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Long-term changes in belowground and aboveground resource allocation of boreal forest stands

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ABSTRACT

Age-related decline of forest stand growth is a common phenomenon, but the associated physiological causes remain uncertain. This study investigated a possible mechanism that could explain stand growth decline observed after canopy closure. We hypothesised that the proportion of resource allocation to roots increases with stand age as a response to a decrease in nutrient availability, which is related to the long-term accumulation of organic matter in boreal forests. Proxies based on soil respiration measurements and stem biomass production were used to describe temporal changes in the proportion of carbon allocated to belowground and aboveground stand components along a 1067-year post-fire chronosequence. The proportion of resources that were allocated belowground increased in the first 200 years following fire and declined thereafter. The inverse pattern was observed for the organic matter decomposition rate. Stand-level decline in wood productivity that was observed during the first 60-year period after fire can be attributed to a greater proportion of carbohydrates being allocated to roots in response to a decrease in nutrient availability. However, the relatively low productivity of old-growth stands was not associated with high belowground allocation, suggesting that other mechanisms operating at the tree- or stand-level may be involved.

1. Introduction

As has been observed in several studies, forest growth rate generally increases during early developmental stages, reaches a maximum that corresponds to a peak in stand leaf area, and then decreases gradually (Gholz and Fisher, 1982; Ryan and Yoder, 1997). A decline in growth rate after canopy closure is a well-known phenomenon (Assmann, 1970) but the underlying mechanisms remain unclear (Ryan et al., 2006). Because the hypothesis of an imbalance between photosynthesis and respiration was not supported by experimental results (Ryan and Waring, 1992), a decline in gross primary productivity or a shift in allocation to stem production are strong candidates for inclusion in a process that would explain the age-related decline in net primary production (Ryan et al., 2004; Drake et al., 2011). Accordingly, several authors have suggested lines of research that involve increases in nutrient limitation or hydraulic resistance (Ryan and Yoder, 1997; Weiner and Thomas, 2001), or changes in stand growth dominance (Binkley, 2004). Consequently, it is possible that no single mechanism can explain this decline which could be caused by site-specific processes that are acting alone or in interaction (Ryan et al., 2006).

In this study, we investigated a region of the boreal forest that is characterised by fire return intervals as long as 500 years (Bouchard et al., 2008), which are due to a cold climate and abundant precipitation (Foster, 1985). Consequently, this region is dominated by old-growth stands that are structurally different from even-aged stands that are commonly found in the boreal forest and regulated by short fire cycles (Boucher et al., 2003). To our knowledge, such old-growth stands have never been sampled in previous studies of boreal stand growth processes, given that the maximum observed stand age was generally less than 200 years (Bond-Lamberty et al., 2004; Vogel et al., 2008; Xu et al., 2012). Including old-growth boreal forests in these studies is important because they are relatively abundant and often characterised by a thick organic layer that results from continuous accumulation of organic matter over time (Fenton et al., 2005). Thick organic layers are known to immobilise large quantities of nutrients and to decrease soil temperature (Bonan and Shugart, 1989), thereby leading to poor growth conditions. Because a decrease in soil fertility has been shown to modify tree carbon allocation to roots (Gower et al., 1992; Haynes and Gower, 1995; Vanninen and

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Mäkelä, 2005), a comparison of old-growth and younger stands could highlight key processes that would be otherwise overlooked.

Tree carbon allocation to roots is difficult to measure directly. For example, excavation of entire tree root systems is time-consuming, and even if done properly, a large quantity of fine roots is usually destroyed by the hydraulic excavation technique that are used to separate roots from the soil matrix. Fine root dynamics (biomass, production, mortality and turnover) may be studied using various approaches such as sequential soil coring (indirect) or the ingrowth bag (direct) method, yet both methods have their strengths and limitations (Yuan and Chen, 2012). Yet, it is possible to estimate the pattern of the proportion of resource allocation to roots at the stand level by using measurements of soil respiration (R_s), which in turn can be partitioned into autotrophic and heterotrophic respiration.

Autotrophic respiration corresponds to the metabolic activities of roots, rhizosphere and mycorrhizae which occur in all forest ecosystems, regardless of soil conditions (Hanson et al., 2000). During the growing season, autotrophic respiration is mainly controlled by concentrations of carbohydrates that have been recently fixed through photosynthesis (Ekblad and Högberg, 2001; Bowling et al., 2002) and, thus, is related to gross primary productivity (Litton et al., 2007). As autotrophic respiration is strongly related to root production (Litton et al., 2007), the proportion of resource allocation to the root system compared to that of the aboveground component of a forest stand can be approximated by the ratio of soil autotrophic respiration to tree stem biomass increment. We used this ratio as a proxy for a "root respiration to stemwood production" ratio; from a physiological perspective, this ratio would be interpreted as reflecting the differential proportion of resource allocation to roots vs. stemwood.

Heterotrophic respiration represents the microbial respiration that depends upon substrate quality and quantity (Ryan and Law, 2005). Heterotrophic respiration can thus be used as a proxy for the decomposition rate of the organic layer, which constitutes an important component of nutrient availability in the boreal forest (Bonan and Shugart, 1989). By using measurements of autotrophic and heterotrophic respiration, together with aboveground biomass increment in forest stands of different ages, it would be possible to investigate temporal changes in the proportion of resources that are allocated to roots in relation to soil resource availability. In the humid boreal forest we investigated, nutrient availability was observed to decrease with time elapsed since the last fire (Ward et al., 2014) and can thus be considered as the soil resource most likely to affect forest productivity.

We investigated a possible mechanism that could explain the decline in stand growth that was observed following canopy closure in the northeastern Canadian boreal forest (Ward et al., 2014). We hypothesised that the proportion of resources that are allocated to roots increases with stand age as a response to a decrease in nutrient availability, which is related to the long-term accumulation of organic matter in boreal forests. To achieve this goal, we sub-sampled 15 stands from a chronosequence previously used by Ward et al. (2014), which covered a post-fire period of over 1000 years in the northeastern Canadian boreal forest. This study is therefore complementary to that of Ward et al. (2014) who studied the temporal changes in organic layer thickness, soil temperature, nutrient availability and stand productivity.

2. Material and methods

2.1. Study area

Sites were located north of Baie-Comeau (49°07′N, 68°10′W), Quebec, Canada, in the black spruce-feather moss bioclimatic subdomain (Robitaille and Saucier, 1998). The regional climate is cold maritime, with a mean annual temperature of 1.5 °C and mean annual precipitation of 1014 mm. Snow generally represents 35% of yearly total precipitation and the growing season lasts for about 155 days. The fire return interval of the study region was estimated at 270 years (Bouchard et al., 2008).

Black spruce (*Picea mariana* (Mill.) BSP) and balsam fir (*Abies balsamea* (L.) Mill.) are the dominant canopy species in these forests, with relatively minor components of white spruce (*Picea glauca* (Moench) Voss.), paper or white birch (*Betula papyrifera* Marsh.), jack pine (*Pinus banksiana* Lamb.), tamarack or eastern larch (*Larix laricina* (Du Roi) K. Koch), and trembling aspen (*Populus tremuloides* Michx.). The low frequency of fire in the area led to the creation of a forest landscape that was composed of 65–70% old-growth, uneven-aged stands (Côté et al., 2010).

2.2. Site characteristics

To investigate the effect of stand age on the proportion of resource allocation to roots, we used a sub-sample of a post-fire chronosequence (see Ward et al. (2014) that included 15 sites, which were aged from 17- to 1067-years-since-fire. The original chronosequence was composed of 30 stands, selected to be as similar as possible in terms of surface deposits, topographic position, exposure and drainage. A particular attention was given to select sites characterised by deep glacial tills with good drainage, which are the dominant biophysical features of the study area (Bouchard et al., 2008). We randomly selected three stands in each of five age classes (0–50 y, 51–100 y, 101–150 y, 151–200 y, >200 y), and established one 0.04 ha circular plot in each stand. Within each plot, the number of stems per species was determined for all trees with a diameter at breast height (DBH, 1.3 m) greater than 9.0 cm. Trees with a DBH between 6.0 and 9.1 cm were inventoried in 20 sub-plots of 4 m^2 that had been established systematically within the 400 m^2 plot, with five sub-plots per cardinal point.

The principal characteristics of the 15 sites are presented in Table 1. The thickness of the organic layer (cm), including living bryophytes, was measured at 16 locations within each plot, i.e., four locations in each of the four cardinal directions with a minimum distance of 3 m between locations. In addition, determinations of the organic layer thickness were made at least 50 cm from any major obstacle (tree stump, rocks, etc.).

Time since last fire (TSF) for stands that were <200-year-old were determined according to the historical fire map of the region, which had been prepared by Bouchard et al. (2008). They extracted basal discs from fire-scarred trees or cored several dominant trees, generally being extracted from trembling aspen and jack pine because of their rapid initial growth. TSF was calculated by subtracting the year of inventory from the year of the last fire event. For the older stands, the lifespan of individual black spruce and balsam fir trees was exceeded (Burns and Honkala, 1990); therefore, extraction of tree increment cores would have not given a precise TSF measurement, as individuals in the first cohort had likely disappeared. In such cases, ^{14}C dating of charcoal samples from the last fire was performed (for more details, see Barrette et al. (2013)).

Aboveground net primary productivity of wood ($ANPP_{wood}$) was estimated as annual production of live stemwood biomass. Five-year wood biomass production was estimated from increment cores that had been taken at 1.3 m and oriented towards the plot centre for all trees with DBH greater than 9.0 cm, using the equations of Lambert et al. (2005) that are valid for a large part of the Canadian territory, including the study area. These equations estimate wood biomass from DBH and were constructed with trees whose DBH ranged from 1.5 to more than 40 cm in the case of balsam fir and black spruce. For saplings with DBH between 5.1 and 9.0 cm, a sub-sample of at least three individuals per tree species