

# Tree-Level Patterns of Lodgepole Pine Growth and Leaf Area in Yellowstone National Park: Explaining Anomalous Patterns of Growth Dominance Within Stands

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## ABSTRACT

The growth of forests is the simple sum of the growth rates of all the trees. The growth of individual trees results from non-linear competition among trees for resources, including efficiency in the use of resources to grow stems, and these characteristics may change as trees and forest age. Lodgepole pine (*Pinus contorta*) forests in Yellowstone National Park showed an unusual pattern of low dominance of large trees (=reverse growth dominance), and we hypothesized this pattern resulted from a pattern of declining resource use efficiency (defined as wood growth per unit of tree leaf area) for large, old trees. Across a 96-site chronosequence, the largest trees continued to increase growth with age. Leaf area increased faster with tree size than did growth, leading to lower

growth efficiency for large trees in stands older than about 125 years. These patterns contrasted strongly with those from a similar study with fast-growing *Eucalyptus saligna*, where strongly positive growth dominance resulted from greater growth efficiency across all sizes and ages. The hypothesis was supported, as the reverse growth dominance was associated with declining resource use efficiency in large, old lodgepole pine trees. Several factors may contribute to the declining growth efficiency of large, old pines, and the contribution of these potential factors could be determined from further investigation.

**Key words:** growth dominance coefficient; individual tree growth; forest productivity.

## INTRODUCTION

The development of most forests follows some common trends, including increases in the average mass of trees, and increases in the total mass of

trees per hectare. These trends are often, but not always, accompanied by trends such as declining numbers of overstory trees per hectare as competition leads to mortality of smaller trees. Other trends are not monotonic; the rate of growth per hectare for a stand often reaches a maximum and then declines (Ryan and others 1997), whereas the growth of the very largest trees within a stand continues to increase (Assmann 1970; Stephenson and others 2014). All these trends develop in

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response to the acquisition and efficiency of use of resources by individual trees, including competition between trees. Competition in forests has often been categorized in terms of dominance, with large trees expected to obtain greater supplies of resources than suppressed trees, leading to faster growth rates for dominant trees. Faster growth by large, dominant trees may also result from greater resource use efficiency, as dominant trees often use resources more efficiently in producing stem wood than non-dominant trees (Binkley and others 2013; Gspaltl and others 2013; Campoe and others 2013).

Patterns observed at the scale of stands develop from interactions among individual trees, and these interactions are often non-linear and asymmetrical between large and small trees (Canham and others 2006; Pretzsch and Biber 2010). Dominance may be very strong in some forests, and moderate in others. The pattern of dominance and tree growth can be characterized in terms of growth dominance, where the pattern of sizes among trees within a stand is compared with the pattern of growth (Binkley 2004). If the growth rate of each tree is proportional to its size, growth dominance is zero. Where dominant trees contribute greater proportions of stand growth compared to stand mass, dominance is positive and the disparity among tree sizes increases over time. In some cases, dominant trees account for a larger share of stand biomass than current growth, indicating reverse growth dominance where the size divergence of trees within forests slows or diminishes. Growth dominance can be indexed with a coefficient that is analogous to the Gini coefficient (Binkley and others 2008). If the growth of each tree in a stand is linearly proportional to tree size, the growth dominance coefficient is 0. Greater growth (in relation to tree size) by larger trees gives a positive coefficient (with a maximum possible of 1.0), and slow growth by large trees gives a negative coefficient (and reverse growth dominance, with a minimum possible of  $-1.0$ ).

Patterns of growth dominance during stand development are not universal. Some cases, such as fast-growing plantations of *Eucalyptus*, develop and sustain strong growth dominance (positive growth dominance coefficients) as biomass accumulates to hundreds of megagrams per hectare (Binkley 2004; Doi and others 2010). Plantations of pine species often show little growth dominance, with growth dominance coefficients near zero throughout a rotation (Martin and Jokela 2004; Fernández Tschieder and others 2012). In other cases, growth dominance patterns in pine forests shift with

management regimes (Bradford and others 2010). Fernandez and others (Fernández and others 2011) suggested that some of the differences in patterns of growth dominance among forests may result from varying levels of plasticity in rates of photosynthesis among species.

Lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) forests in Yellowstone National Park showed an unusual pattern of growth dominance during stand development. Over several centuries, growth dominance coefficients varied from near zero to strongly negative (reversed growth dominance), with no period of positive growth dominance (Binkley and others 2008). A tree that was 1.5 times the size of a smaller tree in the same stand typically grew less than 1.5 times faster. For comparison, the same situation in a eucalyptus plantation might have the larger tree growing two or three times faster than the smaller tree (Binkley and others 2010). We know of no other forest type that shows strong reverse growth dominance, though too few assessments have been conducted to establish how rare this pattern might be for other species and sites.

Why do lodgepole pine trees fail to show strong growth dominance at any phase of stand development? We hypothesized that reverse growth dominance in lodgepole pine stands results from lower efficiency of using light to produce wood in dominant trees than in non-dominant trees, moderating the growth rates of the larger trees. This would be the opposite of the commonly found patterns for other forest types (Binkley and others 2013). Any pattern in efficiency of light use may derive in part from patterns in use and efficiency of use for nutrients and water, as these often covary positively among stands across sites (for example, Stape and others 2004) and among trees within sites (for example, Binkley and others 2002). For example, a pattern driven by a difference in efficiency of nutrient use among trees within a stand would likely drive a similar pattern in light use efficiency, and experimentation would be needed to unravel potential interactions.

## SITE DESCRIPTION AND METHODS

We tested our hypothesis using data from an age sequence of lodgepole pine stands in (and near to) Yellowstone National Park (Kashian and others 2005, 2013). The area is located in the northeastern corner of Wyoming, extending into adjacent Montana and Idaho (general location:  $44^{\circ}$  to  $45^{\circ}$  N,  $110^{\circ}$  to  $111^{\circ}$  W). The summers are cool (average temperature  $13^{\circ}\text{C}$ ) and winters are very cold ( $1^{\circ}\text{C}$

average), with about  $600 \text{ mm y}^{-1}$  precipitation (mostly as snow). The low-fertility soils are mostly sandy loams developed from rhyolitic parent materials. Stand-replacing fires commonly occur at intervals of one to several centuries, and landscapes are dominated by both even-aged and uneven-aged stands of lodgepole pine.

The age sequence included 96 stands, ranging in age from 12 to more than 350 years old. The original sampling was designed to include a range of stand densities within each age class, and all stands were at least 5 ha (and more than 100 m from roads and trails). Tree diameters and heights were measured in three subplots (10 m  $\times$  50 m) at each of the 96 locations. The biomass of stems and foliage of trees younger than 25 years were estimated as

$$\text{Stem mass} = 13.144 \times \text{basal diameter}^{2.888} (r^2 = 0.88)$$

$$\text{Foliage mass} = 7.193 \times \text{basal diameter}^{2.729} (r^2 = 0.70)$$

with mass in g and basal diameter in cm (Litton and others Litton and others 2003). Values in older forests were calculated as

$$\text{Stem mass} = 0.020 \times dbh^{1.535} * ht^{1.447} (r^2 = 0.97)$$

$$\text{Foliage mass} = 0.104 * dbh^{2.419} * ht^{1.447} (r^2 = 0.82),$$

where mass is kg, *dbh* is diameter at 1.4-m height in cm, and *ht* is total height in m (Kashian and others 2013). Specific leaf area (on a projected basis) was assumed to be a constant  $9.52 \text{ m}^2 \text{ kg}^{-1}$  (Kaufman and Troendle 1981) across all stands. Stem increment was estimated based on the current mass of each tree minus the estimated mass of the tree 5 years prior (based on radial increments taken from 30 random trees at each location).

Our hypothesis would be tested ideally with direct measurement of light use at the scale of individual trees, but direct measurement is not possible and modeling approaches require complex parameterization. Fortunately, within stands the interception of light (absorbed photosynthetically active radiation) relates directly and linearly with the leaf area of a tree (Binkley and others 2013). This may not be true at the scale of stands, where self-shading within canopies influences stand APAR/leaf area; at the scale of individual trees, the pattern is linear because trees (within a stand) with more leaf area have proportionally greater spread of crowns. Therefore, we used tree leaf area as a proxy for tree APAR and tested our hypothesis that larger trees within stands would show lower increment/

leaf area. This relationship is sometimes referred to as "growth efficiency" (Waring and others 1980; Waring 1983; Mainwaring and Maguire 2004; Gspaltl and others 2012).

The use of a regression equation to estimate leaf area introduces a notable error in calculations of stem increment per leaf area. Regressions calculate leaf area for average trees; a tree that grows faster than average may have more leaf area than a slower growing tree of the same diameter and calculated leaf area. In such a case, the increment/leaf area would be overestimated for the faster-growing tree. Similarly, slow-growing trees may be calculated to have leaf areas that are too high, leading to an underestimation of true increment/leaf area. Fortunately, this bias is opposite in direction from our hypothesis (fast-growing dominant trees will show lower increment/LA than subordinate trees), and would lead to rejection of the hypothesis rather than to false support.

Within each plot, we ranked trees from smallest to largest based on stem mass, and converted the rankings to percentiles for the tree rank within the plot. The patterns of stem increment, leaf area, and stem increment/leaf area in each stand were fit with curves using CurveExpert version 2.0 (<http://www.curveexpert.net/>). The best-fit equation (based on lowest AIC<sub>C</sub>, Akaike's Information Criterion adjusted for small sample sizes) was then used to estimate the average trend across the percentiles in each stand. The 96 plots were analyzed for patterns of stem increment, leaf area, and stem increment/leaf area as a function of tree percentile and stand age (also with CurveExpert).

The pattern of dominance among trees within stands develops from patterns of individual tree growth, leaf area, or growth/leaf area. We tested the importance of each factor by regressing the growth dominance coefficients for each stand (from Binkley and others 2006) against stem growth, leaf area, and growth/leaf area. We used the values for the 80th percentile tree to represent the class of large trees, and the values for the 40th percentile tree to represent the small trees.

A similar analysis of age, growth, and leaf area was performed for a *Eucalyptus saligna* stand in Hawaii that had been remeasured over a 20-year period (Binkley and others 2003), providing an illustration of how patterns differ between the reverse growth dominance case of lodgepole pine and the strong positive growth dominance of *Eucalyptus*. The age span in the *Eucalyptus* case study was shorter than the lodgepole pine study, but stem biomass of *Eucalyptus* at age 20 (about  $230 \text{ Mg ha}^{-1}$ ) was much greater than that of lodgepole pine after several

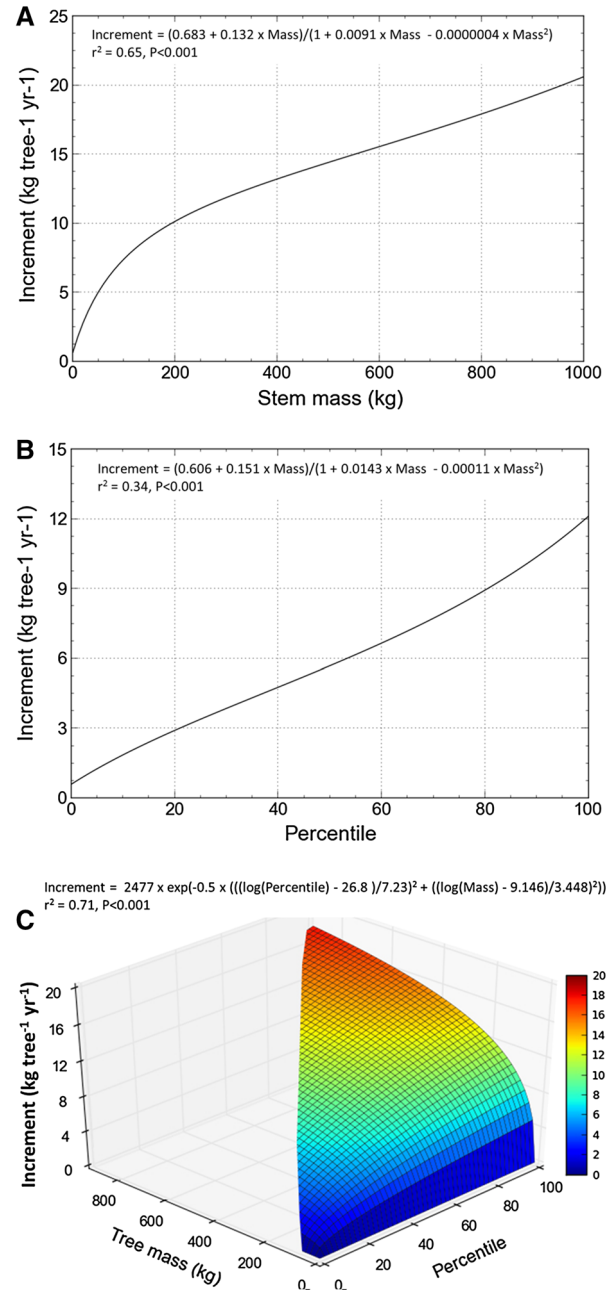
centuries (about  $150 \text{ Mg ha}^{-1}$ ), providing a good basis for contrasting growth patterns despite the age differences.

## RESULTS AND DISCUSSION

Across all stands and ages, larger lodgepole pine trees tended to grow faster than smaller trees; a 400-kg tree would average about 30% more growth than a 200-kg tree (Figure 1A). This is much less than the at least 200% greater growth that would be needed for a stand to show zero or positive growth dominance. The average growth of an 80th percentile tree would be about double that of a 40th percentile tree (Figure 1B). A tree of a given size tended to grow more if it was also dominant within the stand. For example, a 400-kg tree at the 80th percentile within a stand would grow about one-third faster than a 400-kg tree at the 40th percentile in a stand (Figure 1C).

Suppressed trees (low percentile ranking) showed little growth at any age (Figure 2A), and dominant trees in the oldest forests averaged the greatest growth (consistent with the common forest pattern highlighted by Stephenson and others 2014). Leaf area per tree increased with increasing age and increasing dominance (Figure 2B). The increase in growth of dominant trees after age 100 was less than the large increase in tree leaf area, so the combination of these patterns showed that the greatest growth/leaf area occurred in trees of moderate age and dominance (Figure 2C). The patterns in Figure 2 strongly support the hypothesis that lodgepole pine trees fail to show strong growth dominance at the stand scale because the higher leaf area (and light interception) of dominant trees is partially offset by lower stem growth/leaf area. The overall pattern of stand age and dominance (Figure 2C) accounted for about 15% of all the variation in growth/leaf among trees.

Large ratios of growth rates between large (80th percentile) and small (40th percentile) trees were associated with growth dominance coefficients of near zero, whereas smaller ratios of growth for large and small trees occurred in stands with negative growth dominance coefficients (Figure 3), consistent with the pattern reported by Fernández Tschieder and others (2012). The ratio of leaf area of the large versus small trees did not relate strongly to stand growth dominance coefficients. The ratio for large and small trees for growth per leaf area showed a very strong relationship, also supporting the hypothesis. Stands with negative growth dominance coefficients had less difference

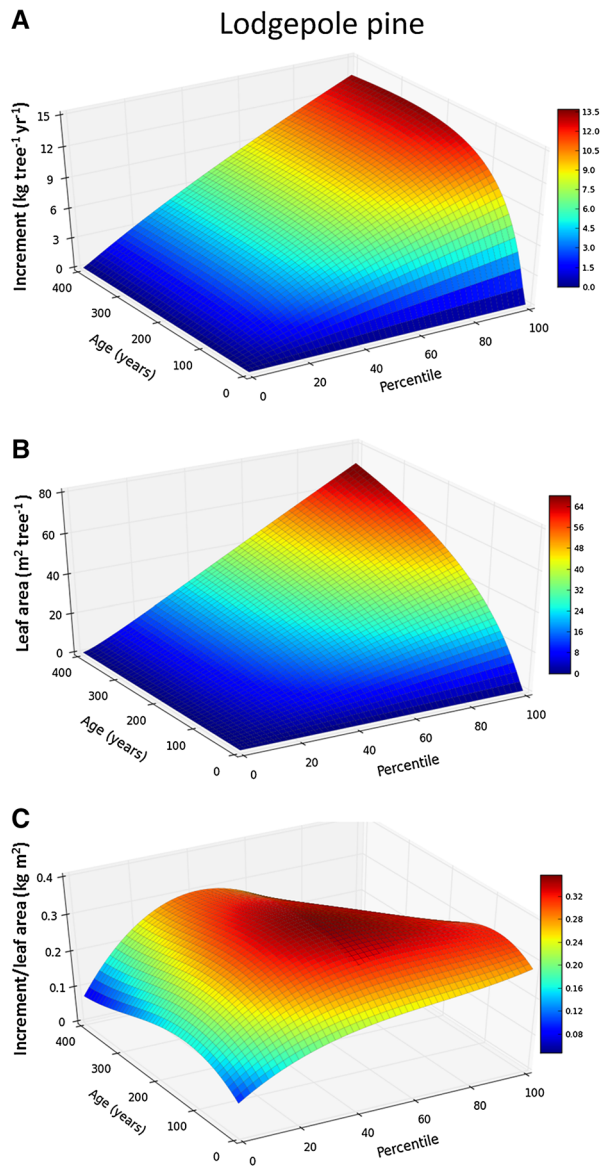


**Figure 1.** Larger trees tended to grow faster than smaller trees across all stands (**A**,  $\text{AIC}_C = 8556$ ), with differences in tree sizes being more important for trees less than 200 kg. Across all stands, dominant (higher percentile) trees tended to grow faster than subordinate trees (**B**,  $\text{AIC}_C = 10990$ ). Including both mass and dominance (**C**) provided a better prediction of increment ( $\text{AIC}_C = 7854$ ).

between large and small trees than did the stands with near zero coefficients.

The pattern found for a forest showing a typical absence of reverse growth dominance is illustrated in Figure 4 with a *Eucalyptus* case study. Both the growth and the leaf area in this plantation were





**Figure 2.** The pattern of stem increment for lodgepole pine forests (**A**;  $r^2 = 0.52$ ) did not increase as steeply for large, old trees as did the pattern for leaf area (**B**;  $r^2 = 0.52$ ), leading to a downward trend of growth/leaf area in old, dominant trees (**C**;  $r^2 = 0.15$ ,  $p < 0.01$ ).

concentrated in dominant trees, and growth/leaf area was always greater for dominant trees at all ages. Increases in tree growth (with increasing tree size) were always larger than increases in tree leaf area.

Indeed, growth dominance of the largest *Eucalyptus* trees within a stand may remain strong even in old stands that exceed 300 Mg ha<sup>-1</sup> of biomass and heights over 40 m (Doi and others 2010). We do not have information on stem growth/leaf area in old-growth stands of *Eucalyptus*. The largest trees in very old stands would have greater heights, crown

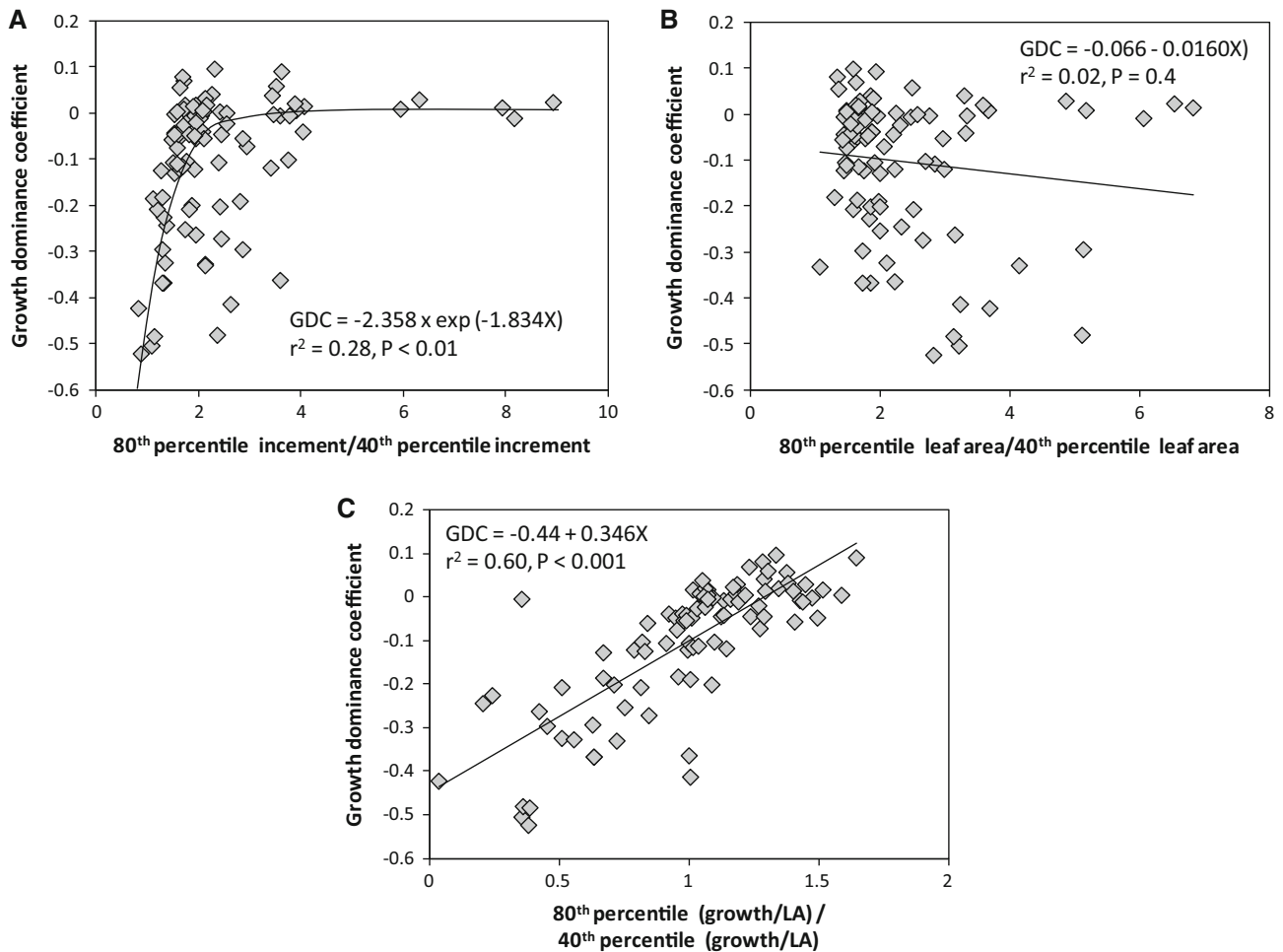
widths, and branch lengths than non-dominant trees, but sustained positive growth dominance means that either leaf area is disproportionately higher or the growth/leaf area remains higher for dominant trees.

The support for the hypothesis leads to the next question: Why does leaf area (and light interception) for lodgepole pine trees increase for large trees without a commensurate increase in stem growth? Additional experimentation is needed to explore this question, and we expect the explanation may include one or more of the following ideas.

Fernández and others (2011) noted that some *Eucalyptus* species have high plasticity in rates of photosynthesis per unit of resource used (such as photosynthesis/light intercepted). Trees with higher resource use may have plasticity to increase efficiency of resource use. They noted that pines may show low plasticity, leading to reduced dominance in pine stands than in *Eucalyptus* stands. Our case for lodgepole pine would be consistent with a high plasticity in a pine species, but in the opposite direction to that noted for *Eucalyptus* by Fernández and others (2011).

The rate of photosynthesis per unit of leaf area (and light interception) could be lower for large trees. Declining specific rates of photosynthesis have been reported for a wide variety of trees (Bond 2000). The importance of potential driving factors is unclear. Increasing tree height is usually associated with reduced water use efficiency (Koch and others 2004; McDowell and others 2011), but the marginal increases in heights for older lodgepole pine trees are probably too slight (see below) for this mechanism to be important. For trees of similar heights, greater crown width and greater branch lengths on older trees might lower water use efficiency (Waring and Silvester 1994; Walcroft and others 1996).

We speculate that the pattern for old lodgepole pine trees could reflect an increasing average age of sapwood rings that are retained to support the crown (for example, Pothier and others 1989). Fifty-year-old trees average radial increments of 1.3 mm y<sup>-1</sup>, dropping to 0.35 mm y<sup>-1</sup> by age 100 and 0.15 mm y<sup>-1</sup> by age 200. The smaller radial increments of older, larger trees is associated with increased crown leaf areas, necessitating more years of sapwood retention to sustain the sapwood area needed to meet crown water demands. Perhaps the conductance of older xylem inhibits efficient water use and photosynthesis per unit of light intercepted. Evidence from studies of other pine species is mixed. Conductance decreased with stand age for *Pinus banksiana*, with a stronger de-



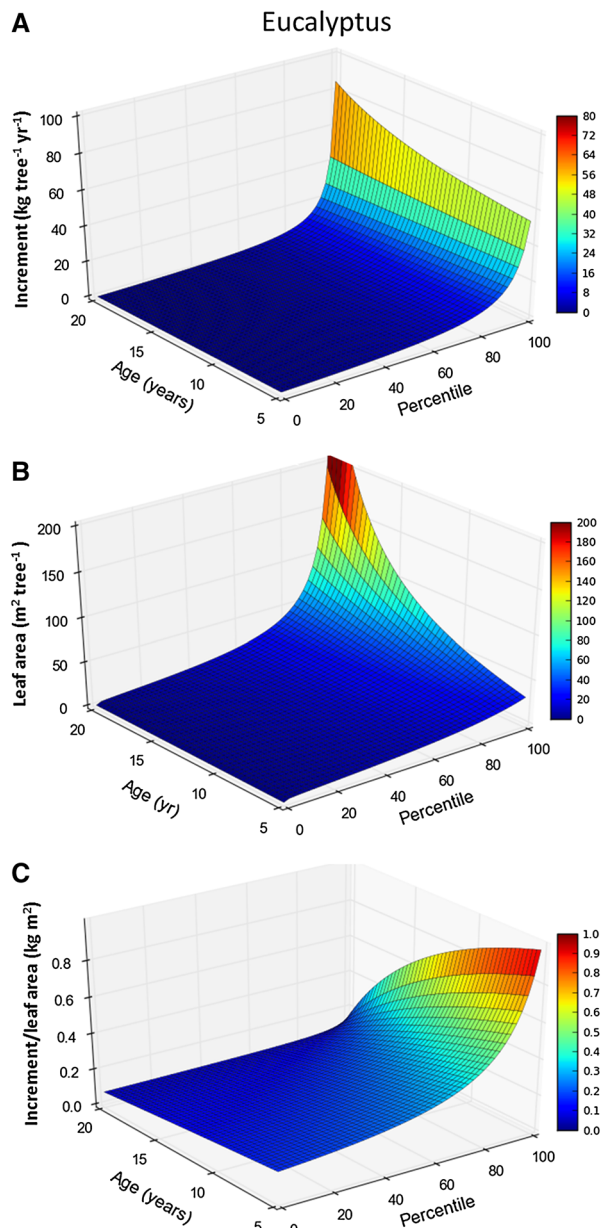
**Figure 3.** The ratios of growth rates of larger trees to smaller trees (represented by the 80th percentile and 40th percentile tree in each stand) accounted for little of the variation the growth dominance coefficients of the stands, except that stands with very high ratios all had coefficients near zero (**A**). The ratio for leaf area (LA) did not relate significantly with the growth dominance coefficients (**B**), though omission of the stands less than 20 years old increased the  $r^2$  to 0.34 ( $p < 0.01$ ; not shown). Growth dominance coefficients increased strong with increasing ratios of growth efficiency (stem growth/LA) for large:small trees (**C**). Stands with low dominance had negative growth dominance coefficients, and showed lower growth efficiency for large trees than small trees.

cline in low-productivity sites that might be similar to our lodgepole pine sites (Pothier and others 1989). A study of the hydraulic characteristics of *Pinus ponderosa* showed that trees over 220 years of age did retain living sapwood for more than 150 years; however, the hydraulic conductivity of sapwood in old trees was not lower than in younger trees (Domec and Gartner 2003), so this possible mechanism may not be important. Direct measurements of photosynthesis and the eco-physiological factors driving any patterns would be needed to provide insights on how plasticity in this case would work against dominant trees with rates of resource use.

It is possible that the increase in leaf area with large tree sizes develops from a lengthening of the

live crowns rather than a spreading of branches that broadens the crowns. More leaf area that is essentially concentrated in tall cylinders would lead to more self-shading within crowns, contrary to the typical pattern of high leaf area trees having broader crowns (Binkley and others 2013). Lengthening the live crowns for large trees could lead to lower light interception per unit leaf area, and lower carbohydrate production for use in growing wood. However, average tree height reached 13 m by age 100 years, rising to 16 m at 300 years, so we do not expect that longer crowns are likely to explain the pattern.

A third alternative is that large, old trees sustain the same rates of photosynthesis per leaf area and light interceptions as smaller, younger trees, but



**Figure 4.** In contrast to lodgepole pine, the pattern for the *Eucalyptus saligna* stand showed large enough increases in increment with dominance (**A**;  $r^2 = 0.52$ ) relative to leaf area (**B**;  $r^2 = 0.81$ ) that larger and dominant trees of all ages were more efficient at growing wood/leaf area than smaller and subordinate trees (**C**;  $r^2 = 0.22$ ,  $p < 0.01$ ).

they allocate proportionally less photosynthate to wood growth and more to respiration or belowground production. Information is not available for partitioning of photosynthate on an individual tree basis. At a stand level, age-related declines in wood growth and aboveground net primary production do not appear to be driven by changes in partitioning. Ryan and others (1997) concluded that

declining growth in an older stand of lodgepole pine in Colorado led to a decrease in total woody biomass respiration, which would not be consistent with increasing partitioning to respiration in our Yellowstone stands. In southeastern Wyoming, Smith and Resh (1999) found that a consistent proportion of stand production was allocated belowground across a 260-year chronosequence. Litton and others (2004) looked at belowground allocation at a stand scale for some of the young (13 years old) and moderate-aged (110 years old) stands of lodgepole pine used in the present paper; total belowground carbon allocation related strongly with aboveground net primary production, so declining production in older stands would not likely result from increasing partitioning belowground.

A final possibility is that tree growth is not carbon-limited for older, larger trees. Low rates of stem growth per unit of leaf area (or light interception) could result from a sink limitation rather than a source (carbon supply) limitation. A variety of studies have shown that trees with low growth rates actually have higher storage of non-structural carbohydrates than fast-growing tree (Körner 2003). This scenario would beg the question, however, of why larger trees produce and sustain crowns in excess of what would be needed to meet actual sink demands for carbohydrates.

How might this case study provide insights for other species and locations? The statistical population of inference for this investigation is the lodgepole pine forests of Yellowstone National Park. We expect the patterns would likely apply to other lodgepole pine stand in the region, as patterns that applied at a geographic scale of hundreds of thousands of hectares might be robust across larger geographic areas.

What insights might apply beyond this single forest type? The answers to this question might depend on how commonly older forests develop reverse growth dominance, where the largest trees contribute less than a proportionate share of stand growth. We don't know how common this pattern might be. Mixed-species forests might be another case where reverse growth dominance might develop. Doi (2008) found very strong reverse growth dominance in the diverse forests on Barro Colorado Island, Panama. Patterns of leaf area and growth/leaf area were not measured for these stands, but we predict that dominant trees would show lower stem growth/leaf area than non-dominant trees. We speculate that the presence of multiple species might lead to a broader range of physiology and growth efficiency, providing more options for non-



dominant trees to show high efficiency and an overall pattern of reverse growth dominance in older forests. These ideas would be very interesting to test in mixed-species forests in both tropical and temperate locations.

Stephenson and others (2014) showed that sustained high growth rates for dominant trees typically persist even for very old trees. We speculate that sites and trees that are exceptions to this general pattern would develop where the efficiency of resource use by large old trees is not sustained.

Many more investigations will be needed into the typical patterns found in forests, and the factors that drive variations in these patterns among forests.

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