Hydraulic limitations in dominant trees as a contributing mechanism to the age-related growth decline of boreal forest stands

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ABSTRACT

Hydraulic limitations in dominant trees may play a role in the growth decline that is commonly observed in aging forest stands. We hypothesized that hydraulic limitations affect dominant trees but not non-dominant trees in aging forests, resulting in changes in growth dominance during stand development. To test this hypothesis, we used a 1067-year-long post-fire chronosequence that was established in the eastern Canadian boreal forest. Within each stand, we estimated transpiration of different sized trees using direct (stem sap flow) and indirect (leaf isotope composition) measurements, which were combined with tree and stand growth estimates (growth dominance coefficient, GD). Stem sap flow measurements indicated that transpiration rate per unit leaf area (E_L) of dominant trees indeed decreased with increasing stand age and, based upon temporal changes in leaf C and O isotope ratios, was related to an increase in stomatal closure. These results suggest that hydraulic limitation of dominant trees increased with stand age. Also, the slope of the relationship between E_L and tree diameter that was calculated for each stand decreased with decreasing GD, implying that hydraulic limitation was responsible for the shift in stand growth dominance that was observed over time. Therefore, hydraulic limitation in dominant trees clearly contributes to reverse growth dominance of old-growth boreal forests, and could be involved in age-related declines in forest productivity.

1. Introduction

The growth rate of most forests initially increases in the early stages of their development, peaks usually at the time of canopy closure, and declines thereafter (Assmann, 1970; Gholz and Fisher, 1982; Ryan et al., 1997). Such age-related declines in forest growth have been widely observed in empirical studies (Binkley and Greene, 1983; Taylor and MacLean, 2005; Xu et al., 2012). However, the underlying mechanisms are still a matter of debate (Ryan et al., 2004). Because the hypothesis of an imbalance between photosynthesis and wood respiration causing the observed decline in growth with stand age (Kira and Shidei, 1967) has been refuted (Ryan and Waring, 1992; Ryan et al., 2004; Drake et al., 2010; Tang et al., 2014), numerous investigations have attempted to identify the mechanisms involved in such growth decline. Several hypotheses have emerged, including increases in nutrient (Murty et al., 1996) or hydraulic (Ryan and Yoder, 1997; Ryan et al., 2006) limitations to photosynthesis, a shift in growth dominance among trees during stand development (Binkley et al., 2002; Binkley, 2004) and an increase in belowground carbon allocation (Gower et al., 1996; Baret et al., 2015). All of these potential

mechanisms have been experimentally supported, but no consensus has yet been reached, which suggests that a combination of site-specific processes rather than a universal mechanism could explain the decline in forest productivity with age. Recent studies also demonstrated that tree-level productivity could increase continuously with tree size (Stephenson et al., 2014) and could not be impacted by tree age (Sillett et al., 2015). Those findings make the determination of mechanisms associated with tree growth over time even more challenging.

The hydraulic limitation hypothesis (Yoder et al., 1994; Ryan and Yoder, 1997) proposed a mechanism to explain the slowing of height growth with tree size and the maximum limits to tree height. It predicts that stomatal conductance to water vapour (g_s) in tall, old trees would be constrained by a reduction in leaf-specific hydraulic conductance (k_l), causing a decrease in photosynthesis and, consequently, in primary productivity (Yoder et al., 1994). Reduction in k_l with tree size could be explained by a greater path length of the water column, an increase in sapwood density (Bowman et al., 2005), a decrease in sapwood conductance (Pothier et al., 1989), and the gravitational pull in tall trees. Because there is a strong interdependence between k_l and g_s (Sperry et al., 1993; Hubbard et al., 2001), low leaf-specific hydraulic

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conductance would also decrease leaf conductance to CO_2, thereby reducing photosynthesis and the annual gross primary productivity (GPP) over the long-term (Gower et al., 1996; Ryan et al., 1997). Overall tree transpiration would be reduced, as it depends upon tree leaf area (Granier et al., 2000), stomatal characteristics (Kelliher et al., 1993; Hogg and Hurdle, 1997) and leaf-to-air vapour pressure deficit (Oren et al., 1999).

Accordingly, a decrease in hydraulic conductance and water flux with tree height and/or age has been observed in many tree species, such as Scots pine (*Pinus sylvestris* L.) (Mencuccini and Grace, 1996; Martinez-Vilalta et al., 2006), loblolly pine (*Pinus taeda* L.) (Drake et al., 2010), maritime pine (*Pinus pinaster* Aiton) (Delzon et al., 2004), European beech (*Fagus sylvatica* L.) (Schäfer et al., 2000) and Oregon white oak (*Quercus garryana* Douglas ex Hook.) (Phillips et al., 2003). Lower net photosynthetic rate and stomatal conductance have also been observed in tall, old trees compared to smaller trees (Bond, 2000; Kolb and Stone, 2000). While a decrease in whole-tree hydraulic conductance affects stomatal aperture (Sperry et al., 1993; Sperry and Pockman, 1993; Sperry, 2000) and leaf gas exchange (Hubbard et al., 2001), age-related effects on total hydraulic conductance per unit leaf area remain unclear (Mencuccini, 2002; Ryan et al., 2006). Inconsistent results could be explained by homeostatic mechanisms that would increase the water transport capacity of the tree relative to the total leaf area (Ryan and Yoder, 1997; Becker et al., 2000). Hydraulic limitation may be not universal and as whole canopy processes are often inferred by measuring small components of the whole system because of the complexity of investigating physiological responses of large canopies, testing the hydraulic limitation hypothesis is challenging (Ryan et al., 2006).

The objective of this study was to investigate how a hydraulic limitation to photosynthesis could contribute to the decline in stand growth that was observed after canopy closure in the northeastern Canadian boreal forest (Ward et al., 2014). This was achieved by using a sub-sample of a chronosequence that covered a period of over 1067 years and, thus, included old-growth stands (Ward et al., 2014; Baret et al., 2015). Previous work in the region has shown that declining growth of dominant trees was observed soon after canopy closure and was responsible for the decline in stand growth (Baret et al., 2017). According to the hydraulic limitation hypothesis, we postulated that the transpiration rate of dominant trees, but not that of dominated trees, should decrease in aging forests. This should result in a shift in growth dominance from dominant to non-dominant trees during stand development. To test this hypothesis, we used stem sap flow measurements, leaf-level isotope composition, and tree and stand growth estimates.

2. Materials 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 about 155 days. These climatic conditions are associated with slow growth of trees whose maximum height rarely exceeds 25 m. The fire return interval of the study region was estimated to be 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.). Low fire frequency 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 test the hydraulic limitation hypothesis in boreal forest stands, we used the same post-fire chronosequence as that of 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 select 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. Tree height of all trees was also measured with an electronic dendrometer (Vertex III, Haglöf, Sweden). Foliage and stem biomass 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 1.3 m height and oriented toward the plot centre for all trees with a DBH > 9.0 cm. The orientation of increment cores toward the plot centre prevents the introduction of any bias in estimates of wood biomass increment and sapwood area. Bark growth over the 5-year period was considered negligible and therefore no correction was applied. Increment cores were used to estimate tree sapwood area (S_a), while tree projected leaf areas (L_a) were estimated using relationships between L_a and S_a, as described by Ward et al. (2014).

Time since last fire (TSF) for stands that were < 200-years-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, which were generally extracted from trembling aspen and jack pine because of their early establishment after fire. TSF was calculated by subtracting the year of inventory from the year of the last fire event. For 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 not provide a precise TSF measurements, as individuals from 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 Ward et al. 2014).

The relationship between tree size and growth rate within the sampled forest stands was characterized according to their growth dominance patterns (Binkley, 2004; Binkley et al., 2006). Growth dominance in individual stands was evaluated based upon the method that was described by West (2014). For each stand, trees were arranged in ascending order of DBH; the cumulative stem increment was plotted as a function of the cumulative stem mass to form a growth dominance curve. A growth dominance coefficient (GD), similar to a Gini coefficient, was calculated for each stand as:

$$GD = 1 - \sum_{i=1}^{n} (s_i - s_{i-1})(d_i + d_{i-1})$$

(1)

where s_i is the cumulative proportional size of tree i, and d_i is the cumulative proportional growth of tree i. Consequently, a stand with strong growth dominance (GD > 0) means that the contribution of dominant trees to stand growth is greater than their contribution to stand mass. Conversely, a stand showing reverse growth dominance (GD < 0) indicates that dominant trees account for a larger share of stand biomass than does current growth. When growth of each tree is linearly proportional to tree size, GD is equal to zero.