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Light absorption and use efficiency in forests: Why patterns differ for trees and stands

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ABSTRACT

The production of stem wood by trees and stands depends on the absorption of light, and the efficiency of converting light into stem wood. Larger trees within a stand tend to absorb more light and use it more efficiently in growing wood; greater growth of large trees typically results from a combination of increased light absorption (about three-fourths of the effect) and increased efficiency of light use (about one-fourth of the effect). Similarly, more productive forests commonly show greater light absorption and higher efficiency of light use; differences of 50–80% are commonly reported for both light absorption and for light use efficiency in comparisons of forests that differ in species composition, site fertility, and silvicultural treatments. These quantitative assessments of production ecology require estimation of light absorption at the appropriate scale, because patterns of light absorption in relation to leaf area differ fundamentally for trees and stands. Three types of relationships between light absorption and leaf area are important, and the typical patterns differ among types. The absorption of light through the crown of an individual tree (Type I) typically follows a logarithmic trend where each successive layer of leaves absorbs a consistent proportion of incident light. This pattern is often related to Beer's Law for absorption of light. The second type of relationship considers light absorption in relation to leaf area index within a set of stands; Type II comparisons of light absorption across ranges of stand leaf area indexes do not usually show a logarithmic trend, and expectations for the pattern among stands should not be based on Beer's Law. The third type of relationship focuses on total light absorption as a function of a tree's total leaf area; Type III comparisons for sets of trees within a stand generally show linear (or even exponential) increases in light absorbance with increasing leaf area, again deviating from an (inappropriate) application of Beer's Law. This distinction in patterns between light absorption and leaf area of trees and stands is particularly important when hypotheses are tested about the stem growth/leaf area (often termed growth efficiency, or leaf area efficiency). At the stand level (Type I), the logarithmic (or flat) relationship between light absorption and leaf area index may lead to different outcomes for hypotheses tested as a function of light absorption and those tested in relation to leaf area. At the level of individual trees (Type III), hypothesis tests based on light absorption or leaf area will provide similar answers, owing to the linear (or slightly exponential) relationship between light absorption and leaf area.

1. Introduction

The absorption of light by leaves is the foundation for all production by trees and stands. The growth of both trees and stands depends in part on the amount of light absorbed by leaves, but also on the efficiency of converting absorbed light into biomass, and the allocation of photosynthate to various tissues. Studies comparing growth differences that result from differences in species composition (within sites), site fertility (with constant species composition), and silvicultural treatments (within sites) typically show that higher growth rates are associated with 50–80% greater absorption of light (Fig. 1A and B). Similar increases are common in the efficiency of light use (stem growth per unit light absorbed). Within stands, larger trees generally grow faster than smaller trees. A comparison of 40th percentile trees (by stem volume or mass) with 80th percentile trees typically shows 75–100% greater light absorption by the larger trees, coupled with a 25–30% increase in light use efficiency (Fig. 1C and D).

Quantitative insights into the production ecology of trees and stands depend on accurate characterization of light absorption. Forest managers and scientists have used a variety of direct and

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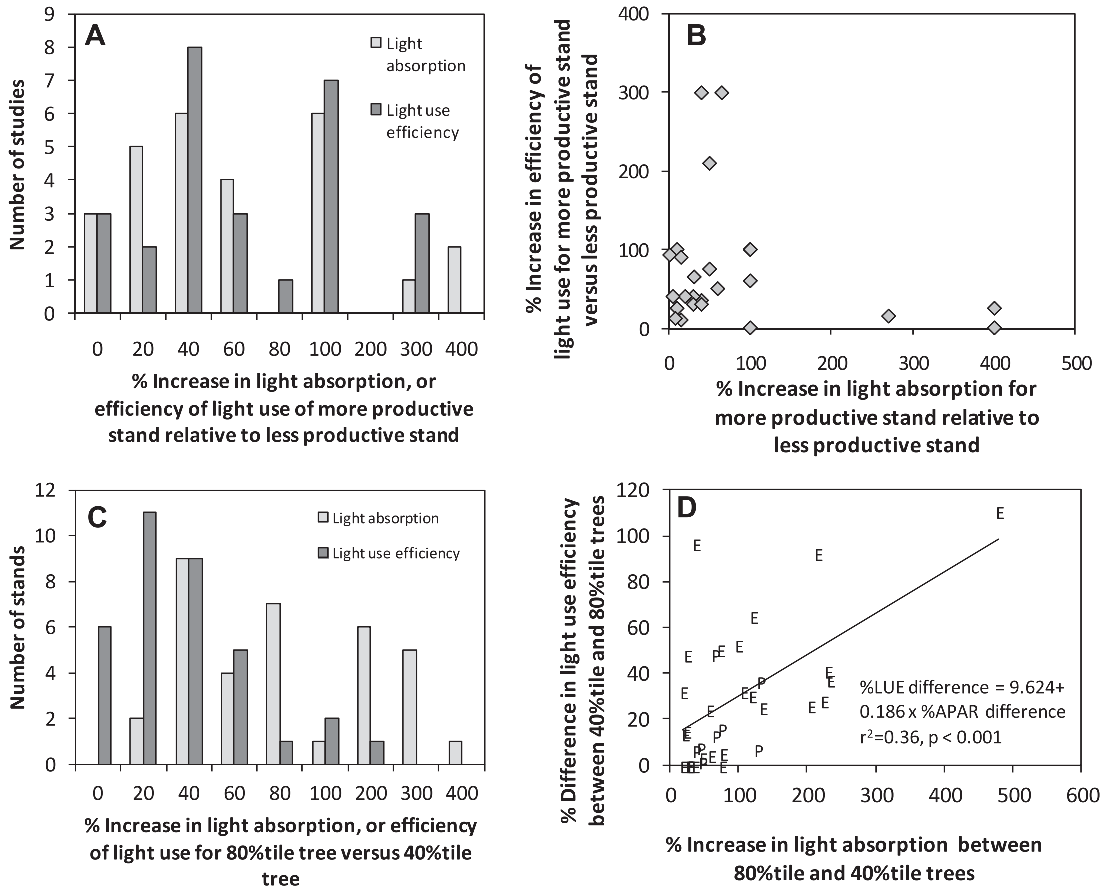

Fig. 1. When one forest is more productive than another forest, as a result of species composition, geographic site productivity, or silvicultural treatments, the faster growth may result from increased light absorption, increased efficiency of using light to grow stem wood, or both. Increases in light absorption and efficiency of light use are about equally common as drivers of differences in stand level growth (A), from data summarized in Binkley, 2011). There is no pattern across studies in the magnitude of change in light absorption versus light use efficiency (B), but notably no studies reported a negative interaction (lower light use efficiency with higher light absorption), or very large differences in both factors together. Within a stand, large trees typically grow faster than small trees; comparing the average light absorption for 40th percentile trees and 80th percentile trees (based on stem mass or volume) showed that light absorption is typically 65% (median) to 100% (mean) higher for the 80th percentile tree, whereas light use efficiency is typically 24% (median) to 28% (mean) higher (C), from data in Binkley et al. 2004; Binkley et al., 2010; Campoe et al. 2013a; Forrester et al., 2013; Gspaltl et al., 2013). Within a stand, the larger trees tend to show both increased light absorption and increased efficiency of light use (D); (E = *Eucalyptus*, P = *Picea*), and no stands showed a negative interaction.

indirect approaches over the past century to gauge the effectiveness of trees and stands in absorbing light (Pretzsch, 2010). The development of individual tree crowns has been characterized by crown dimensions (such as the live crown ratio of the foliated length of the stem as a proportion of total stem height) and individual tree leaf area (often estimated from diameter, or from cross-sectional sapwood area). Canopy development for stands has been indirectly indexed by measures of stand basal area or stand density index; stands with low basal area typically grow less stem wood than stands with moderate or high basal areas, largely owing to smaller canopies and lower absorption of light. In the past few decades, direct estimates of stand leaf area have become common, by summing the leaf area of individual trees, or through measures related to light-absorption characteristics.

Crown and canopy characteristics determine the amount of light absorbed by trees and stands, but the relationships between crown or canopy structure and light absorption are not simple. A difference of 50% in leaf area between stands will not show the same influence on light absorption as a 50% difference in leaf area between two trees within a single stand. In this review we explore the relationships between leaf area and light absorption, and explain why patterns fundamentally differ at the scales of canopies within trees (or stands), sets of whole trees, and sets of stands.

2. Three categorical types of light absorption in relation to leaf area

Questions about the influence of leaf area on light absorption fall into three distinct categorical types (Fig. 2). Type I considers the attenuation of light passing through the crown of a tree, or the canopy of a single stand. A layer of leaves tends to absorb a fraction of incident light, depending on leaf angle, leaf clumping, and albedo factors. Light that passes through the first layer of leaves may be partially absorbed by the second layer, and so on. If each layer of leaves absorbs the same proportion of incident light, the resultant curve of light absorption as a function of leaf area will give a logarithmic trend. A doubling of the leaf area in a crown, or leaf area index (LAI, the layers of leaves per ground area) of a single stand, would typically provide less than a doubling of light absorption.

Another categorical type is the relationship of light absorption to leaf area when compared across a set of stands. Light absorption within a single stand would likely follow the Type I expectation, but a comparison among stands (Type II) may show an entirely different pattern. One stand may have double the leaf area of another, but the difference in light absorption would depend on structural differences between the stands (leaf angles, leaf clumping on shoots, and especially on the extent of gaps between crowns). Gi-