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A hypothesis about the interaction of tree dominance and stand production through stand development

Dan Binkley[*]

Department of Forest, Rangeland and Watershed Stewardship, Graduate Degree Program in Ecology, and Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523, USA

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Abstract

The development of forests over time involves changes in rates of growth of trees and stands, and changes in the competition and dominance between trees plays a large role in the overall development of stands. A hypothesis proposes that changes in the growth of trees and stands result from regular changes in dominance and the efficiency of resource use by dominant and non-dominant trees. Dominance is low prior to canopy closure, and efficiency of resource use is high for all trees. Increasing dominance near canopy closure reduces the efficiency of resource use by non-dominant trees, lowering overall stand growth. Later in stand development, the efficiency of resource use also declines for the largest trees, reducing the level of dominance in the stand. The dominance part of this hypothesis was examined for 150 years of stand development in two mixed-species stands in the Coast Range of Oregon. A quantitative index of dominance was minimal prior to the peak in stand growth near age 25–30 years, and then increased sharply as stand productivity declined. Dominance then declined after age 100 years as the growth rate of the 300 largest trees/ha began to decline. The dominance portion of the hypothesis was supported, and further testing may be useful.

Keywords: Forest production; Age-related growth decline; Douglas-fir; Western hemlock; Resource use efficiency

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1. Introduction

Two patterns are observed in the development of most even-aged forests: trees differentiate into various dominance classes (Oliver and Larson, 1996), and overall forest growth increases, peaks, and then declines (Ryan et al., 1997). These two patterns are driven by a host of interacting processes, including: the supply and use of resources (such as light, water, and nitrogen), competition for resources, and differences in the efficiency of trees (and species) in using resources to grow. Binkley et al. (2002a) examined the interaction of these two patterns, and proposed that the decline in stand-level wood growth that commonly occurs shortly after canopy closure may be driven primarily by shifts in dominance among trees, and by the ensuing declines in efficiency of resource use by the suppressed trees. The processes that account for growth declines near canopy closure may differ from those that constrain growth rates late in stand development (B.J. Bond, M.G. Ryan, personal communication).

In this paper, I propose that the decline in stand-level growth near canopy closure is driven by increasing dominance of larger trees, leading to declining

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[*] Tel.: +1-970-491-6519; fax: +1-970-491-2796.
E-mail address: dan@cnr.colostate.edu (D. Binkley).

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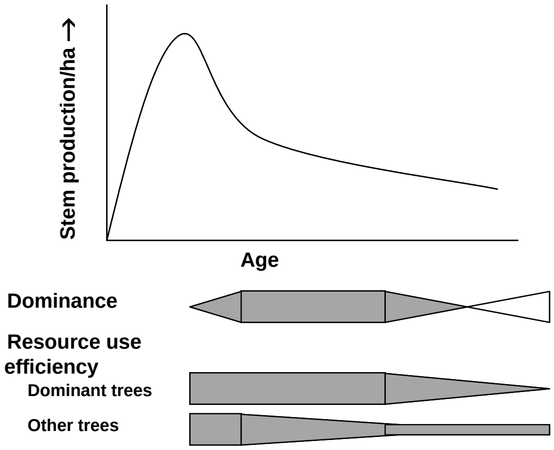

Fig. 1. Hypothesized trends in dominance and resource use efficiency (stem production per unit of resource used) in relation to changes in stem production through stand development. Dominance is low prior to the peak in stem production (near the time of canopy closure; Ryan et al., 1997), and efficiency of resource use is high for dominant trees and other trees. Increasing dominance then leads to reduced efficiency of resource use of non-dominant trees (Binkley et al., 2002a), and a decline in total stand stem production. The efficiency of resource use by dominant trees is sustained until some point then declines, with a concomitant decline in dominance. Very large, old trees may no longer dominate stand production, leading to a "reverse" dominance (unfilled triangle in dominance bar) late in stand development.

efficiency of resource use by smaller trees. With further stand development, the ability of large trees to dominate smaller trees declines as the spacing between trees increases, and large, old trees enter a phase where their growth no longer keeps pace with their increasing dominance of site resources (Fig. 1). The hypothesis was developed from experiments with *Eucalyptus* plantations in Hawaii (Binkley et al., 2002a, 2003; Ryan et al., in press), and in old-growth forests in the Rocky Mountains (Binkley et al., 2002b). The relationship between dominance and age-related (or size-related) decline in forest production would of course be complicated by any time-related changes in other factors, including nutrient supply in the soil (Ryan et al., 1997).

A full test of the hypothesis is difficult, as intensive studies in plantations typically do not progress to very late stages of stand development, and long-term data on growth of old, unmanaged forests is sparse. I tested some key expectations of these ideas about dominance and age-related decline for a period of 150 years using records from over 70 years of development of two stands in the Coastal Range of Oregon (from the Permanent Study Plot program, a partnership between the H.J. Andrews Long-term Ecological Research Program and the US Forest Service Pacific Northwest Research Station). This single test cannot address the full hypothesis, but the test provides a good illustration of the dominance components of the overall hypothesis, and the outcome of the test could undermine the hypothesis.

2. Methods

The changing dominance of trees through stand development was examined for two nearby stands in the Cascade Head Experimental Forest. Data for the first eight decade years of stand development were taken from the 0.2 ha Plot #11, with remeasurement of tagged trees at ages 21, 26, 31, 43, 55, 60, 71 and 76 years. This unmanaged stand developed after pasture abandonment in 1925 (Berntsen, 1961; Binkley et al., 1992; Binkley, in press). The site index for Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) was about 40 m at 50 years. After the first 10 years of stand development, the stand contained about 4500 conifers/ha (Douglas-fir, western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and Sitka spruce (*Picea sitchensis* (Bong.) Carr.)) and 3000 red alder/ha (*Alnus rubra* Bong.).

The older unmanaged stand established following the catastrophic Nestucca wildfire in the late 1840s. Plot #14 is a 0.4 ha experimental area in the Cascade Head Experimental Forest's permanent plot system for Douglas-fir growth; Acker et al. (2000) provide production and biomass information for some other plots that regenerated primarily to western hemlock and Sitka spruce after the same fire. The diameters of permanently tagged trees were measured at age 85 (in 1935), 90, 96, 101, 106, 138, 133, 139, 144 and 149 years.

Stem mass was estimated from tree diameters with the biomass equations (from the Oregon State University Forest Science Data Bank, Means et al., 1994):

$$\log_e(\text{alder mass in kg}) = -2.669 + (2.463 \log_e(\text{diameter in cm}));$$

$\log_e(\text{Douglas-fir mass in kg}) = -3.0396 + (2.5951 \log_e(\text{diameter in cm}))$;
$\log_e(\text{hemlock mass in kg}) = -2.681 + (2.447 \log_e(\text{diameter in cm}))$;
$\log_e(\text{spruce stem mass in kg}) = -8.55 + (2.457 \log_e(\text{diameter in mm}))$.

The patterns of stem mass and growth were evaluated by summing the stem mass of all trees within each plot for each period; the largest 300 trees/ha in each time period were also examined to indicate the age-related trends in the dominant cohort of trees.

Dominance is commonly defined by canopy classes, such as dominant, codominant, intermediate, and suppressed (Oliver and Larson, 1996). For the purpose of this hypothesis, a functional definition of dominance is needed. I defined dominance in relation to the pattern of cumulative distributions of stem mass and growth. Trees were arranged from smallest to largest for each time period, and the cumulative distribution for stem mass was compared with the cumulative distribution for stem growth. A stand showing no dominance would have 20% of the stand increment produced by the trees that comprise each 20% tile of the stem mass. A stand with strong dominance would have notably more than 20% of the total stand growth contributed by the largest trees that comprise the top 20% of stem mass. An old stand with massive, slow-growing trees might even show "reverse" dominance, where the trees comprising the top 20% of stem mass contribute notably less than 20% of the stem increment of the stand.

In the hypothesis test, I expected to find low dominance prior to the peak of stand increment, which would be consistent with the idea of high efficiency of resource use by all trees prior to the period of full canopy closure. After that point, the dominance of the larger trees should accelerate, driving down stand-level increment as a result of falling efficiency of resource use by suppressed trees. Later in stand development, other ecophysiological factors should constrain the growth of the dominant trees (despite sustained high resource use), accentuating the decline in stand-level increment and relaxing the degree of dominance in the stand. These tests examine the key dominance components of the hypothesis in Fig. 1, but do not test the components of resource use efficiency.

3. Results and discussion

How comparable were the two stands? At age 76 years, the stem mass of the younger stand was comprised of 7% western hemlock, 17% Sitka spruce, 37% Douglas-fir, and 38% red alder. The stem mass of the older stand at age 85 years was just 1% red alder, along with 3% Sitka spruce, 23% western hemlock, and 73% Douglas-fir. These differences at a similar age indicate that the younger stand probably had substantially more red alder and Sitka spruce in its early development than the older stand. Despite these notable differences in species composition, the patterns of growth, biomass accumulation, and dominance appeared to chart similar trends (Fig. 2). The pattern of stem mass and gross stem increment indicated that the older stand may have been somewhat larger and more productive when it was the same age as the younger stand. This could result from the influence of red alder in the younger stand; the rate of mortality among the alder was large from age 50–76 years, and the total alder stem mass declined over this period (Binkley, in press). The self-thinning trajectory of the younger stand would be consistent with the trajectory of the older stand (Fig. 2). Most importantly, the trends in mass and growth of the dominant cohort (largest 300 ha^{-1}) looked similar.

If these two stands can be taken to represent the general trend that would be followed by a single stand over 150 years, the major features would include:

1. An accumulation of more than 500 Mg/ha of stem mass in a century.
2. A peak in the rate of stem increment near age 25–30 years, followed by a rapid decline of 40% or more.
3. A peak in the growth of the dominant cohort of trees (largest 300 ha^{-1}) near 80 years, followed by a gradual decline.

The dominance trends also appeared to be congruent between the two stands. At age 24 years, the younger stand showed little dominance, as the cumulative wood increment matched the cumulative stand biomass (Fig. 3a). The smallest trees comprising 20% of the stem mass accounted for 20% of the stem increment, and the largest 20% accounted for 17% of the growth. Dominance was much stronger by 74 years, when the smallest 20% contributed only 9% of

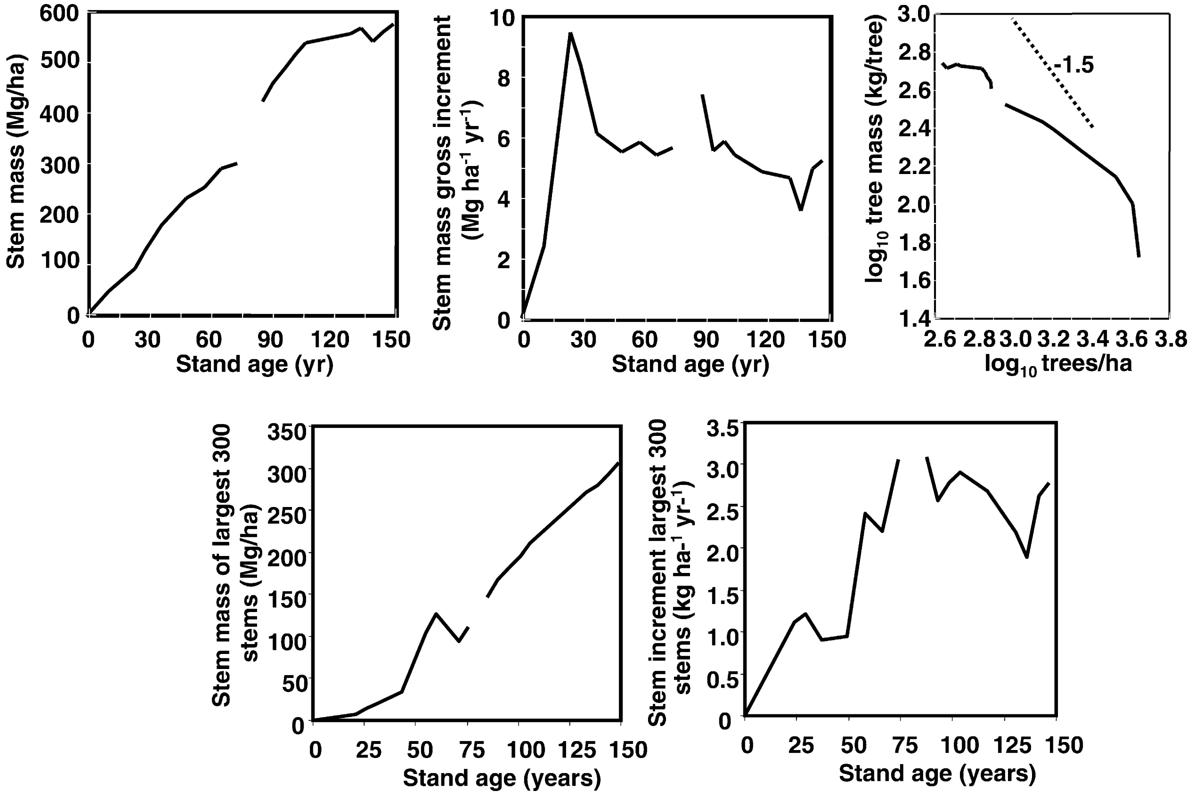

Fig. 2. Patterns of stem mass, increment, and self-thinning for all trees in both stands (upper graphs), and for the largest 300 trees/ha (the dominant cohort; lower graphs). The gaps in the lines denote the non-overlapping period of record for the two stands.

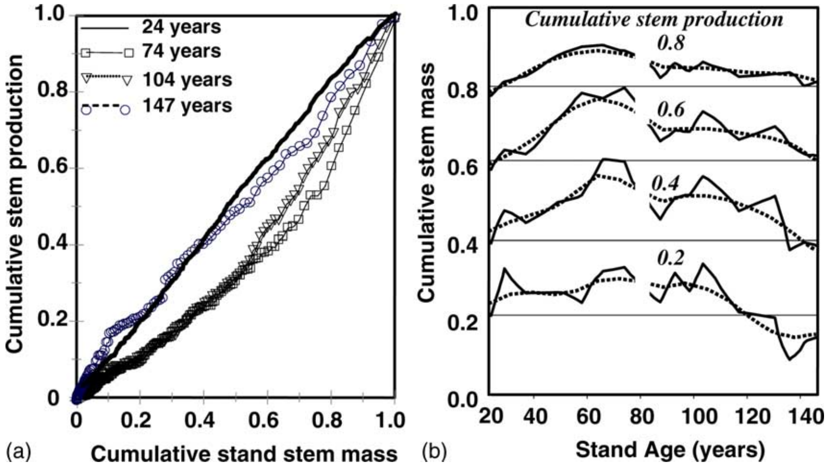

Fig. 3. Cumulative stem production as a function of cumulative stem mass, with trees ranked from smallest to largest (a); the downward progression of the line to age 74 years indicates increased dominance, whereas the return toward the 1:1 line in later years indicates reduced dominance. The same information integrated across all time periods (b), with cumulative stem production as the jagged lines (or smoothed isolines). Curves above the horizontal grid lines of cumulative mass indicate the occurrence of dominance (see text for more explanation).

stand growth, and the largest 20% contributed 39% of the total growth. This increasing dominance is evidenced as a ''sagging'' in the relationship in Fig. 3a. Dominance at age 104 years in the older stand had relaxed somewhat, with the trees comprising the smallest 20% of stem mass accounting for 11% of the total increment, and the largest 20% accounting for 30%. Dominance had disappeared by 147 years, when both the smallest and largest 20% each accounted for 21% of the stand growth. The timeline of dominance matched expectations for stand-level decline in growth; the onset of substantial dominance coincided with the beginning of the decline in stand-level growth, and the later decline in the growth of the dominant cohort (largest 300 trees) marked the end of dominance.

The dominance trends for all periods are illustrated in a three-dimensional plot in Fig. 3b. In this case, stand age comprises the *X*-axis, and the cumulative stem biomass is the *Y*-axis. When the cumulative production matches the cumulative mass (1:1), the cumulative production lines would fall on the horizontal grid lines. Strong dominance is evident where the cumulative production lines rise above the cumulative stem mass grid lines. Between ages 20 and 110 years, the 20% tile trend for cumulative production was higher than the 20% tile line for cumulative biomass, indicating that about 30% of the stand biomass (ranked from small trees to large trees) needed to be included to capture just 20% of the stand production. Similarly, at age 60 years the trees comprising 90% of the stem mass provided only 80% of the production; the largest trees comprising 10% of the stem mass accounted for 20% of the stand production. These dominance trends are consistent with the hypothesis (Fig. 1).

Some of these dominance trends have also been noted in other forests. For example, monocultures of *Eucalyptus saligna* (Sm.) in Hawaii showed an onset of dominance at 2 years, coincident with the beginning of the decline in stand-level growth (Binkley et al., 2003). Dominance increased through age 10 years (stem mass of 130 Mg/ha) when the largest 20% of trees contributed 55% of stand production, then relaxed somewhat by age 20 years when the largest 20% contributed just 40% of stand production. The growth rate of the largest trees comprising 20% of the mass declined after age 10 years, consistent with reduction of dominance. These patterns were consistent with the hypothesized interaction of stand dominance and growth over time in early stages of stand development; increasing dominance accounted for the onset of declining stand-level growth, and declining later growth of the dominant trees resulted in a reduction in dominance.

The pattern of cumulative stand biomass and production for 18 old-growth forests (>250 years) in the Colorado Rockies showed not only a lack of dominance by big trees, but a greater proportional production by smaller trees (Binkley et al., 2002b). The trees comprising the smallest 20% of the stand mass accounted for about 45% of stand production, whereas the trees comprising the largest 20% of stand mass contributed just 8% of stand growth. This would be a case of ''reverse'' dominance, where the growth of the largest trees is less than their proportional contribution to stand mass. This pattern is also consistent with the basic hypothesis of dominance and stand growth declines in old forests; the growth of large, old trees was limited by some ecophysiological feature that also prevented the large trees from dominating the production of the stand.

This hypothesis of the interaction of dominance and stand production may be applicable in a variety of areas. For example, the apparent disparity between some comparisons of ''young'' and ''old'' trees and forests might be removed by having a quantitative measure of whether a decline is associated with increasing or decreasing levels of dominance. For example, hydraulic limitation was refuted as a hypothesis for age-related decline in a *Eucalyptus* plantation near the time of canopy closure (Barnard and Ryan, 2003), but supported in several cases involving trees far beyond the age of canopy closure (Ryan and Yoder, 1997; Ryan et al., 2000; Schäfer et al., 2000). Stand development could also be associated with changing rates of resources use, such as light interception as a result of changes in stand structure (fewer trees, longer crowns, greater spatial heterogeneity). The hypothesis presented here focuses on rates of growth per unit of resource used, and how changes in efficiency would drive trends whether resource use declined over time or not. We clearly need more information on age-related trends in rates of resource use, and in the efficiency of resource use (production per unit resource used) at the level of individual trees and stands. Measurements of individual-tree resource use are now feasible with recent technological advances in laser methods of determining leaf distributions in canopies (Lefsky et al., 2002), and heat-flow methods of estimating whole-tree water use (Granier et al., 1996).

Another application might be a resolution of the apparent contradiction in expectations of how the efficiency of resource use relates to dominance. Binkley et al. (2002a) predicted that dominant trees would be more efficient in using resources than suppressed trees, whereas Smith and Long (2001) predicted the opposite; both might be true if the predictions refer to periods of increasing dominance and decreasing dominance.

The hypothesis might also provide quantitative identification of stages of stand development (Oliver and Larson, 1996; Franklin et al., 2002). The 150-year-old forest in the Coast Range of Oregon showed a relaxation in dominance, whereas the old-growth forests in Colorado appeared to be farther along a development curve where "reverse" dominance had developed with smaller trees accounting for proportionately more stand growth than larger trees. It would be interesting to see graphs of longer-term changes in dominance (of the type in Fig. 3b) and how these relate to structural classifications of forest development.

A final application would be an explanation of why some plantations fail to show the typical age-related decline in production that commonly occurs near canopy closure (Ryan et al., 1997), such as high productivity plantations of radiata pine (*Pinus radiata*) in New Zealand (Garcia, 1990), intensively fertilized loblolly pine (*Pinus taeda* L.) in the southeastern United States (H.L. Allen, personal communication), and irrigated and fertilized stands of hybrid poplars in the Pacific Northwest (P. Payne, personal communication). In these cases, the hypothesis predicts that sustained production must be matched by low levels of dominance.

The evidence presented here supports the hypothesis of the interaction of dominance and changes in stem growth through stand development, and I hope that future studies will challenge the idea, either refining it or refuting it.

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