 to 1984, and birch dieback from 1938 to 1948. Stand developmental patterns were caused by species characteristics and multiple interacting disturbances, resulting in mortality, growth reductions, releases, and establishment of new cohorts. Balsam fir was present in all stands, but its tendency to establish and release from advanced regeneration following budworm-caused mortality resulted in cyclical proportions of fir in the canopy. Red spruce was less vulnerable to spruce budworm and longer lived, allowing them to persist and better withstand disturbance. Periodic growth index values less than 0.9 for fir and spruce were correlated with mortality of softwoods caused by defoliation, which resulted in release and growth index values >1.1 for sugar maple. Our results demonstrated substantial variation in mixedwood development patterns over a 60-year period within a small (45 km) area.

1. Introduction

Forest management planning is based on understanding and modeling stand development patterns that result from complex interactions among species characteristics, the environment, and disturbances. Natural disturbances have important effects on stand developmental patterns (e.g., Yemshanov and Perera, 2002), and species-specific disturbance agents interacting with different species longevity can drive pulses of mortality and growth reduction of some species in combination with release and growth enhancement of other species. For effective forest management we need to understand how such disturbances and interactions result in species composition and stand development changes over time.

In Atlantic Canada, the dominant natural disturbance is periodic outbreaks of spruce budworm (*Choristoneura fumiferana* Clem.), which cause substantial, species-dependent mortality of host balsam fir (*Abies balsamea* (L.) Mill.) and spruce (*Picea* sp.) (e.g., MacLean, 1980; MacLean et al., 2002). Spruce budworm outbreaks cause growth reductions of host species and growth increases of non-host species (e.g., Hennigar and MacLean, 2010). Fire return intervals in this area are long, averaging 625 years (Wein and Moore, 1977). However, even in non-outbreak periods, large variability in balsam fir-spruce volume development patterns occur, ranging from decreasing, stable, or increasing volume over time (Taylor and MacLean, 2005), with 29% of 585 permanent sample plots in New Brunswick, Canada from 1987 to 1998 exhibiting decreasing volume. Decline resulted from increased rates of mortality, influenced by ecoregion, species, and combined effects of past insect outbreak and wind disturbances (Taylor and MacLean, 2005), occurring up to 29 years after defoliation ceased (Taylor and MacLean, 2009).

Mixed tolerant hardwood/spruce-fir stands (hereafter termed mixedwoods) are characteristic of the Acadian forest region in Atlantic Canada, where temperate tree species of the northeastern United States intermix with boreal forest species. Mixedwood stands provide habitat for a variety of species (e.g., Girard et al., 2004; Ritchie et al., 2009), are an important source of timber for forest industry, and undergo lower spruce budworm defoliation of

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host species than in pure softwood stands (Su et al., 1996). Concerns about reductions of mixedwood stands have been raised (Betts et al., 2003; Higdon et al., 2005; Etheridge et al., 2005) because common forestry practices tend to shift tree species composition toward either softwood or hardwood dominance (Bergeron and Harvey, 1997; Etheridge et al., 2005).

An analysis of forest composition from 1946 to 2002 for a 190,000 ha industrial forest in New Brunswick, Canada showed that softwood area was similar (40% versus 42%), but mixedwood decreased from 37% to 18%, and hardwood increased from 10% to 25% (Etheridge et al., 2005). Only 18% of unharvested mixedwood stands in 1946 remained the same type by 2002, with 56% transitioning to hardwoods (Etheridge et al., 2006). Amos-Binks et al. (2010) identified five different stand development patterns on this landbase, based upon 1946 softwood (SW) content (70–80%, termed SW versus 30–60%, termed mixedwood (MW)) and change in SW content from 1946 to 2006 (SW-stable, SW-declining, MW-fluctuating, MW-stable, and MW-declining). Over the period from 1946 to 2002, SW content change ranged from +18% to −62%. SW content declined because of high balsam fir mortality due to old age and a 1950s spruce budworm outbreak, plus birch (*Betula* sp.) dieback in the 1940s (Gibson, 1953; Baskerville, 1965; Bourque et al., 2005), with higher declines of SW on southerly aspects and at higher mean elevations (Amos-Binks et al., 2010). The SW-stable class had a higher proportion of red spruce (*Picea rubens* Sarg.).

Amos-Binks et al. (2010) attempted to use spruce budworm defoliation data, from annual aerial surveys, to explain the varied stand development trajectories, but although decreases in SW composition and SW canopy cover in MW- and SW-declining stands coincided with the 1947–1956 spruce budworm outbreak, defoliation data did not explain the differences. This may be because of the relatively coarse nature of available aerial defoliation survey data. Dendrochronology has been shown to be an effective tool to examine both disturbance dynamics (Fraver and White, 2005a; Bouchard et al., 2006) and to quantify effects of spruce budworm outbreaks (MacKinnon and MacLean, 2004; Taylor and MacLean, 2008). Therefore, in this paper, we used a dendrochronological analysis of tree growth in the same 32 mixedwood stands, representing declining, fluctuating, and stable stand development classes, studied by Amos-Binks et al. (2010) to: (1) identify periods of natural disturbance that may have influenced stand dynamics of balsam fir—shade tolerant hardwood stands; (2) determine growth patterns and periods of tree release for two spruce budworm host species and two non-host tree species, and their relationship to mortality; and (3) analyze how natural disturbances influenced composition and developmental patterns of the five stand classes.

2. Methods

2.1. Study area

The study area is the J.D. Irving, Limited Black Brook District, located in northwestern New Brunswick, Canada, at the northern limit of the Acadian forest region (Rowe, 1972). A detailed description of characteristics of the study area was presented by Amos-Binks et al. (2010), and only a summary will be given here. The 190,000 ha privately-owned landbase has been intensively managed since the 1950s. Prior to acquisition of the lands by J.D. Irving, Limited in 1944, much of the southern portion of the landbase had been under cutting license for 40 years (Lussier and Grenier, 1947), while the less accessible northern portion had remained unharvested prior to 1939 (Grenier, 1945).

The majority (94%) of the Black Brook District is located in the northern portion of the Central Uplands Ecoregion (New Brunswick Department of Natural Resources, 2003), made up of Ordovician to Devonian meta-sediments and rich soils. Abundant average annual precipitation (approximately 1300 mm) is accompanied by a cool climate (New Brunswick Department of Natural Resources, 2003). The distribution of hardwood and softwood species reflects effects of daily shifts of cold air from higher elevations to the valleys. Valleys have a high concentration of balsam fir and spruce whereas tolerant hardwoods (yellow birch (*Betula alleghaniensis* Britt.), sugar maple (*Acer saccharum* Marsh.), and beech (*Fagus grandifolia* Ehrh.) occupy upper slopes, hills and ridges. Slopes contain a mixture of balsam fir, spruce, and tolerant hardwoods in mixedwood stands. Southern slopes maintain a warmer topoclimate that favors tolerant hardwood species. Low fire frequencies have resulted in sparse fire-dependent species like white pine (*Pinus strobus* L.) and trembling aspen (*Populus tremuloides* Michx).

2.2. Stand selection and sampling

A total of 32 unharvested stands representing five stand development classes were sampled, where the classes were defined based on 1946 softwood content (70–80% cover, termed SW versus 40–60%, termed MW) and change in softwood content from 1946 to 2006 (stable, declining, or fluctuating) based on photo interpretation of 50 m × 50 m grid cells in each stand on sets of aerial photographs from 1946, 1966, 1982, and 2006. Stand selection methods, development patterns, locations, and photo-interpretation methods are described in detail in Amos-Binks et al. (2010). Although a complete history of these stands is unavailable, many of the stands on this landbase were probably initiated by the spruce budworm outbreak in the 1870s (Etheridge et al., 2005). Three other well known spruce budworm outbreaks occurred on the landbase during the 1910s, 1950s and 1970s–1980s. In addition, significant mortality among birch species occurred in the area due to birch dieback in the 1940s (Gibson, 1953). Photo-interpretation and ground verification indicated that no harvesting occurred in the sample stands after 1946, but there may have been partial harvesting between 1870 and 1945.

The 32 stands (mean size 13.4 ha; range 3.1–27.2 ha) were sampled in 2008 with three variable radius (prism, 2 m^2/ha basal area factor) plots per stand. Prism plots were established in specific 50 m by 50 m grid cells in each sample stand, selected based on the grid cell's percentage of softwood cover in each photo-interpretation measurement year (Amos-Binks et al., 2010), to match the mean softwood content of the stand over time. Plot locations were first determined by compass and GPS and later confirmed using >180 differentially corrected points per plot. Diameter at breast height (DBH), height, species, and crown class (dominant, co-dominant, intermediate, or suppressed) were recorded for all trees >8 cm DBH within the plot. Two increment cores were extracted at breast height (1.37 m) 90–180 degrees in orientation from each other and parallel to the topographic contour, when possible, from every second dominant or co-dominant tree in each plot to a maximum of five trees per species [balsam fir, red spruce, white spruce (*Picea glauca* [Moench] Voss), eastern white cedar (*Thuja occidentals* L.), yellow birch, sugar maple and red maple (*Acer rubrum* L.)] per plot, or 15 trees per species per stand. When spruce budworm host species (balsam fir or spruce) were not present or sparse within the plot, cores were extracted from host trees outside the plot. A total of 1163 increment cores were analyzed. Cores were stored in plastic straws sealed with tape in a freezer.

2.3. Increment core measurement and data analyses

Increment cores were mounted on core boards and sanded to a fine polish using progressively finer sand paper to a grit of 1000 using standard core preparation techniques (Swetnam et al., 1988). Cores were measured to the nearest 0.01 mm using the