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## Long-term changes in stand growth dominance as related to resource acquisition and utilization in the boreal forest



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### ABSTRACT

Temporal changes in stand growth dominance, i.e. a measure of the relative contribution of different-sized trees to the total stand growth, may play a role in the commonly observed decline in forest productivity over time through a shift in resource acquisition and utilization between dominant and non-dominant trees. We hypothesized that the expected decreases in both growth dominance (GD) and relative growth rate (RGR) over time were related to decreases in leaf biomass of dominant trees or increases in allocation to leaf biomass of non-dominant trees. To better understand these potential relationships, we quantified stand growth dominance and some functional components (specific leaf area, leaf weight ratio, net assimilation rate, nitrogen per unit leaf area and nitrogen use efficiency) of the relative growth rate of dominant and non-dominant trees along forest development stages in the eastern Canadian boreal forest using a 1067-year-long post-fire chronosequence. As expected, stand growth dominance decreased with stand development, and was closely related to differences in RGR between dominant and non-dominant trees. Decline in both growth dominance and differences in RGR between 100 and 200 years after fire was related to greater biomass partitioning to leaves in non-dominant trees, coupled to better light acquisition capacity of non-dominant trees, which appeared in stands that were >75-years-old. In old-growth stands, the growth advantage of non-dominant trees over dominant trees involved other mechanisms, such as higher photosynthetic rates and better resource use efficiency in the non-dominant trees. Overall, the observed decrease in stand growth dominance with increasing age was explained mainly by declining resource acquisition and utilization in dominant trees rather than through improved resource acquisition and utilization of non-dominant trees.

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### 1. Introduction

The development of most forests follows common trends, beginning with an initial increase in tree growth rate that peaks at an early age, followed by a decline after canopy closure (Assmann, 1970; Ryan et al., 1997). Accordingly, the pattern of changes in tree and stand productivity has been related to the spatiotemporal dynamics of forest structure (Latham et al., 1998; Harrod et al., 1999; Youngblood et al., 2004). Indeed, forest structure can influence the competitive interactions between trees (Stoll et al., 2002) by reinforcing or magnifying the hierarchy of plant size (Perry, 1985). Aboveground inter-tree competition is often considered as size-asymmetric in even-aged stands

(Weiner, 1990), with large trees having access to a disproportionate quantity of light compared to suppressed trees. This can often explain the faster growth of large, dominant trees, together with greater resource use efficiency, which is defined as stemwood production per unit leaf area (Binkley et al., 2013; Campoe et al., 2013; Gspaltl et al., 2013).

Binkley (2004) proposed that the relationship between tree size and growth rate within forest stands predictably changes through stand development. These changes were quantified through the growth dominance coefficient that represents the relative contribution of different-sized trees to the total stand growth by considering their relative contribution to the total stem mass (West, 2014). A positive growth dominance indicates that the relative contribution of large trees to total stand growth is larger than their relative contribution to total stem mass. Inversely, a reverse growth dominance indicates that the relative contribution of small

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trees to entire stand growth is larger than their relative contributions to stand stemwood biomass. According to Binkley (2004), a positive growth dominance is expected in young stands, while a reverse growth dominance should characterize old-growth stands, i.e., stands in which senescence mortality begins to affect dominant trees (Bouchard et al., 2008). These temporal changes in growth dominance may play a role in the commonly observed decline in stand productivity over time (Ryan et al., 1997; He et al., 2012), but these observations are supported by few empirical studies. Indeed, the observation of this pattern requires long-term forest surveys that include the old-growth phase (Binkley et al., 2006), while most studies have hitherto focused on forests prior to maturity (Martin and Jokela, 2004; Fernández and Gyenge, 2009; Fernández Tschieder et al., 2012).

In the rare cases where reverse growth dominance was observed in old-growth stands (Binkley et al., 2006), the causes of this process were never clearly determined. It could result from growth acceleration of non-dominant trees, declining growth of dominant trees, or a combination of both processes (Binkley et al., 2006). Despite many research efforts over the years, factors that could also explain the age-related decline in forest productivity are still poorly understood, or at least not universally acknowledged. Recent results suggest that such a decline is related to the declining growth of dominant trees, with the possible influence of increasing belowground carbon allocation, nutrient limitation, hydraulic resistance and canopy abrasion (Ryan et al., 1997, 2004; Binkley et al., 2002; Rudnicki et al., 2003).

Changes in growth dominance over time are presumably driven by differences in resource acquisition and resource use efficiency among trees of varying ages and sizes (Binkley et al., 2004). These growth components can be quantitatively analyzed through the decomposition of tree relative growth rate (Williams, 1946) into indices of resource acquisition, leaf photosynthetic activity, and allocation to wood production (Evans, 1972). Comparing the relative growth rate (and their components) of different-sized trees in stands offers insight into the effects of stand structure on forest growth. In addition, tree biomass partitioning between leaves, stem and roots depends upon the environment, i.e., the most limiting resource, and on the constraints of plant size (McCarthy and Enquist, 2007). When comparing the growth of trees of different sizes, it is thus important to separate the effects due to changes in both size and environment.

In this study, we investigated the pattern of changes in growth dominance of boreal forest stands by comparing indices of resource acquisition and resource use efficiency between dominant and non-dominant trees. This was achieved by using a chronosequence that covered a post-fire period of over 1067 years and was composed of 30 stands, of which one-half had reached the old-growth stage (Ward et al., 2014; Baret et al., 2015). As proposed by Binkley (2004), we first hypothesized that growth dominance should gradually shift from positive in young stands to negative in older stands. We expect that this temporal pattern of growth dominance would be explained mainly by a decrease in the relative growth rate of dominant trees, while non-dominant tree RGR should remain relatively constant over time. By decomposing the relative growth rate of dominant and non-dominant trees into functional components (specific leaf area, leaf weight ratio, net assimilation rate, nitrogen per unit leaf area and nitrogen use efficiency), we further hypothesized that these temporal changes in relative growth rate would be explained by a decrease in resource acquisition and utilization of dominant trees while the opposite would be observed for non-dominant trees. The results from this study should help to explain the long-term dynamics of boreal forest structure as well as the age-related declines in forest 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 sub-domain (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 varied between 270 and >500 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.) (Table 1). The low frequency of fire in the area has led to the creation of a forest landscape that is composed of 65–70% old-growth, uneven-aged stands (Côté et al., 2010).

### 2.2. Site and tree characteristics

To investigate the temporal changes of growth dominance in boreal forest stands, we used the same post-fire chronosequence that was employed by Ward et al. (2014) and Baret et al. (2015). This chronosequence was composed of 30 stands, which were aged from 17- to 1277-years-since-fire. The sites were selected to be as similar as possible in terms of surface deposits, topographic position, exposure and drainage. Particular attention was given to selecting sites that were characterized by deep glacial tills with good drainage, which are the dominant biophysical features of the study area (Bouchard et al., 2008).

In each stand, we established one 0.04-ha circular plot. Within each plot, we measured the diameter at breast height (DBH, 1.3 m) of all trees with a DBH > 9.0 cm. The foliage biomass, the stem biomass and the stem increment were estimated for each tree using their DBH, together with the biomass equations of Lambert et al. (2005) for Canadian tree species. Five-year wood biomass production was estimated from increment cores that had been taken at breast height and oriented toward the plot center for all trees with a DBH > 9.0 cm. The projected leaf area (LA) of each cored tree was estimated using relationships between LA and sapwood area, as described by Ward et al. (2014). Stem increment and LA values allowed us to compute the annual aboveground wood biomass that was produced per unit leaf area, calculated at the tree-level. Tree species composition and tree size distribution along the chronosequence are presented in Table 1 and Fig. 1, respectively.

A sub-sample of the chronosequence was also used to collect tree foliage and determine their nitrogen concentrations. This sub-sample was composed of three stands that were randomly selected within each of five age classes (0–50 yr., 51–100 yr., 101–150 yr., 151–200 yr., >200 yr.) of the chronosequence, except for the 0–50 yr class for which only one stand was sampled because two stands did not contain trees with DBH > 9 cm. From the end of September to the end of October 2012, foliage samples were collected in each stand to determine foliar nitrogen concentrations and specific leaf area of trees from two social classes. These two social classes consisted of dominant trees, which corresponded to 20% of trees in the plot with the largest DBH, and suppressed trees (hereafter, non-dominant trees), which corresponded to 20% of individuals in the plot with the smallest DBH. For four black spruce or balsam fir trees per social class within each of these 13 plots, we collected three branches of the upper side of the

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