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Effects of partial harvesting on species and structural diversity in aspen-dominated boreal mixedwood stands

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ABSTRACT

Partial harvesting is thought to result in more structurally diverse forest stands, providing a promising alternative to clearcutting and helping balance timber production and biodiversity conservation. Evidence for this hypothesis is based mostly on understory vegetation communities, with little information available on how partial harvesting affects tree species and structural diversity. In this study, we examined overstory and understory tree species and structural diversity of boreal mixedwoods over 20 years in stands that were unharvested, partially harvested with 40% canopy removal, and clearcut. As expected, clearcutting reduced overstory tree species and structural diversity relative to that of unharvested stands; partial harvesting, however, did not affect neighbourhood (area of 4 trees including one subject tree and 3 neighbours) or stand diversity until after a forest tent caterpillar outbreak that occurred during years 3–5 post-harvesting. The insect-induced trembling aspen (*Populus tremuloides* Michx.) mortality was higher in the partially harvested than in the unharvested areas decreasing structural diversity at both neighbourhood and stand scales. In comparison, within-stand variations (horizontal complexity or spatial heterogeneity) in neighbourhood diversity values (Shannon species diversity, Shannon structural diversity by 2-m height class, and structural diversity by height variation) increased following the insect outbreak. The post-harvesting temporal dynamics of overstory diversity appeared time dependent and related to harvest removal, forest tent caterpillar defoliation, and growth of released balsam fir (*Abies balsamea* (L.) Mill.) and aspen regeneration. In all treatments, understory diversity was decreased by clearcutting, which stimulated profuse aspen suckering, and abundant balsam fir regeneration. We conclude that partial harvesting with 40% canopy removal did not significantly change tree species or structural diversity of boreal mixedwood stands in northeastern Ontario, Canada. Changes in overstory diversity following a forest tent caterpillar outbreak, however, suggest that partial harvesting that removes more of the canopy and reduces individual tree dominance may increase species diversity and within-stand structural variation but reduce structural diversity in the overstory.

1. Introduction

In North American boreal forests, mixedwood stands dominated by trembling aspen (*Populus tremuloides* Michx.) are notable for their relatively high productivity, diverse stand types, and rich understory communities (De Grandpré and Bergeron, 1997; Reich et al., 2001; Chen and Popadiouk, 2002; Cavard et al., 2011). Following stand-replacing disturbances in these forests, shade-intolerant hardwoods, mostly trembling aspen and white birch (*Betula papyrifera* Marsh.), regenerate profusely and quickly dominate sites with shade-tolerant conifers including black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) Mill.) establishing in the understory (Lieffers and Beck, 1994; Man and Lieffers, 1999; Peters et al., 2006; Nlungu-Kweta et al., 2014). This two-story vertical structure changes over time due to tree and understory vegetation growth in gaps caused by aging, windthrow, or insects (Chen and Popadiouk, 2002; Hart and Chen, 2006), resulting in a range of stand composition and structure. This structural diversity could be reduced by use of the clearcut silvicultural system, which may simplify stand structure (Haeussler et al., 2007; Witté et al., 2013).

Structure is a key element of stand biodiversity and influences the type and amount of coarse woody debris (Brassard and Chen, 2006), site productivity (Man and Lieffers, 1999; Chen et al., 2003; Légaré et al., 2005), and diversity of understory plants, insects, birds, wildlife, and soil flora and fauna (Bartemucci et al., 2006; Brassard et al., 2008). Stand structural diversity is associated with varied tree species and sizes

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(Gadow et al., 2012; Man and Yang, 2015) and can be assessed at different scales (Man and Yang, 2015). Stand-scale assessments provide considerable insight into overall structural diversity, including species composition and vertical complexity (Swindel et al., 1984; Staudhammer and LeMay, 2001; Brassard et al., 2008; Thakur et al., 2014), while neighbourhood assessments capture within-stand spatial variations (both horizontal complexity and vertical complexity), an important aspect of stand structural diversity, complexity, and heterogeneity (Lahde et al., 1999; Zenner and Hibbs, 2000; Man and Yang, 2015).

Partial harvesting has been recognized as an alternative to clearcutting that balances the needs for timber production with those of maintaining biodiversity and ecosystem function (Lieffers and Beck, 1994; Bergeron and Harvey, 1997; Harvey et al., 2002; Man et al., 2008a; Witté et al., 2013). Stand structure and composition changes occur after harvesting due to differential removal of tree species and size classes (MacDonald, 2000; Prévost and Pothier, 2003; Brais et al., 2004) and varying regeneration and growth responses of shade tolerant and intolerant tree species (Prévost and Pothier, 2003; MacDonald et al., 2004; Lennie et al., 2009; Prévost and DeBlois, 2014). Because partial harvesting results in the structure and attributes of both harvested and unharvested canopies, it is thought to produce more structurally diverse forests than clearcutting or no cutting (Harvey et al., 2002; Haeussler et al., 2007). However, research to examine the relationship between partial harvesting and biodiversity has mostly focused on understory vegetation communities (Beese and Bryant, 1999; Deal, 2001; Haeussler et al., 2007). Little information is available on how tree species and structural diversity respond to partial harvesting.

The objective of this study was to examine tree species and structural diversity of aspen-dominated boreal mixedwood stands 20 years after partial harvesting. The field sites were established during winter 1995 in northeastern Ontario, Canada (Macdonald, 2000) and post-harvesting regeneration and vegetation responses have been reported for the first 5 years by Macdonald et al. (2004) and for 11 years by Man et al. (2008a). In this study, we examined species and structural diversity of the overstory canopy (stand and neighbourhood assessments with stem mapping data) and understory tree layer immediately before and 1, 3, 5, 11, and 20 years after harvesting. We hypothesized that since partially harvested canopies contain the structure and attributes of both harvested and unharvested canopies, species composition and structure in the overstory canopy as well as the understory tree layer will be more diverse than that in clearcut or unharvested stands.

2. Materials and methods

2.1. Site description and treatments

The site conditions, experimental design, and harvesting treatments are described in detail by MacDonald (2000) and MacDonald et al. (2004) and summarized briefly here. The study site is an aspen-dominated mixedwood stand east of Cochrane, Ontario (49°04′N, 80°26′W). The soil is lacustrine-origin, fresh to moist, and fine-textured. The pre-harvest basal area (BA) of the overstory canopy was about 36 m^2/ha, dominated by trembling aspen (72%), with small amounts of black spruce (15%), jack pine (7%) (*Pinus banksiana* Lamb.), white spruce (3%), balsam fir (2%), and white birch (< 1%). The average age of dominant trees was 73-year-old for trembling aspen and 72 for black spruce. Most understory trees were balsam fir (3555 stems/ha), followed by trembling aspen (482 stems/ha), white birch (247 stems/ha), black spruce (208 stems/ha), and white spruce (13 stems/ha). Woody shrub species were mainly speckled alder (*Alnus rugosa* [DuRoi] Spreng.), mountain maple (*Acer spicatum* Lam.), and beaked hazel (*Corylus cornuta* Marsh.) (MacDonald et al., 2004).

This experiment was set up using a randomized complete block design with 4 harvesting treatments replicated 4 times. The harvesting was originally designed to remove 0 (unharvested), 36 and 68 (partially harvested), and 100% (clearcut) of the merchantable overstory basal area (BA) of all trees ≥10 cm diameter at breast height (DBH). However, due to site constraints and the need to protect advance conifer regeneration, actual BA reduction approached 40% for the two partially harvested treatments, resulting in 8 replications (MacDonald et al., 2004). Harvested plots (100 m × 100 m) were full-tree logged with a feller-buncher and a grapple skidder during January and February 1995. To achieve 40% harvesting level, there was removal of 20% of the overstory targeting large trembling aspen and balsam fir in 16-m-wide leave strips, along with a clearcut in the 5-m-wide skid trails (MacDonald, 2000). Careful logging was applied to minimize damage to advance regeneration and residual trees (Groot et al., 2005).

2.2. Data collection and analysis

Overstory trees were surveyed in a 25 m radius circular plot (0.2 ha) centered within the 1-ha harvested areas. Before and after harvesting, all trees ≥4.0 m tall were tagged and assessed for height and DBH, as well as individual stem location relative to distance and azimuth to plot centre. Understory trees were assessed in 12, 2 m × 2 m plots, equally spaced on the circumference of the circular overstory plot. Trees < 4.0 m were identified by species and measured for total height. Changes in overstory tree diameter, height, density, and basal area, and understory tree density and height after harvesting are shown in Fig. 1.

Changes in overstory diversity following partial harvesting were assessed at neighbourhood and stand scales. Neighbourhood assessments were based on stem mapping data at a scale of 4 trees—1 subject tree and 3 closest neighbours—following methods developed by Man and Yang (2015). Neighbour search was done with algorithm nn2 within the R package RANN version 2.4.1 (Arya et al., 2014). Edge effects and neighbour overlap were dealt with using the procedures documented by Man and Yang (2015). Neighbourhood diversity included Shannon species H' (Shannon and Weaver, 1949), Shannon structural diversity by 2-m height class, and structural diversity by height variation, along with within-stand variations (coefficients of variation calculated as a ratio between standard deviation and mean) of these neighbourhood diversity values (Man and Yang, 2015). For comparison, structural complexity index was also calculated as an area ratio between neighbourhood triangles of tree top and tree base (Zenner and Hibbs, 2000) using Delaunayn triangulation function within the R package geometry version 0.3-6 (Habel et al., 2015).

Stand-scale assessments included Shannon species H' and Shannon structural H' on 2-m height class for overstory trees and 3 height classes for understory trees: small seedlings (0–0.30 m), large seedlings (0.31–1.30 m), and saplings (1.31–4.00 m) (Staudhammer and LeMay, 2001). For overstory structural diversity, height variation (standard deviation) was also assessed (Man and Yang, 2015).

Analysis of variance was used to determine effects of harvesting treatments on overstory and understory tree species and structural diversity. Six assessments conducted at 0, 1, 3, 5, 11, and 20 years after harvesting were treated as repeated measures. Based on visual assessment and Shapiro-Wilk's test of residuals, data transformation was not required. When treatment or treatment by time interaction was significant ($p < .05$), multiple contrasts of treatment means were performed for each measurement time with P values adjusted with Bonferroni correction (Howell, 2012). All analyses were conducted using Proc Mixed and autoregressive (order 1) covariance structure for repeated measures data (SAS 9.3, SAS Institute Inc., 2011).

3. Results

Neighbourhood and stand diversity differed significantly by harvesting treatment and time since harvesting, except for within-stand spatial variation in the structural complexity index (SCI) that did not vary among harvesting treatments or over time (Table 1). At neighbourhood scale, overstory species H' (H_s) (means = 0.69, 0.72, and