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Dynamics of understorey biomass, production and turnover associated with long-term overstorey succession in boreal forest of Canada

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ABSTRACT

Understorey vegetation hosts the most species diversity in temperate and boreal forests and contributes substantially to ecosystem functions. Despite its ecological importance, the dynamics of understorey biomass, production and turnover rates following stand-replacing disturbance and throughout forest succession remain poorly understood. Using a replicated chronosequence spanning 8, 16, 34, 98, 146 and 210 years following fire, we examined the dynamics of understorey biomass, production and turnover associated with stand development and overstorey types (broadleaf, mixedwood, and conifer) in the central boreal forest of Canada. Across all ages and overstorey types, biomass, production and turnover rates of woody plants, herbs, and bryophytes were on average 2.71, 0.10, and 0.13 Mg ha^{-1}; 0.24, 0.13, and 0.08 Mg ha^{-1} year^{-1} and 9.7%, 127.3%, and 67.6% year^{-1}, respectively. Total understorey biomass and production increased continuously with stand age and reached the maximum in 146-year-old stands. Herbaceous biomass and production, peaked in 16-year-old stands, and remained stable thereafter with a slight increase in 146-year-old stands; in contrast, woody plant and bryophyte biomass and production peaked in 98- and 146-year-old stands. Herbaceous and woody vegetation turnover rates were higher in young stands, and those of bryophytes were higher in older stands. Total, woody and herbaceous biomass, production and turnover rates were higher under deciduous broadleaf overstorey, while values for bryophytes were higher in conifer stands, with mixedwood being intermediate. Overstorey mixture had no overall effect on total, woody, herbaceous biomass and production other than the expected from the averages of their broadleaf and conifer stands, but reduced bryophyte biomass and woody turnover. Our findings suggest that understorey biomass, production and turnover rates in the boreal forest are mainly driven by time since colonization and the resource availability and heterogeneity mediated via overstorey composition. Our results highlight the roles of stand development and overstorey composition in understorey biomass, production and turnover and their importance for modeling total forest ecosystem contribution to the global forest carbon.

1. Introduction

In boreal and temperate forest ecosystems, most of the species diversity is in the understorey (Whigham, 2004; Gilliam and Roberts, 2014). Despite the small proportion in biomass from understorey plants, the understorey contributes substantially to total ecosystem carbon and nutrient cycles due to higher turnover rates than overstorey trees (Chapin, 1983; Gilliam, 2007; Cavard et al., 2011). In particular, understorey plants are the most important component of senesced material returned to soil at early successional stages following stand-replacing disturbance, taking up available nutrients and returning them rapidly to the soil, thus contributing to soil nutrients pools and slowing down nutrient loss from runoff (Siccama et al., 1970; Zavitkovski, 1976; Chapin, 1983; Reiners, 1992; Palviainen, 2005). Quantifying understorey biomass, production and turnover rates is thus essential to accurate estimates of carbon and nutrient cycles in forest ecosystems.

In boreal forests, overstorey biomass increases rapidly following stand-replacing disturbance, peaks at canopy transition from the dominance of pioneer species to late-successional species (Gao et al., 2017). Understorey biomass, production and turnover rates are also expected to change with overstorey development, as a result of changes in understorey resource availability and time available for understorey species to colonize (Bartels and Chen, 2015; Kumar et al., 2017b). For example, at the stand initiation stage, high light and nutrient

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availability and abundant growing space result in rapid colonization of herbaceous species in the understorey (Hart and Chen, 2006, 2008; Kumar et al., 2017b). With further development of the stand, resource pre-emption by the overstorey reduces the resources available to the understorey, thereby decreasing the cover and biomass of previously established shade-intolerant and nutrient-demanding herbaceous species (Reiners, 1992; Gilliam and Turrill, 1993; Gilliam et al., 1995; Bartels and Chen, 2010; Reich et al., 2012; Halpern and Lutz, 2013). However, species tolerant of low resource conditions, such as bryophytes and shade tolerant woody plants, increase in abundance with stand development because of more time needed for colonization (Alaback, 1982; Gilliam et al., 1995; DeLuca et al., 2002; Zackrisson et al., 2004). As the stand further matures, the understorey environment becomes more heterogeneous as a result of canopy breakup, increasing both woody and non-woody biomass of understorey vegetation (Huston, 1979; Chen and Popadiouk, 2002; Bartels and Chen, 2010; Kumar et al., 2017a). Although previous studies have estimated understorey production, particulary focused on old-growth forests and woodlands (Hanley and Brady, 1997; Gonzalez-Hernandez et al., 1998; Kolari et al., 2006), the dynamics of understorey production, in particular by various life forms, in relation to long-term overstorey stand development remain poorly understood (but see Bond-Lamberty et al., 2004; Mack et al., 2008).

Post-disturbance availability of tree species propagules varies greatly depending on pre-disturbance forest species composition; post-disturbance boreal forests can thus be dominated by either broadleaf, conifer or their mixtures at any given stage of stand development (Ilisson and Chen, 2009; Taylor and Chen, 2011). Overstorey species composition strongly influences understorey biomass, production and turnover rates through modification of resources, particularly availability and variability of light, water and soil nutrient resources and other effects such as physical characteristics of the litter layer (Légaré et al., 2002; Barbier et al., 2008; Augusto et al., 2015). Deciduous broadleaf overstorey transmits more light to the understorey and deciduous litter is higher in base cations and pH than conifer litter, thus favouring herbaceous and woody plants, while inhibiting bryophytes (Paré and Bergeron, 1996; Légaré et al., 2005; Hart and Chen, 2006; Chytrý et al., 2010; Chávez and Macdonald, 2012). In contrast, coniferous litter is high in lignin content and carbon to nitrogen ratio with low soil pH and nutrient contents, favouring bryophytes (Prescott, 2002; Augusto et al., 2015). Mixedwood stands can provide a heterogeneous environment in the understorey and exhibit greater variability in understorey resources (Bartemucci et al., 2006; Macdonald and Fenniak, 2007; Chávez and Macdonald, 2010), which might result in the higher understorey biomass, production and turnover rates. However, empirical evidence for overstorey effects on understorey biomass, production and turnover rates is limited, with contrasting results (Gonzalez-Hernandez et al., 1998; Cavard et al., 2011; Zhang et al., 2017).

This study examines the effect of stand development following stand-replacing fire and overstorey composition type on understorey biomass, production and turnover rates in the central boreal forests of Canada. We specifically address the following questions: (1) how do biomass, production and turnover rates of understorey total, woody, herb, and bryophyte change following stand-replacing fire? (2) Do age-related dynamics in understorey biomass, production and turnover rates differ among forest compositional types? (3) Do conifer-broadleaf mixtures lead to higher understorey productivity, biomass, and turnover rates than we would expect from the average of their components (i.e., overyielding)? (4) Does this mixture effect change with stand development stage? We hypothesized that following fire, understorey herbaceous biomass, production and turnover rates would be higher in the early stages of stand development because of the rapid colonization rates of fast-growing herbaceous species, whereas those for bryophytes would be higher in the intermediate stages of stand development since they require more time for colonization. Woody as well as total understorey biomass, production and turnover rates would also be higher in intermediate stages because long-lived woody plants would have sufficient time to maximize their biomass and production before turning into part of canopy layer (trees) or turning over due to maturation (shrubs). Furthermore, given the known effects of overstorey compositions on the understorey, we hypothesized that independent of stand age deciduous broadleaf overstorey would support higher understorey total, herb and woody biomass, production and turnover rates relative to those formed by coniferous overstorey. For mixedwood stands, we further hypothesize that mixtures would result in overyielding of understorey biomass, production and turnover rates since mixtures have heterogeneous environment in the understorey and exhibit greater spatial and temporal variability in understorey resources than single-cover-type-dominated stands (Bartemucci et al., 2006; Macdonald and Fenniak, 2007).

2. Material and methods

2.1. Study area

The study was conducted in the boreal forests north of Lake Superior and west of Lake Nipigon in the Black Spruce Forest Management Unit, located approximately 100 km north of Thunder Bay, Ontario, Canada (49°23′N to 49°36′N, 89°31′W to 89°44′W). The area falls within the Moist Mid-Boreal ecoclimatic region (Ecoregions Working Group, 1989) and is characterized by warm summers and cold, snow-rich winters. Mean annual temperature and mean annual precipitation from 1981 to 2010 were 1.9 °C and 824 mm (app. 29% as snowfall), respectively, at the closest climatic station of Cameron Falls (Environment Canada, 2016). The overstorey on mesic sites is typically dominated by *Pinus banksiana* Lamb., *Populus tremuloides* Michx., *Betula papyrifera* Marsh., *Picea mariana* [Mill.] B.S.P., *Picea glauca* [Moench] Voss and *Abies balsamea* [L]. Mill. Common understorey shrubs and herbaceous species in the study area are *Acer spicatum* Lam., *Rubus pubescens* Raf., *Alnus incana* [L]. Moench, *Corylus cornuta* Marsh., *Calamagrostis canadensis* Michx., *Maianthemum canadense* Desf., *Viola renifolia* A. Gray, and *Aster macrophyllus* L. (Hart and Chen, 2008). Wildfire is the most common natural disturbance agent in the study area, with fire-return intervals varying spatially and temporally from 40 to 820 years (Senici et al., 2013), and a fire return interval of approximately 100 years for the past century (Senici et al., 2010).

2.2. Sampling design

To determine the effect of time since fire, we selected stands on mesic sites covering a wide range of stand age classes. As a result of available fires in the study area, we were able to sample six time since stand-replacing fire (TSF) classes, representing early stand initiation, late stand initiation, stem exclusion, early canopy transition, late canopy transition, and gap dynamics stages, respectively (Chen and Popadiouk, 2002). At any given stand development stage on mesic sites in the region; stands originated from fire can be dominated by conifer, broadleaf or mixed-species in the overstorey (Ilisson and Chen, 2009; Taylor and Chen, 2011): in so far as possible we sampled all three overstorey stand types (i.e. broadleaf, conifer, and mixedwood) for each stand age class. We targeted three replicates for each age and overstorey compositional type, however, due to the infrequency of fire and the preference of local forestry companies for harvesting mature stands, we were only able to find two replicates for 146-years-old mixedwood and broadleaf stands with road or boat access, resulting in a total of 52 stands sampled.

The selected stands were spatially interspersed across large areas to minimize spatial autocorrelation. All selected stands were > 1 ha in area, and visually homogeneous in structure and composition. To minimize effects of edaphic variability, all selected stands were located on mesic sites on flat or mid-slope positions, with no slope exceeding