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Light absorption and light-use efficiency of juvenile white spruce trees in natural stands and plantations

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ABSTRACT

Aboveground tree growth is influenced by light availability, light capture, and the efficiency captured light is converted into growth. All three factors are influenced by neighborhood species composition and stand structure and can be modified with silvicultural treatments. The objective was to examine the absorption of photosynthetically active radiation (APAR), light-use efficiency (LUE), and aboveground biomass growth of juvenile white spruce (*Picea glauca* (Moench) Voss) trees in plantations and planted in naturally regenerated stands with diverse species composition. Trees were sampled across a range of sizes, and measurements of white spruce and neighborhood trees were collected at ages seven and eight. Light absorption of individual trees was modeled with MAESTRA accounting for species-specific crown structures of neighboring trees. APAR increased linearly with leaf area in both treatments. The correlation was more influenced by neighborhood competition than self-shading, since self-shading was minimized by crown spread and height growth. Biomass growth increased with increasing APAR in both treatments, but growth for a given unit of APAR was greater in the natural stands, possibly due to greater below-ground biomass allocation in plantations due to lower stand densities. LUE declined slightly across the range of tree size, which contrasts most other studies. The decline could be due to juvenile age of the trees and inherent slow growth of spruce species.

1. Introduction

Light absorption, light availability, and the efficiency that absorbed light is converted into biomass are major factors influencing the growth of trees and forest stands (Binkley et al., 2013a). Stand growth often increases linearly with absorbed photosynthetically active radiation (APAR), where the slope of this relationship is the light-use efficiency (LUE; growth per unit APAR) (Monteith, 1977; Landsberg and Gower, 1997). The same relationship for individual trees is not always linear due to variation in crown shape, leaf area distribution, and the effects of neighborhood species composition and stand structure (Chen et al., 1996; Ishii and Asano, 2010; Binkley et al., 2013a). Stand improvement treatments, such as thinning and shifts in species composition, alter light conditions within a stand, inducing individual trees crown growth and greater light capture (Forrester et al., 2013). Such treatments can also produce short-term increases in LUE and aboveground growth, as shown in *Eucalyptus nitens* (H. Deane & Maiden) Maiden and *Picea abies* (L.) Karst. monocultures (Forrester et al., 2013; Gspaltl et al., 2013). Few studies have examined how tree APAR, LUE, and aboveground growth varies across a gradient of silvicultural intensity from plantations to naturally-regenerated stands for a single species. This information would help explain the adaptability of a species to a wide range of neighborhood conditions.

There is evidence that stands with higher tree diversity also absorb more light, have greater LUE, and grow more biomass than monocultures (Chen et al., 2003) due to species differences in shade tolerances, canopy position, and crown structure (Forrester et al., 2012b). Most of the studies that examined individual tree light absorption and LUE were limited to monocultures (Binkley et al., 2013b) with the exception of a few studies (Charbonnier et al., 2013; le Maire et al., 2013; Forrester and Albrecht, 2014). Forrester and Albrecht (2014) found *P. abies* and *Abies alba* Mill. had greater APAR and LUE in mixed- than monoculture

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neighborhoods, which they contributed to mixed neighborhood effects on modifying crown architecture. Comparatively, both *Eucalyptus grandis* W. Hill ex Maid. and *Acacia mangium* Willd. had greater tree APAR but lower LUE in monocultures than in mixture that resulted in the monocultures having greater production (le Maire et al., 2013). Richards and Schmidt (2010) compared APAR of three tropical species in monoculture and mixture that differed in growth and successional stage, and found a trees of a fast growing early successional species absorbed more radiation when growing within a monoculture of slower growing species. When tree APAR was compared across the three species growing in a monoculture with 50% of the trees taller than the target tree, they ranked moderately fast growing > slow growing > fast growing, likely due to shade sensitivity of the fast growing early successional species. All of these studies have been model simulations or well controlled species assemblages. Natural stands can have much greater species diversity and canopy complexity, and thus heterogeneous light conditions that may affect APAR, LUE, and aboveground growth.

Acadian forests of northeastern North America are an example of forests with high species diversity, since they lie at the intersection of eastern broadleaf forests to the south and boreal forests to the north, with species composition similar to both (Braun, 1950). White spruce (*Picea glauca* (Moench) Voss) is common across the boreal and Acadian forests of northern North America. Seedlings and saplings typically occupy lower canopy strata during early stages of stand development, and can grow 2000–3000 cm^3 $year^{-1}$ of stem volume between 40% and 60% of available light, respectively (Filipescu and Comeau, 2007). White spruce is also commonly planted in monocultures in the eastern part of its range, where light availability, and thus growth, are maximized by controlling all non-spruce vegetation (Burgess et al., 2010). Prior to crown closure, Nelson et al. (2012) found six year old white spruce in plantations grew 0.4 m $year^{-1}$ in height. Information is lacking regarding white spruce grows LUE, especially at the individual tree scale. Differences in stand LUE and light interception were not found in mixed white spruce-trembling aspen (*Populus tremuloides* Michx.) stands across a range of species proportion (Groot et al., 2014). Even though the white spruce component absorbed more light, it was offset by the greater LUE of trembling aspen. Given that white spruce grows in a variety of stand conditions, from monocultures to simple mixtures in boreal forests to diverse mixtures in Acadian forests, it is important to understand how growth, light absorption, and LUE varies in across a range of neighborhood conditions.

The objective of this study was to examine the light absorption behavior of white spruce seedlings and saplings in plantations and interplanted in young naturally regenerated stands with diverse species composition in the Acadian forests. We hypothesized that (1) the effects of shading from neighboring trees has a greater influence over light absorption than self-shading due to heterogeneous canopy structure and species differences in crown form and leaf architecture, (2) light absorption is a better predictor of total aboveground biomass growth than crown leaf area due to self- and neighborhood shading effects, and (3) LUE will increase with tree size and decrease as neighborhood competition increases.

2. Methods

2.1. Study site

The study was located on a site that was clear-cut harvested in 1995 with ~2.3 m^2 ha^{-1} of residual basal area on the Penobscot Experimental Forest (PEF) in the Acadian forest of east-central Maine (44°50′37″N, 68°37′39″W). The site regenerated to a mixture of shade intolerant hardwood species and shade tolerant conifer species including trembling aspen, bigtooth aspen (*Populus grandidentata* Michx.), paper birch (*Betula papyifera* Marsh.), gray birch (*Betula populifolia* Marshall), red maple (*Acer rubrum* L.), balsam fir (*Abies balsamifera* (L.) Mill.), eastern hemlock (*Tsuga canadensis* L.), and red spruce (*Picea rubens* Sarg.) (Nelson et al., 2013).

Climate at the PEF is classified as cool and humid. The 30-year (1951–1980) mean annual temperature at Bangor, Maine, USA (~16 km from the site) was 6.6 °C, with an average low of −7.0 °C in February and average high of 20.0 °C in July. Precipitation averages 1060 mm per year with 48% occurring between May and October. Annual snowfall averages 2390 mm, and the frost-free period in the region ranges from 140 to 160 days per year. A weather station at the study site during the 2011 and 2012 growing seasons (May to September) recorded a mean air temperature of 16.8 °C, mean volumetric soil water content of 0.10 m^3 m^{-3}, and mean above-canopy, daytime photosynthetic active radiation (400–700 nm) of 640 μmol m^{-2} s^{-1}. Soils at the study site are Wisconsian till origin and range from loamy, mixed, active, acid, frigid, shallow, Aeric Endoquepts to coarse-loamy, isotic, frigid, Aquic Haplothods.

The full experimental design was a 3 × 3 factorial of silvicultural intensity and species composition, plus an untreated control, with each treatment replicated four times across the site in 2004. Treatments included thinning/overtopping release, thinning/overtopping release plus enrichment planting, and plantations, all across a compositional gradient ranging from pure hardwood to nearly pure conifer (A.S. Nelson et al., 2014). The growing stock used for plantations and enrichment planting were open-pollinated white spruce container seedlings and cuttings of four different hybrid poplar (*Populus* species) clones. White spruce seedlings were provided by a local tree nursery, with 65-cm^3 rooting volume, mean height of 15.5 cm (range 7.5–28.0 cm), and mean ground line diameter of 2.6 mm (range 1.0–9.0 mm) at the time of planting.

2.2. Study design

The current investigation focused on planted white spruce in 4 of the 10 treatments including natural stands shifted to conifer (EC) and mixedwood (EM) composition, and two plantation treatments planted either in pure white spruce (PC) or 67% white spruce and 33% hybrid poplar crop trees mixtures (PM). All trees were planted at a 2 m × 2 m spacing. In the EC and EM treatments, naturally regenerated trees were thinned to a 2 m × 2 m crop-tree spacing using herbicides and brush saws, and 50% of the crop-trees were planted with white spruce (EC) or white spruce and hybrid poplar (EM). In the PM treatment, hybrid poplar cuttings were planted in clumps to minimize growth reductions of white spruce seedlings (Nelson et al., 2012). Basal area in 2011 was 0.78 ± 0.44 m^2 ha^{-1} (PC), 3.40 ± 1.28 m^2 ha^{-1} (PM), 6.97 ± 2.73 m^2 ha^{-1} (EC), and 10.12 ± 4.54 m^2 ha^{-1} (EM) (Table 1).

Three planted white spruce trees were selected in each treatment plot (n = 12). A study-wide inventory in 2010 was used to stratify white spruce trees into three height classes (<170 cm, 171–420 cm, and >420 cm) and one individual per height class was selected in each plot to ensure adequate representation of tree size. Competitor trees around each white spruce tree were identified using the search cone method (Biging and Dobbertin, 1992) with a 60° angle from the base of the crown. Competitors were limited to a horizontal distance of 5 m due to high stem densities in the EC and EM treatments. This method ensured that trees both larger and smaller than the white spruce trees were included.