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Editorial

Why one tree grows faster than another: Patterns of light use and light use efficiency at the scale of individual trees and stands

1. Introduction

Perhaps the most fundamental question in forestry is why one tree grows faster than another. The patterns of growth for individual trees determine the patterns of growth for stands, over time and in response to silvicultural treatments. For example, the stand-growth response to thinning from below (removing small trees) versus thinning from above (removing dominant trees) is essentially determined by the factors influencing the growth of individual trees, and how these factors change.

At first glance the growth of a tree may simply be viewed as a function of tree size; bigger trees generally grow faster than smaller trees. Given that faster growth is a common way for trees to get bigger, this tautological pattern provides no new information to explain differences among trees in growth rates. Some foresters have tried to explain differences in tree growth rates in terms of growing space: larger trees grow faster because they have more growing space. Unfortunately, growing space is not quantifiable and changes over time (Oliver and Larson, 1990), so the idea of growing space also provides no information to test for causes of differences in growth rates.

2. Key insights from the papers

A resource ecology perspective has the opportunity to provide new information and understanding about growth rates. The growth of a tree is a function of resource acquisition (light, water, nutrients), the efficiency of using resources to generate photosynthates, and the partitioning of photosynthates to various tissues and functions in the tree (Binkley et al., 2004). Measurements of resource use were problematic for most of the 20th Century, though proxies such as leaf area could be used to explain how one stand grew faster than another, or how a treatment such as fertilization changed stand growth (Waring, 1983). Direct measurements of stand-level light use have now become routine, but direct measurements at the scale of individual trees remains problematic.

Fortunately, advances in modeling of tree canopies now allows estimation of light use at the scale of individual trees. This special issue of *Forest Ecology and Management* presents a set of studies with four tree genera on four continents that examined how light use and light use efficiency accounted for differences in growth among trees within stands, and how these individual-tree patterns influenced stand-level growth.

A review by Binkley et al. (2013) focused on how light interception at the scale of individual tree crowns differs from interception by stand canopies. Within a tree crown, light interception may follow a classic Beers' Law expectation of each layer of leaves intercepting a constant fraction of incoming light; each additional layer of leaves captures successively less light. This expectation might lead to confusion when estimating light interception by a tree that has twice the leaf area of another tree; in most cases, a doubling of crown leaf area also doubles light interception, because big trees spread out crowns across larger ground areas rather than stacking more vertical layers of leaves. At the level of individual trees, patterns of stem growth per unit light interception relate linearly to growth per unit of leaf area. The pattern breaks down at the level of stands, however, illustrating a key distinction among scales in leaf area and light interception.

le Maire et al. (2013) explained why mixing *Acacia mangium* with *Eucalyptus grandis* in Brazil did not lead to higher growth than in *Eucalyptus* monoculture. The mixed plots had a 2-story canopy (with *Eucalyptus* above *Acacia*, Fig. 1) with greater light interception, but both Acacia and Eucalyptus used light with lower efficiency than in monocultures. Taller trees of both species used more light than shorter trees, and taller Acacia trees showed higher light use efficiency while height had little effect on Eucalyptus light use efficiency.

Campoe et al. (2013a) characterized patterns in individual tree light use and light use efficiency across a productivity gradient within a stand of *Eucalyptus grandis* in Brazil (Fig. 2). Overall, the largest 20% of the trees in the plantation accounted for more than double the growth of the middle 20% of trees in the final year of the plantation's rotation. The greater growth of dominant trees was driven exclusively by greater light use, as light use efficiency did not differ between these two size classes. The more productive half of the plantation grew about 20% more stemwood than the less productive half of the plantation, and this difference resulted primarily (80–90%) from greater light use efficiency in the more fertile portions, with much smaller contribution (10–20%) from higher light use.

Forrester et al. (2013) examined how light use and light use efficiency accounted for the growth response to silvicultural treatments (thinning, pruning, and fertilization) in a plantation of *Eucalyptus nitens* in Australia. At mid rotation, faster growth of larger trees resulted more from higher light use efficiency than from higher light use. Differences in light use efficiency became largely unimportant near the end of the rotation, when differences in light use explained almost all of the differences in growth among trees. Both factors were important in the overall stand-level responses to siliviculture, as well as the pattern of stem growth with tree age. Stand growth showed the typical pattern of a peak (between year 4 and 5) and subsequent decline; this pattern was explained by a continuous increase in light use, and a continuous decrease in light

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use efficiency. A similar decline in light use efficiency with stand age accounted for age-related decline of Eucalyptus growth in other studies (e.g. Ryan et al., 2004, 2010); the next step of explaining the reason behind the decline in efficiency remains an important area for future research.

Gspaltl et al. (2013) explored light and growth patterns in eight even-aged Norway spruce (*Picea abies*) stands in Austria, spanning three age classes (from 40 to 130 years, Fig. 3) and two thinning regimes (thinned and unthinned). Across all ages and thinning treatments, larger trees used more light, and used the intercepted light more efficiently to grow wood. Large (80th percentile) trees averaged about 30% greater light use efficiency than small (20th percentile) trees.

Campoe et al. (2013b) examined the production ecology of a 9-year-old plantation of loblolly pine (*Pinus taeda*, Fig. 4) 2 years after initiation of irrigation and fertilization in a factorial design. Across all treatment, large trees (80th percentile) grew 3.4 times more than small trees (20th percentile), with greater light interception accounting for two-thirds of the higher growth, and greater light use efficiency accounting for the other third. Fertilization boosted growth of the largest (greater than 80th percentile) trees by two-fold, mostly by increasing light use efficiency (71% contribution) rather than light use (29% contribution). Irrigation plus fertilization led to a tripling of growth of the largest trees, again with the contribution of light use efficiency (85%) being more important than light use (15%).

Fig. 1. A 50:50 mixture of *Eucalyptus grandis* with *Acacia mangium* developed a two-storied canopy (with narrow-leaved Eucalyptus crowns above broader leaved Acacia crowns) with greater light interception than in monocultures of either species, but lower efficiency of light use in producing stemwood (see le Maire et al., 2013).

3. Generalizations and next steps

Hypotheses about relationships between light use and stem growth at the scale of individual trees may be tested with estimates of light use when complex sampling and modeling allow estimation of individual-tree light use (as in the papers in this special issue). The consistent, linear relationship between light interception and individual tree crown leaf area provides an encouraging opportunity for testing the same hypotheses when more challenging modeling is not feasible.

Within a stand, dominant trees show high efficiency of light use, typically greater than average trees. The total growth of a stand is driven heavily by the combination of greater light use and higher efficiency of light use of the larger trees. Thinning a stand from below would typically remove the trees with both low light use and low efficiency. Thinning from above can substantially reduce stand-level growth as the harvested trees would typically be among the most efficient trees in the stand, and subordinate residual trees may take time to increase both light use and efficiency.

The evidence for high light use efficiency for dominant trees is strong in the studies in this special issue, as well as in other plantations (Binkley et al., 2002, 2010). Would dominant trees in very old forests still show the same (or greater) efficiency of light use as subordinate trees in the same forests? Some forests show "reverse growth dominance" where the larger trees account for a higher proportion of current stand mass than stand increment (Binkley, 2004; Binkley et al., 2006). We suspect these forests may indeed show lower efficiency of light use by dominant trees, and look forward to experimental tests of this prediction.

How do dominant trees accomplish higher efficiency of light use in growing stemwood? Higher rates of photosynthesis per unit of leaf area may account for a portion of the extra growth. We suspect that greater partitioning of photosynthate to wood growth in larger trees is the likely explanation for higher efficiency, but we currently lack suitable methods for measuring much of the carbon mass balance at the scale of individual trees (for stand-level allocation insights, see Epron et al., 2012; Mäkelä, 2012). Few studies have documented the effect of dominance class on rates of tree respiration, but methods are currently available. No study has yet measured the belowground carbon flux for individual trees within a stand, and we hope this major gap in knowledge will shrink as innovative approaches are developed in coming decades.

The papers in this special issue found that dominant trees get more light and use this light efficiently. The degree of uniformity of tree sizes within a stand may influence the efficiency of light use and total stand growth (e.g. Binkley et al., 2010). A major question remains about spatial relationships between trees: how much space does such a dominant tree need? This is not the unquantifiable concept of "growing space" as defined above, but simply that part of the stand's area which is needed by a dominant tree to receive so much light and to develop such a crown as needed to use the light so efficiently Gspaltl et al. (2012). How many dominant, efficient trees can fit into a hectare, and why?

Of course light is not the only resource required by trees; most trees and most stands are limited in production rate by water