Relationships between patterns of stand growth dominance and tree competition mode for species of various shade tolerances

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A B S T R A C T

The principal objective of the study aimed at establishing formal relationships between stand growth dominance and mode of inter-tree competition for stands dominated by different tree species. We selected permanent sample plots (PSP) that were established in eastern Canada and which were dominated by five tree species of differing degrees of shade tolerance: trembling aspen (*Populus tremuloides* Michx.), jack pine (*Pinus banksiana* Lamb.), white birch (*Betula papyrifera* Marsh.), black spruce (*Picea mariana* [Mill.] BSP), and balsam fir (*Abies balsamea* [L.] Mill.). The PSPs were used to calculate growth dominance coefficients (GD), together with the intercept (TCM_{int}) and slope (TCM_{slp}) of plot-level relationships between stem mass increment and stem mass, which were used to describe tree competition mode. GD decreased linearly with increasing stand age for all species, with highest GD values being observed in stands dominated by trembling aspen and lowest values being observed in stands dominated by shade-tolerant black spruce and balsam fir. Increasing stand diameter diversity was associated with a linear decrease in GD for all tree species. GD decreased with increasing TCM_{int}, whereas it increased with increasing TCM_{slp}. The linear relationships between GD and tree diameter diversity could estimate stand growth dominance without having to determine the recent growth of all trees. Also, the close relationship between GD and inter-tree competition mode suggests that this combined information is meaningful in helping to implement silvicultural treatments such as tree selection for partial cutting.

1. Introduction

Individual-tree growth dynamics are strongly influenced by competition-induced mortality in premature forest stands (Bigler and Bugmann, 2003), whereas senescence, disease and windthrow are important causes of tree mortality in aging stands (Sturtevant et al., 1997). Moreover, the social status of dead trees is likely to change gradually with stand age. For example, mortality that is observed in young, even-aged stands affects mostly smaller trees because of strong competition exerted by dominant trees (Pretzsch and Biber, 2010). In contrast, mortality of dominant trees is much more frequent in older stands (e.g., Lowe et al., 2011). Knowledge of these temporal changes in tree mortality patterns may have important silvicultural implications, for example, in guiding selection of trees that are to be harvested during partial cuts. In older stands, determination of trees that are dying is difficult because mortality is irregular and can affect all tree sizes (Landsberg and Sands, 2011). Yet, tree mortality that is not caused by disturbance agents (e.g., wind) is generally preceded by diameter growth decline (Bigler and Bugmann, 2003), which suggests that it can be predicted from individual-tree growth dynamics.

Binkley (2004) proposed that temporal changes in tree growth dynamics could explain the stand growth decline generally observed with age. This hypothesis predicts that the relative contribution of dominant trees to total stand growth decreases with age, while that of non-dominant trees increases concomitantly, thereby leading to a phase of reverse growth dominance. Although this hypothesis has received some support from studies that have been conducted in old stands (Binkley et al., 2006; Doi et al., 2010), the temporal sequence ending with reverse growth dominance has not been thoroughly documented. For example, temporal variation in stand growth dominance may differ among tree species of varying degrees of shade tolerance, with shade-intolerant, fast-growing species showing strong growth dominance, even at advanced ages (Doi et al., 2010; Fernández et al. 2011). Growth dominance of a given stand may be related to the prevailing mode of competition between trees, as suggested by Doi et al. (2010), Fernández Tschieder et al. (2012), and Looney et al. (2016). These authors proposed that strong growth dominance at young ages could reflect size-asymmetric competition, whereby large individuals obtain a disproportionate share of resources relative to their size (Weiner, 1990). In contrast, reverse growth dominance should correspond to partial size-symmetric or completely symmetric competition, where all individuals tend to use the same amount of resources, irrespective of their size
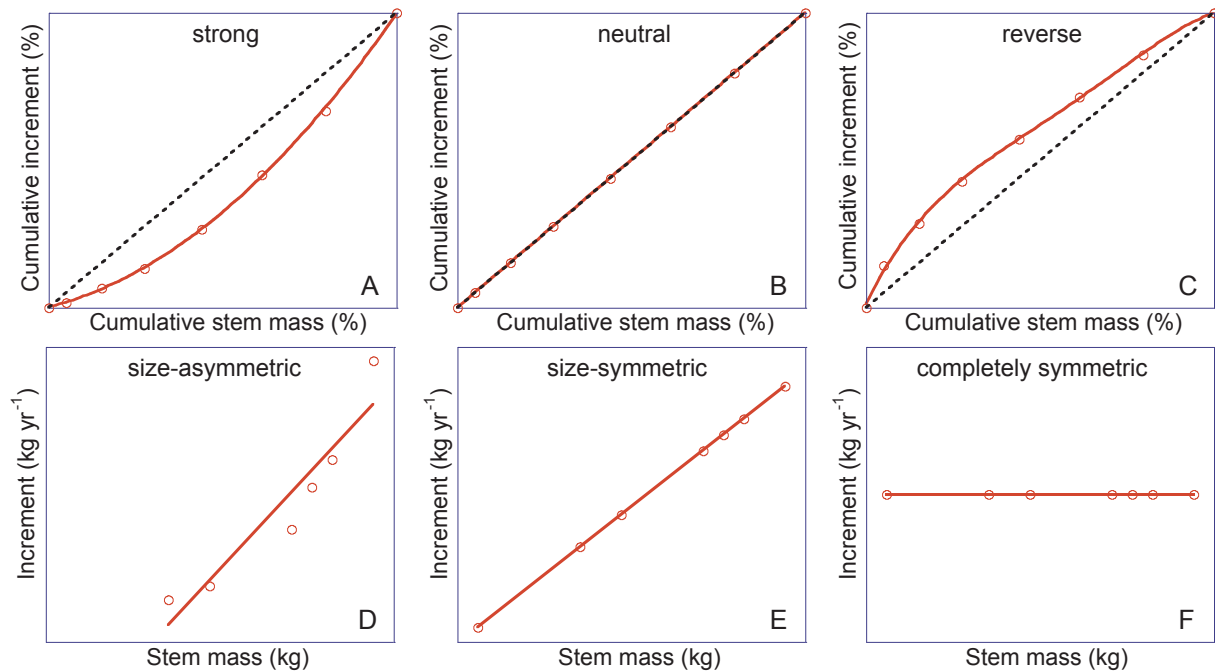
Fig. 1. Predicted correspondence between patterns of growth dominance (A, B and C), as described by Binkley et al. (2006), and tree competition modes (D, E and F), as described by Pretzsch and Biber (2010).

(Weiner, 1990). This proposed relationship between growth dominance and tree competition mode (two important descriptors of forest stand dynamics with complementary interpretations) has yet to be empirically tested.

The principal objective of the present study, therefore, is to establish formal relationships between stand growth dominance and mode of inter-tree competition for stands that are dominated by different tree species. Moreover, in order to estimate the growth dominance of stands without having to determine the recent growth of all trees, the secondary objective was to characterize patterns of growth dominance as a function of stand state variables, particularly stand age, density and diameter diversity. Stand growth dominance can be quantified (Binkley et al., 2006) by ordering trees of a sample plot from smallest to largest and then relating their cumulative growth to the cumulative stem mass (Fig. 1A–C). For its part, tree competition mode can be characterized by calculating the intercept and slope of a relationship between the growth and stem mass of all trees in a given sample plot (Fig. 1D–F; Pretzsch and Biber, 2010).

A positive growth dominance coefficient corresponds to a stand within which the relative contribution of small trees to total stand growth is lower than their relative contributions to total stem mass (Fig. 1A). This type of growth dominance is thought to result from size-asymmetric competition (Fig. 1D), which occurs when dominant trees have disproportionate access to resources compared to non-dominant trees (Pretzsch and Biber, 2010; Fernández Tschieder et al., 2012; Looney et al., 2016). When trees of all sizes contribute equally to stand growth, stand growth dominance is neutral (Fig. 1B). This response should correspond to size-symmetric competition (Fig. 1E) between trees, thereby indicating that soil nutrients or water are limiting rather than light (Pretzsch and Biber, 2010). Finally, reverse growth dominance is observed when relative contributions of small trees to entire stand growth are larger than their relative contributions to stand stemwood biomass (Fig. 1C). This situation is expected to correspond to partial size-symmetric or completely symmetric competition between trees (Fig. 1F), defined as theoretically equal access to growth resources for all trees, regardless of their size.

Three hypotheses have emerged from the preceding concepts. First, as suggested by the results of Binkley et al. (2006) and Fernández et al.

(2011), the growth dominance coefficient is hypothesized to decrease with increasing age for all species. Yet, for a given age, higher growth dominance coefficients should be associated with shade-intolerant, fast-growing species, particularly when they are established on good quality sites. Second, because multi-cohort stand structures often characterize old-growth stands with negative growth dominance coefficients (Binkley et al., 2006; Castagneri et al., 2012), the growth dominance coefficient is hypothesized to decrease with increasing tree size diversity. Third, as illustrated in Fig. 1, stand growth dominance is hypothesized to be closely linked to the mode of tree competition; the latter has a direct effect on the relative growth of different-sized trees, which is summarized by the growth dominance coefficient at the stand scale. These hypotheses were tested with stands that were dominated by five tree species of different shade-tolerances using a large network of permanent sample plots, which had been established in eastern Canada.

2. Materials and methods

2.1. Plot selection and measurements

The sample stands were selected from a network of permanent sample plots (PSP), which had been established by the *Ministère des Forêts, de la Faune et des Parcs du Québec* (MFFPQ) from 1970 onward across the mixedwood and boreal vegetation zones of the Province of Quebec, Canada. PSPs were established in stands originating from a stand-replacing disturbance, such as fire, clear-cutting or windthrow, and which had not been subjected to silvicultural treatments. PSP selection was based on three criteria. First, selected stands were composed of at least 75% of merchantable basal area (BA) at the first measurement, in very shade-intolerant trembling aspen (*Populus tremuloides* Michx.) and jack pine (*Pinus banksiana* Lamb.), shade-intolerant white birch (*Betula papyrifera* Marsh.), shade-tolerant black spruce (*Picea mariana* [Mill.] BSP), or very shade-tolerant balsam fir (*Abies balsamea* [L.] Mill.). Second, selected PSPs were measured at least twice and had to include at least three dominant or co-dominant trees of the target species, for which age and total height (H) were measured. Third, these PSPs had to include at least four individuals of