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Response of aspen stands to forest tent caterpillar defoliation and subsequent overstory mortality in northeastern Ontario, Canada

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ABSTRACT

Overstory mortality, understory tree recruitment, and vegetation development were assessed in trembling aspen (*Populus tremuloides* Michx.) stands following two recent episodes of forest tent caterpillar defoliation (*Malacosoma disstria* Hbn.) in northeastern Ontario. The results suggest that poplar (aspen and balsam poplar (*Populus balsamifera* L.)) mortality increased with consecutive years of insect defoliation occurring from the mid-1980s to mid-2000s and the proportion of poplars in the overstory, but decreased with improved pre-defoliation tree vigour (DBH increment). The first outbreak, which lasted from the mid-1980s to early 1990s, was more severe in terms of insect defoliation and contributed more to poplar mortality and decline. The decline began in the late 1990s and peaked in early 2000s. Poplar regeneration and understory shrubs responded rapidly to foliage loss to insect defoliation and mortality of overstory poplars. The regenerated poplars were able to maintain their growth under developing shrubs and residual overstory canopy and numbers were sufficient to compensate for the poplar trees lost to insect infestation. The defoliation-induced overstory decline will accelerate the transition of aspen stands to conifer dominance through enhanced conifer recruitment and growth, and reduced hardwood overstory in aspen-dominated stands, while hardwood dominance will persist in pure aspen stands. From a timber supply perspective, the decline caused by forest tent caterpillar defoliation could delay the availability of aspen stands for harvesting by 40–50 years.

1. Introduction

Forest tent caterpillar (*Malacosoma disstria* Hbn.) (FTC) is the most serious defoliator of trembling aspen (*Populus tremuloides* Michx.) and balsam poplar (*Populus balsamifera* L.) in Canada (Peterson and Peterson, 1992). The FTC outbreaks, typically 3–6 years in duration, can affect large areas (Sippell, 1962; Hildahl and Campbell, 1975) reducing tree growth and vigour but seldom inducing tree mortality (Ghent, 1958; Hildahl and Campbell, 1975; Peterson and Peterson, 1992). In northeastern Ontario, several FTC outbreaks have occurred since 1948. The most recent outbreak occurred from the mid-1990s through 2004 and peaked in 2001, immediately after the previous outbreak which occurred in the mid-1980s through the early 1990s and peaked in 1992 (Cooke et al., 2009).

The repeated long periods of defoliation, coupled with a period of drought, have resulted in extensive mortality of overstory trees (often referred to as "decline" or "stand dieback", see Frey et al., 2004) in aspen stands in the affected areas of northeastern Ontario (Candau et al., 2002). First detected in 2000 through aerial survey, the affected area covered 516,395 ha by 2004. The mortality level of trembling aspen and balsam poplar in these declined stands varied and could reach nearly 100% (B. Fox, OMNR, unpubl. data). The overstory canopy decline is expected to release understory conifers and accelerate forest succession from hardwood to conifer dominance (Greene et al., 1999; Shepperd et al., 2001; Chen and Popadiouk, 2002). The long-term dynamics of these declined stands are, however, largely unknown, due to lack of quantitative information on regeneration responses and post-decline stand structure. This affects forest planning and long-term wood supply analysis for northeastern Ontario mills.

The future dynamics of affected aspen stands likely depend on the composition of both overstory and understory communities prior to FTC outbreaks, the level of insect defoliation and resultant overstory mortality, and time since disturbance. Reduction of the overstory canopy stimulates aspen and balsam poplar regeneration as well as the growth of understory vegetation and conifers. As such, the density of understory poplars following insect defoliation is lower than that after clearcutting or fire, and often inadequate for replacing trees lost to insect infestation (Frey et al., 2004). Regeneration responses of aspen stands to insect defoliation and overstory

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decline have not been quantified and how regenerated poplars perform under heavy shrub competition and shade of residual overstory trees remains unknown.

In this study, we investigated aspen stands of various ages, overstory composition prior to recent FTC outbreaks, and post-defoliation mortality to quantify changes in residual stand structure of both overstory and understory following FTC defoliation and subsequent decline. Specifically, we assessed (1) changes in overstory basal area, density, and composition, (2) mortality of overstory poplars in relation to stand composition, age, insect defoliation and pre-defoliation diameter growth, and (3) understory recruitment and vegetation responses to insect defoliation and overstory mortality. The ultimate goal is to better understand how affected stands may evolve over time and what the implications of this large-scale decline are for forest management planning and long-term wood supply in northeastern Ontario.

2. Methods

2.1. Study stands

Forest health monitoring aerial mapping surveys (carried out by Ontario Ministry of Natural Resources' (OMNR) Forest Health and Silviculture Section and the Canadian Forest Service (CFS) between 2000 and 2004) were used in conjunction with Ontario Forest Resource Inventory (FRI) to facilitate stand selection for field survey. Candidate stands were: (1) were fully stocked (crown closure ≥0.70) prior to recent FTC outbreaks in the mid-1980s and dominated by poplars (aspen and balsam poplar) (≥70% basal area (BA)) on fresh to moist, fine loamy to clayey soils (the dominant site type is ES 7f, see Taylor et al., 2000); (2) had a range of post-defoliation poplar mortality – from low (cumulative mortality <35%; most live trees are healthy) to heavy (cumulative mortality ≥70%; most live trees show signs of dieback); and (3) had a range of stand ages – from young (31–50 years old) to mature (51–70 years old) and overmature (>70 years old). Selected stands were assessed in the field for composition, age, crown closure, and level of poplar mortality. All stands were located in a 200 km × 80 km area between Smooth Rock Falls and Hearst in northeastern Ontario where the FTC defoliation and subsequent decline since 2000 is concentrated.

A total of 48 stands were chosen for the study. Average stand age at time of assessment was 63, but ranged from 35 to 90 years (Table 1). Five stands were under 50, 26 were 50 to 69, and 17 were 70 years or older. The pre-defoliation mean stand density was 856 stems ha^{-1} and mean basal area (BA) was 29.7 m^2 ha^{-1}, including all the live and recently dead trees in the overstory at time of measurement. Hardwood species, mainly trembling aspen (61%), balsam poplar (35%), and white birch (*Betula papyrifera* Marsh) (4%), constituted 89% of the average overstory canopy by basal area and 84% by density. The dominant conifer was balsam fir (*Abies balsamea* (L.) Mill.), with small amounts of white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea mariana* (Mill.) B.S.P.).

2.2. Data collection

Within each selected stand, three circular plots of 11.28 m radius were established to assess overstory trees using the field protocols established by the Ontario Growth and Yield Program (Hayden et al., 1995). The three plots formed a triangle with 40 m between plot centres. Each overstory plot had four 2 m × 2 m subplots for understory tree and vegetation assessment, placed at 90° intervals along the circumference of the circular overstory plot.

All live overstory trees (>10 cm diameter at breast height (DBH)) and large saplings (>4 m tall and ≤10 cm DBH) within overstory plots were tagged and tallied for species, DBH, and crown class (dominant, co-dominant, and understory) in late fall 2005 and early spring 2006. Standing and fallen down dead trees in each plot were identified to species and measured for DBH. According to Alban and Pastor (1993) and our observations, hardwood trees that were well decomposed and conifers that had lost all bark were presumed to have died prior to the early 1990s outbreak and were excluded from the overstory assessment.

The abundance of understory vegetation and trees were quantified in 4 m^2 subplots in the summer of 2006 as follows: (1) percent ground cover of shrubs, grasses, herbaceous plants (herbs), ferns, and mosses, (2) stem counts for three dominant tall shrubs: speckled alder (*Alnus rugosa*), mountain maple (*Acer spicatum*), and beaked hazel (*Corylus cornuta*), by height classes of small (0.50–2.0 m) and large (>2.0 m), and (3) stem counts for understory hardwoods and conifers by species and height classes of small seedling (≤0.20 m), large seedling (0.21–1.30 m), and small sapling (1.31–4.0 m).

In each stand, outside the overstory plots, stem disks were collected at 0.20 m aboveground from a minimum of three regenerated aspen and balsam poplar and tall understory shrubs (by species) randomly selected near the centre of the triangle formed by three overstory plots. Additionally, outside the overstory plots increment cores were also collected from three live dominant overstory aspen and balsam poplar. Stem disks and cores were processed and measured for ring width to nearest 0.01 mm, using the Tree Ring Increment Measurement (TRIM) System (Fayle and McIver, 1986). Ring width data from stem disks were used to determine age and basal diameter growth rate of regenerated poplars and shrubs. Increment cores from live overstory poplars were used to verify FRI stand age and provide pre-defoliation diameter increment as an indicator of tree vigour (Waring et al., 1980).

Insect defoliation, in terms of the total/consecutive years of defoliation during each of the FTC outbreaks, was obtained from annual FTC defoliation surveys (carried out by the Forest Insect and Disease Survey and Forest Health Monitoring staff of CFS from 1933 to 1997 and by CFS and OMNR's Forest Health and Silviculture Section from 1998 to 2005). Survey mapping is done from aircraft in combination with ground checks. Sketching of defoliated areas is done on 1:125,000 or 1:250,000 maps, which are then digitized and electronically stored. Five FTC outbreaks were identified in the study area with defoliation peaking in the early 1940s, early 1950s, late 1970s, early 1990s, and early 2000s. Stands with negligible or light defoliation (<30%) are classified as healthy or 'not defoliated' and those with moderate (30–69%) and severe (≥70%) defoliation as 'defoliated' stands. The number of years of defoliation for each selected stand was determined by overlapping GPS locations and the digitized defoliation maps.

2.3. Data analysis

Stand composition was calculated as proportions of BA and density (stems ha^{-1}) of hardwood in the overstory relative to totals for the stand. Similarly, stand mortality following the recent FTC outbreaks was determined as total amounts or proportions of BA and density of dead trees compared to all stems.

Regression and correlation analyses were conducted to examine the relationships of stand attributes and insect defoliation with poplar mortality and understory development, using Proc Reg and Proc Corr in SAS Release 9.1 (SAS Institute Inc., Cary, NC). First, multiple regression was run to identify factors that influence poplar mortality through stepwise selection (the level of significance for variables to enter or stay was 0.15). The factors examined included: pre-defoliation poplar BA, proportion of poplar, stand total density, stand age, DBH increment of live overstory poplars, and insect defoliation. Then, data from all stands were pooled to examine the