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# Effect of local stand structure on leaf area, growth, and growth efficiency following thinning of white spruce

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ABSTRACT

We examined the influence of stand structure surrounding individual dominant and codominant trees on leaf area, tree growth, and growth efficiency (stem growth per unit leaf area) in young white spruce (*Picea glauca* (Moench) Voss) plantations. Objectives were to (i) test the hypothesis that individual tree volume increment and growth efficiency increase with increasing growing space, and (ii) determine the relative importance of growth efficiency and leaf area to stem volume increment in young spruce following thinning. Growing space was expressed as area potentially available (APA) to each tree. Relative current annual volume increment (annual increment divided by the mean increment for the 3 years immediately preceding thinning) increased linearly with increasing APA 2 and 3 years after thinning, supporting our hypothesis that tree volume increment increases with APA. Growth efficiency however, was not related to APA. Leaf area was positively related to APA 3 years after thinning, and current annual volume increment was related to leaf area. Leaf area per tree increased from 17.8 $m^2$ to 29.8 $m^2$ over the 3 years (2011–2013) following thinning and was 16.5–18.7 $m^2$ for unthinned trees over the same period. Growth efficiency decreased from 1.35 to 0.64 $dm^3\ m^{-2}$ for thinned trees and from 0.74 to 0.55 $dm^3\ m^{-2}$ for unthinned trees from 2010 to 2013. Growth efficiency did not differ between thinned and unthinned trees, but it was significantly lower in year 3 than year 1 after thinning ($p = 0.0178$) and significantly lower than the prethinning growth efficiency ($p = 0.0034$). Our results show that thinning increased individual tree volume increment by increasing leaf area of remaining trees and not by increasing their growth efficiency.



## 1. Introduction

Tree growth is a function of the amount of foliage, the rate of photosynthesis per unit of foliage, allocation of photosynthate to components and conversion rates to new structural matter (Brix, 1983). The unit leaf area rate or net assimilation rate, i.e. the dry weight increase per unit of foliage over time (Briggs et al., 1920; Evans, 1972), can be used as a surrogate for photosynthesis and conversion rates because these are difficult to measure for entire plants over long periods of time (Brix, 1983). For forestry purposes, growth efficiency, defined as stem wood growth per unit of foliage by Waring et al. (1980), can be used instead of net assimilation rate. The amount of foliage is strongly correlated with absorbed photosynthetic active radiation (Binkley et al., 2010; Gspaltl et al., 2013) and can be regarded as the potential production capacity of a tree (Brix, 1983). Growth efficiency is a measure of resource use efficiency (Brix, 1983; Gspaltl et al., 2013) and tree vigor (Waring et al., 1980).

Several studies have reported on the relative importance of leaf area and growth efficiency in determining tree growth response to thinning. Average rates of stem growth per tree were 3–8 times greater in thinned than in unthinned balsam fir (*Abies balsamea* (L.) Mill.) stands, and stem growth was correlated with foliar weight, however, growth efficiency of dominant and codominant trees in thinned stands were similar to those of similar trees in unthinned stands (Lavigne, 1988). Over a 7-year period, mean annual stemwood biomass increment was 34% greater for thinned Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) than unthinned trees, and leaf biomass increased by 0.58 kg $year^{-1}$ for thinned trees compared to a decrease of 0.03 kg $year^{-1}$ for unthinned trees (Brix, 1983). Stem growth per unit leaf area was only 14% greater for the thinned than unthinned trees indicating that the major growth response to treatment was caused by an increase in the

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amount of foliage (Brix, 1983). Five-year stem growth and leaf area per tree were greater at intermediate spacings (4.0–5.2 m) in thinned Douglas-fir plantations and, in contrast to other studies, stem growth per unit leaf area generally increased with increasing spacing (Binkley and Reid, 1984). Determining the relative role of leaf area and growth efficiency on stand treatment responses is important, because it may account for much of the variation found among treatments or between studies on different sites, and may allow more precise predictions of growth responses (Binkley and Reid, 1984).

Each individual tree in a stand has a finite amount of growing space, which can be approximated by its crown projection area (Assmann, 1970) or leaf area (O'Hara, 1988). The use of crown projection area to represent growing space assumes that trees are limited only by horizontal or lateral competition (Assmann, 1970; O'Hara, 1988). However, as stands develop and trees differentiate, a dominant tree can increase in height and intercept the sunlight of a nearby suppressed tree without lateral expansion, and the suppressed tree with limited growth due to the reduced light may decline in growth without a reduction in horizontal growing space (O'Hara, 1988). Leaf area includes a vertical dimension of growing space (O'Hara, 1988; Gspaltl et al., 2012) and provides a better measure of growing space occupancy than crown projection area (O'Hara, 1988). However, allocation of growing space by leaf area is more difficult operationally than crown projection area. Individual tree growing space can be expressed as area potentially available (APA) (Assmann, 1970), which is defined as the area of an irregular polygon constructed around a subject tree (Brown, 1965; Moore et al., 1973). The APA also has been suggested as a surrogate measure of the degree of potential root spread, available belowground resource pool, and/or degree of crown crowding (Mainwaring and Maguire, 2004). Thus APA may be operationally more practical than allocating growing space by leaf area (Mainwaring and Maguire, 2004), and may have merit in analysis of growth response to thinning, where residual trees remaining following thinning respond to suddenly increased growing space and light conditions. Trees in closed-canopy stands fully occupy their APA but trees in recently thinned stands may not, and the relative occupancy may be related to increase of leaf area per tree in thinned versus unthinned stands. This may introduce a time since thinning effect on growth per tree. Therefore APA may provide a quantitative basis for relating thinning intensity to individual tree growth (Moore et al., 1973).

Mainwaring and Maguire (2004) found a decrease of volume growth per APA with increasing APA for ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) and lodgepole pine (*Pinus contorta* Dougl. ex. Loud.). Similarly, Sterba (2005) found that tree growth per crown projection area decreased with increasing crown projection area for a given social class in mixed stands of Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.). Studies on the influence of APA on leaf area and growth per unit leaf area, which may account for the increased growth of residual trees following thinning, are needed. Knowledge of the relationship among volume increment, growth efficiency, foliage amount, and APA can help forest managers design silvicultural treatments that can potentially optimize both foliage distribution among trees and growth efficiency, and, thereby, increase tree growth. Growth models that use resource use efficiency could also benefit from data on the relationship between efficiency of individual trees and their growing space (APA). Application of such relationships in models may lead to better growth predictions than using an average stand growth efficiency that does not account for differences between individual trees.

We examined effects of APA on leaf area, volume increment, and growth efficiency for 3 years after commercial thinning in young white spruce plantations. Objectives of this paper were to: (i) test the hypotheses that individual tree volume increment and growth efficiency increase with APA in young white spruce plantations; and (ii) determine the relative importance of growth efficiency and leaf area to stem volume increment in young spruce trees following thinning. This forms part of a larger study that determined effects of alternative commercial thinning treatments on stand growth, deadwood, and plant and animal response (MacLean et al., 2015; Omari and MacLean, 2015).

## 2. Materials and methods

### *2.1. Study area*

The study was carried out in the Black Brook District, a 220 000 ha forest, owned by J.D. Irving, Limited (JDI) in northern New Brunswick, Canada (47°9′51″–67°55′27″).

The Black Brook District is located in the Southern Uplands Ecoregion, which is underlain by meta-sedimentary and calcareous sedimentary bedrock, and drained to the South and West by tributaries of the Saint John River (New Brunswick Department of Natural Resources and Energy (NBDNRE), 1998). Elevation ranges from 180 to 600 m, increasing from South to North. The Black Brook district contains some of the most intensively managed forests in Canada with over 85 000 ha of primarily spruce plantations. Clearcuts are generally replanted within one year of harvest, with mechanical site preparation before planting and herbicide application 1–3 years after planting, if required. Plantations are often cleaned at 10–15 years, commercially thinned at 20–40 years, and final harvesting is done between ages 35–55 years old. Further details on the study area can be found in Omari and MacLean (2015).

### *2.2. Study design*

The commercial thinning installations described in Omari and MacLean (2015) were used in this study. Six >20 ha white spruce plantations aged between 22 and 30 years, selected on the basis of similar stand characteristics, were commercially thinned in the fall of 2010 or winter of 2011. Each plantation was divided into four blocks (minimum block size of ~5 ha) and randomly assigned one of four treatments: (1) an unthinned control, and three 40% basal area removal thinning treatments; with (2) slash and tops remaining on site (status quo); (3) branches and tops extracted from the site (biomass removal); and (4) 11–12 clumps of unthinned trees left per treatment block, and one-half of the trees in each clump girdled to create snags (enhanced structure). Five 0.04 ha circular permanent sample plots (PSPs) were randomly located in each treatment block. Approximately 12% of each thinned treatment block area was harvested as trails. Harvest trail width and spacing were approximately 3.5 m and 23 m, respectively.

### *2.3. Data collection*

Two of the plantations (Roussel Brook and Canton) were randomly selected, and one plot randomly selected in each of the unthinned and status quo thinned treatments of each plantation. In the surrounding area of each selected plot, dominant and codominant trees were marked and measured for diameter at breast height (DBH), total height, and crown width before destructive sampling in fall 2013. Three trees were selected in each unthinned plot and 12 trees in each status quo thinned plot. Trees in the thinned treatment were selected based on number of trees removed around each tree and proximity of the tree to an extraction trail. The eight or nine closest surrounding trees around each