



# Patterns of growth dominance in forests of the Rocky Mountains, USA

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## Abstract

We used data from 142 stands in Colorado and Wyoming, USA, to test the expectations of a model of growth dominance and stand development. Growth dominance relates the distribution of growth rates of individual trees within a stand to tree sizes. Stands with large trees that account for a greater share of stand growth than of stand mass exhibit strong growth dominance. Stands with large trees that contribute less to stand growth than to stand mass show reverse growth dominance. The four-phase model predicts that forests move from a period of little dominance (Phase 1), with trees accounting for similar contributions to stand growth and stand mass. Phase 2 is a period of strong growth dominance, where larger trees account for a disproportionately large amount of total stand growth. Growth dominance declines during Phase 3 as growth of the larger trees slows. A final Phase 4 shows reverse growth dominance when the growth of larger trees is less than their proportional contribution to total stand mass. The datasets supported the expectation of reverse growth dominance in old forests of ponderosa pine, Engelmann spruce and subalpine fir, lodgepole pine, and mixed stands of aspen and conifers. Pure aspen stands did not show reverse growth dominance. An age sequence of lodgepole pine failed to show the expected Phase 2 period of strongly developed growth dominance. Future work needs to combine quantitative descriptions of patterns in growth dominance with experimental manipulations of resource supplies and environmental conditions to connect forest dynamics at the scales of individual trees, groups of trees, and stands.

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## 1. Introduction

The development of forests over time leads to changing competitive environments for each tree, with some trees increasing dominance over others (Oliver and Larson, 1996; Franklin et al., 2002; Long et al., 2004). Larger, dominant trees typically capture more light (and perhaps other resources such as soil water and nutrients) than smaller trees, which provides a positive feedback that further accentuates differences in tree

sizes. This expectation would be true only if the efficiency of converting captured light into biomass for large trees was similar (or greater) than the light use efficiency of smaller trees. Patterns of size distributions of trees have been quantified with a variety of spatial (North et al., 2004; Boyden et al., 2005a) and non-spatial approaches (Neumann and Starlinger, 2001; Lexerød and Eid, 2006).

Dominance has commonly been represented as frequency diagrams for stem sizes (such as the inverse-J shaped distribution common in all-age forests) or growth. Cumulative frequency diagrams illustrate the proportion of a stand's trees (or mass, or growth) that fall above or below any given value. For example, Binkley et al. (2003a) found that the largest 20% of trees in old-growth forests of Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) contributed

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half of the total stand biomass, but only one-fourth of the current increment. The cumulative distribution for stand growth can also be plotted as a function of the cumulative distribution for stand biomass, yielding a growth dominance curve (Binkley et al., 2003a). The growth dominance curve would follow the 1:1 line if the proportional contributions of each size class of trees were the same for biomass as for increment. If large trees accounted for a greater proportion of stand growth than for stand mass, then the growth dominance curve would fall below the 1:1 line (Binkley, 2003b). The growth dominance curve would arc above the 1:1 line if relatively low growth rates of large trees accounted for a smaller portion of total stand growth than of stand biomass,

indicating “reverse growth dominance” where the large, structurally dominant trees do not dominate the growth of the stand (illustrated in Fig. 1).

Binkley (2004) proposed that stand development entails a systematic change in the growth dominance curve of stands, and that this pattern may play a role in the commonly observed decline in stand growth in older forests. This model included four phases (Fig. 2):

1. An early phase where open-grown trees experience little competition, and the growth of each tree is proportional to the fraction it comprises of total stand mass (growth dominance curve follows the 1:1 line).

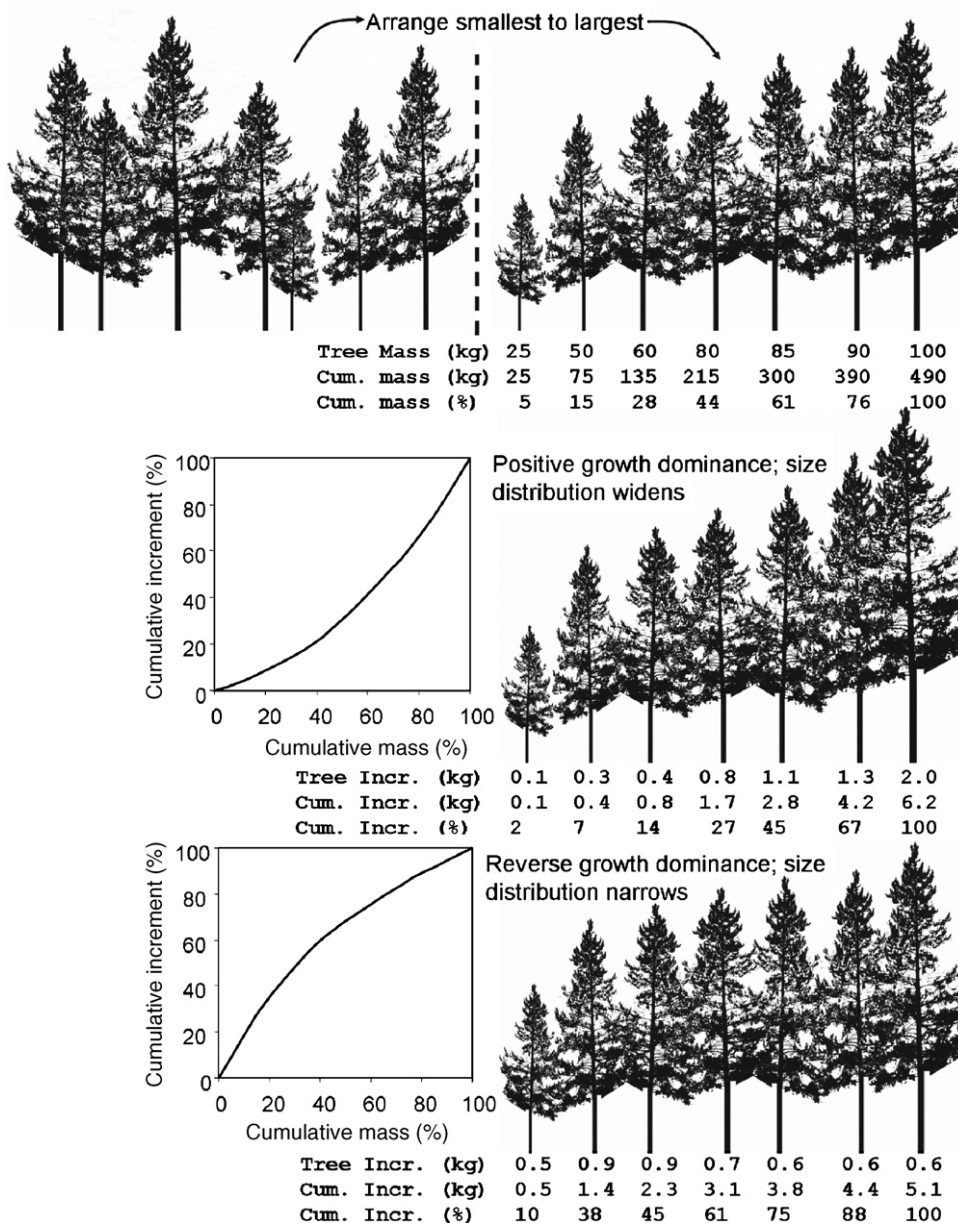


Fig. 1. To evaluate growth dominance, trees in a stand are ordered by size (top) and summed to provide a cumulative distribution. Plotting the cumulative increment (for the same ordering of trees) on the Y-axis yields a positive growth dominance (middle) if dominant trees account for a large proportion of stand growth (middle), and tree sizes become more varied within the stand. If dominant trees provide a lower proportional share of stand growth, reverse growth dominance (lower) results, and tree sizes become more similar over time.

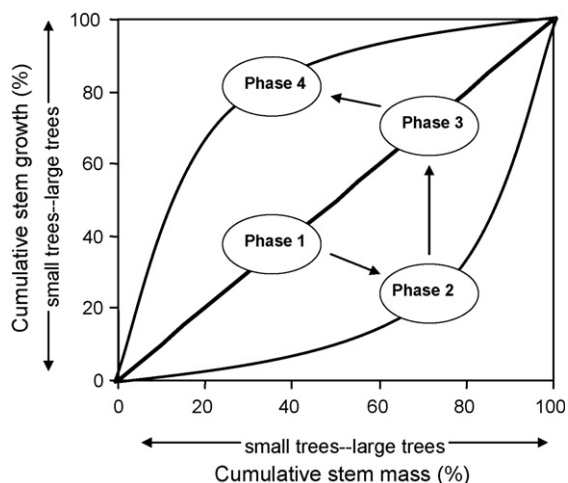


Fig. 2. Conceptual model of four phases of growth dominance in stand development (after Binkley, 2004). Cumulative stem biomass for the stand is plotted on the X-axis, with trees ranked from smallest to largest (as in Fig. 1). Early in development (Phase 1), competition between trees is low and each tree's contribution to the total stand growth is proportional to its mass (1:1 line). In Phase 2, larger trees have gained substantial dominance, increased their use of site resources, and suppressed the growth of smaller trees, all of which account for the steep ascent of the curve at upper end of the X-axis. Growth dominance subsides as one or more factors drives a reduction in the growth rate of dominant trees (Phase 3), and a condition of "reverse growth dominance" may develop (Phase 4) where the contribution of large trees to total stand growth is less than their proportional mass, and the curve flattens at the top.

2. A phase of increasing growth dominance, where the growth of the largest trees is greater than their current contribution to total stand mass. While this condition persists, growth dominance is strong, the distribution of stem sizes becomes broader, and the growth dominance curve falls below 1:1.
3. A declining phase of growth dominance, as growth of the largest trees begins to decrease as a proportion of total stand growth (growth dominance curve returns to the 1:1 line).
4. A phase of "reverse growth dominance" where the growth of the largest trees is less than their proportional contribution to stand mass, and the growth dominance rises above the 1:1 line.

Forests would proceed gradually through these phases, rather than jump discretely from one to another.

In this paper, we evaluate the evidence supporting this four-phase model by examining patterns in 142 stands of aspen (*Populus tremuloides*; 17 stands), ponderosa pine (*Pinus ponderosa*; 1 stand), lodgepole pine (*P. contorta* var. *latifolia*; 96 stands), and Engelmann spruce/subalpine fir (28 stands) in Colorado and Wyoming. Old forests were evaluated for all species, and comparisons between young and old forests were possible with data sets for aspen and lodgepole pine.

## 2. Analytical approach

The growth-dominance approach is illustrated in Fig. 3 for an old-growth ponderosa pine stand (described below). The top two graphs (Fig. 3a and b) are simple frequency distributions,

with size or growth of trees on the X-axis and the percent of trees in each class on the Y-axis. Some interpretations about the relationship between tree size and growth can be made from these two graphs. For example, about 53% of the trees fell into the smallest class based on mass, but only 45% fell into the smallest class based on growth. Fig. 3c provides a finer resolution representation where the growth of each tree is related to the tree's size. The variation in the pattern is substantial, but larger trees grew significantly faster on average than smaller trees. The expected growth of a 500 kg tree would be 0.58 kg/year, compared with 0.96 kg for a 1500 kg tree. The growth of the three-fold-larger tree was less than twice the growth of the smaller tree, indicating reverse growth dominance because the larger tree would account for less of the stand growth than of the stand mass.

Fig. 3d puts tree size and growth into a stand-level representation by ranking trees from the smallest to the largest, and plotting the cumulative percent of the trees on the Y-axis. The largest 20% of the trees (those falling above the 80% point on the X-axis) accounted for about 70% of the total stand mass, but only about half of the total stand growth.

The pattern in these cumulative curves (Fig. 3d) can be analyzed by calculating a Gini coefficient, which is the area below the 1:1 line minus the area below the cumulative curve (sometimes called the Lorenz curve), as a proportion of the total area beneath the 1:1 line (Dixon et al., 1987; Neumann and Starlinger, 2001; Lexerød and Eid, 2006). The Gini coefficient would be 0 when all observations line up along the 1:1 line (and all trees showed the same growth), and a maximum approaching 1.0 if all trees except one had zero growth. The Gini coefficient for the cumulative, ranked stem mass of the ponderosa pine stand was 0.68 (Fig. 3d), compared with 0.53 for the cumulative, ranked stem increment. The higher Gini coefficient for mass than for increment indicates that large trees accounted for a larger proportion of the stand's mass than for the stand's increment, again demonstrating a case of Phase 4 reverse growth dominance.

The difference in Gini coefficients for cumulative stand mass versus stand increment could be used as an index of the degree of dominance in a stand. Alternatively, we developed a related approach by placing the two curves in Fig. 3d into the single relationship of the growth dominance curve (Fig. 3e). The X-axis is the cumulative distribution for stem mass, and the Y-axis is the cumulative increment distribution. We calculated a coefficient of growth dominance, similar to the Gini coefficient. The growth dominance coefficient is the area below the 1:1 line minus the area below the growth dominance curve, as proportion of the area beneath the 1:1 line. Stands with strong growth dominance have a curve that falls below the 1:1 line, and a positive growth dominance coefficient (as with the Gini coefficient). Stands showing reverse growth dominance have curves that rise above the 1:1 line (as in Fig. 3e), so the area below the curve is greater than the area below the 1:1 line, providing a negative growth dominance coefficient of  $-0.25$  for the old growth ponderosa pine stand.

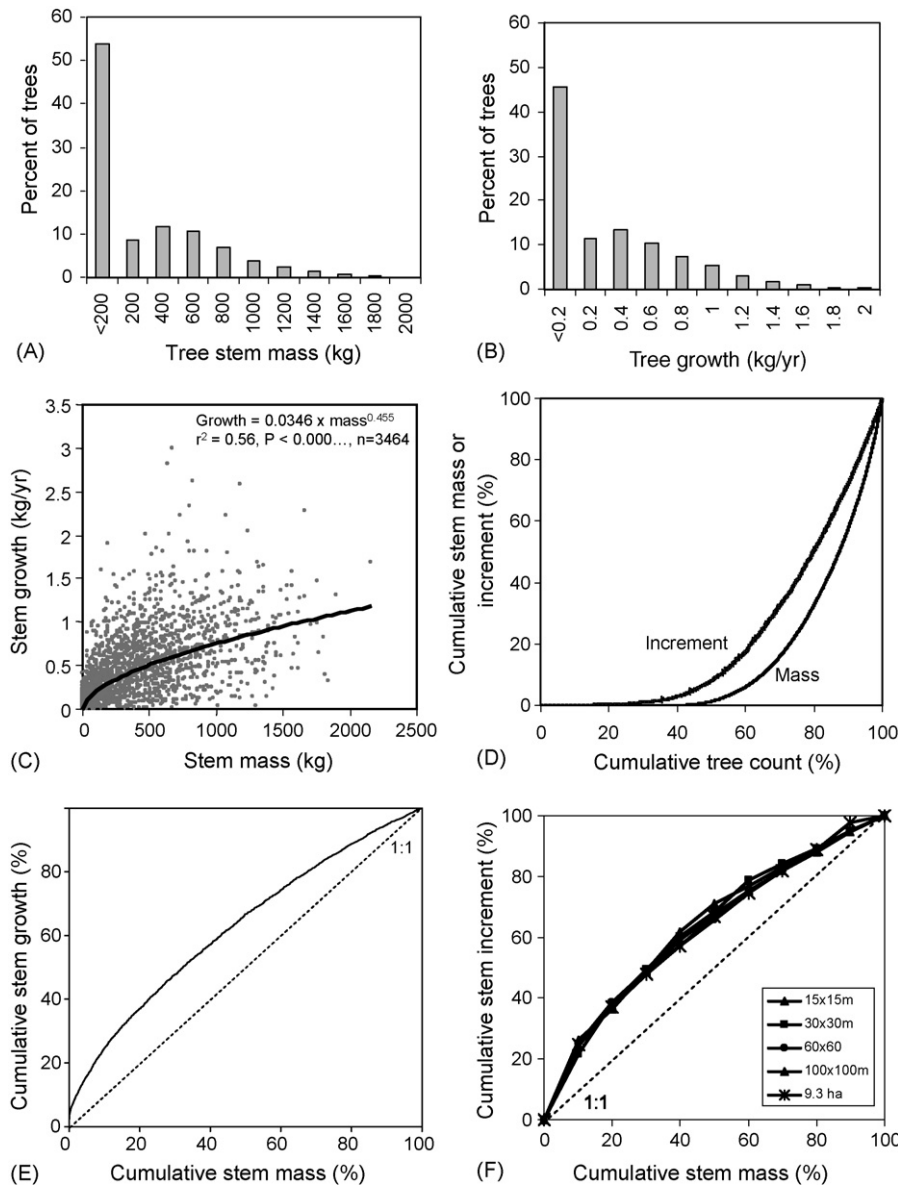


Fig. 3. Illustration of growth dominance representation for a 9.2-ha old-growth stand of ponderosa pine at the Manitou Experimental Forest: frequency distributions for stem mass (a) and increment (b) can be combined with information on stem increment in relation to tree size (c) to produce a cumulative distributions (d) that shows the largest 20% of the trees accounted for about 70% of the total stand stem mass, but contributed just half of stand increment. The growth dominance curve (e) plots the cumulative increment distribution as a function of the cumulative mass distribution. The calculated growth dominance curves for this stand did not vary across a spatial scale of more than two orders of magnitude, based on six subplots of varying sizes from within the stand (f).

### 3. Methods

We used existing data sets from several studies to determine growth dominance patterns in relation to stand age, age structure, and species composition. The unit of observation for our analysis is a stand; some stands were represented by data from a single plot, and other stands were sampled with multiple subplots.

#### 3.1. Old-growth ponderosa pine

A single 9.3 ha stand of ponderosa pine was measured in the Manitou Experimental Forest, 40 km northwest of Colorado Springs, CO (Boyden et al., 2005b). All trees were stem

mapped and measured repeatedly; in this paper we use data from 1991 and 2001 for stem biomass and increment to test the prediction of reverse growth dominance (Phase 4) in old forests. Given that the size of plots varied across the other studies included in this analysis, we examined the effect of plot size on the dominance curve by subsampling the 9.3 ha stand with six 15 m × 15 m subplots (225 m<sup>2</sup>), six 30 m × 30 m subplots (900 m<sup>2</sup>), six 60 m × 60 m subplots (3600 m<sup>2</sup>), and six 100 m × 100 m subplots (1 ha).

#### 3.2. Old-growth spruce/fir

We used data from three studies of old-growth stands of Engelmann spruce and subalpine fir (some stands also

contained some lodgepole pine). Fourteen old-growth stands were sampled in the Loch Vale watershed in Rocky Mountain National Park in Colorado in 1984 (Arthur and Fahey, 1992), and again in 2002. Plot size was 0.04 ha; our analysis omitted any trees present in 1984 that did not survive to 2002. Nine stands were sampled in 2004 and 2005 within the Fool Creek Watershed at the Fraser Experimental Forest in Colorado, with four circular subplots (168 m<sup>2</sup>) per stand. Tree increments were determined on tree cores, and applying biomass regression equations to tree diameters for 1984 and 2002. The same four-subplot design was used to sample five stands in the Glacier Lakes Experimental Forests in the Medicine Bow Mountains of southeastern Wyoming. These stands were also used to test the prediction of reverse growth dominance in old forests.

### 3.3. Aspen

Fornwalt (1999) measured three subplots in each of two adjacent aspen stands in the Medicine Bow Mountains. In the younger, denser stand the trees ranged in age from 15 to 25 years, compared with 60 to 120 years (most over 100 years) in the older stand. The subplots were 15 m × 15 m in the denser young stand, and 20 m × 20 m in the old stand. Tree growth was determined from increment cores taken from 20% of the trees in each plot. Previous diameters correlated very highly with current diameters ( $r^2 = 0.99$  for older stand, and 0.98 for younger stand) so this relationship was used to estimate growth for trees that were not cored. This pair of stands was used to test the expectation of strong dominance in the young stand, and reverse growth dominance in the old stand. A lack of replication at the stand level restricts our statistical analysis to testing for patterns within stands, and differences between stands, but without a direct test of stand age *per se*.

Kaye et al. (2005) sampled 15 stands of aspen (100–140 years old) in Rocky Mountain National Park in 2002, and determined diameter increments using cores of all trees. Seven of the circular 314 m<sup>2</sup> plots were pure aspen, and eight had substantial conifer encroachment (averaging about one-third of stand basal area). Given the old age of these stands, we tested for the expected reverse growth dominance, and whether species composition altered the dominance curve.

### 3.4. Lodgepole pine

We used data from previous and current work in Yellowstone National Park (Litton et al., 2003; Turner et al., 2004; Kashian et al., 2005a, 2005b) to examine patterns in growth dominance in relation to stand age, density, and cohort structure. Trees were sampled either within three 10 m × 50 m plots (all stands >25 years old) or along three 50-meter belt transects of variable width. Forests younger than 40 years were represented by 19 stands, along with 10 stands between 40 and 80 years old, 24 stands between 80 and 150 years old, 21 stands between 150 and 250 years old, and 22 stands over 250 years old. Biomass increments were calculated from increment cores and allometric equations developed by Arcano et al. (unpublished data) for stands older than 25 years, and from basal disks and

allometric equations developed by Turner et al. (2004) for stands younger than 25 years. The lodgepole equations all estimated total aboveground tree biomass, whereas the equations for the other species in this paper estimated only stem wood plus bark. The broad array of lodgepole pine stands allowed us to test the full range of the dominance model in Fig. 2, as well as examine differences in dominance that might result from stand density, and from the presence of multiple age cohorts. No measure of density (number of stems/ha; stand basal area; or stand density index) related significantly with the growth dominance coefficients (either alone or in multiple regressions with stand age), so stand density effects are not shown.

We tested the significance of differences between growth dominance curves by comparing groups (such as stands at different sites, or aspen stands with and without conifers) of growth dominance coefficients with ANOVA (SYSTAT 11), with a critical alpha of 0.05. We also tested whether the average growth dominance coefficient for each group differed from 0 (=1:1 line) by calculating the 95% confidence interval for each group's mean. The distribution of Gini coefficients may not be normal (Giles, 2004); however, the variance in growth dominance coefficients within all the groups of stands passed the Kolmogorov–Smirnov normality test, with one exception. The variance among growth dominance coefficients was not normal for the group of <40-year-old stands of lodgepole pine in Yellowstone National Park, but the growth dominance coefficients were all very close to 0 for this group, so the lack of normality did not compromise the overall analysis. We also tested for the effect of stand age on the growth dominance coefficients using linear regression.

## 4. Results

The patterns for the old-growth stand of ponderosa pine (Fig. 3) were described above in the presentation of the analytical approach. This imbalance between mass and increment resulted in a hump in the growth dominance curve (Fig. 3e), indicating the expected Phase 4 pattern of reverse growth dominance. The growth dominance curve was consistent across plot sizes that spanned more than two orders of magnitude (Fig. 3f); the growth dominance coefficients ranged from –0.22 to –0.25 across the range of plot sizes. Differences in plot sizes among studies should not confound the basic interpretation of growth dominance curves.

Old-growth spruce/fir stands also showed a Phase 4 growth dominance curve, with the larger trees accounting for proportionally less of the increment than of the mass at the stand level (Fig. 4). The growth dominance coefficient for the stands in Loch Vale in Rocky Mountain National Park averaged –0.33 (standard deviation among stands = 0.10), which did not differ significantly from the average coefficient (–0.39) for 18 other stands across the Park (calculated for the stands reported in Binkley et al., 2003a). The old-growth forests at Glacier Lakes in Wyoming showed an average growth dominance coefficient of –0.21 (S.D. 0.12), compared with –0.24 (S.D. 0.08) for the old-growth forests at Fraser, CO.

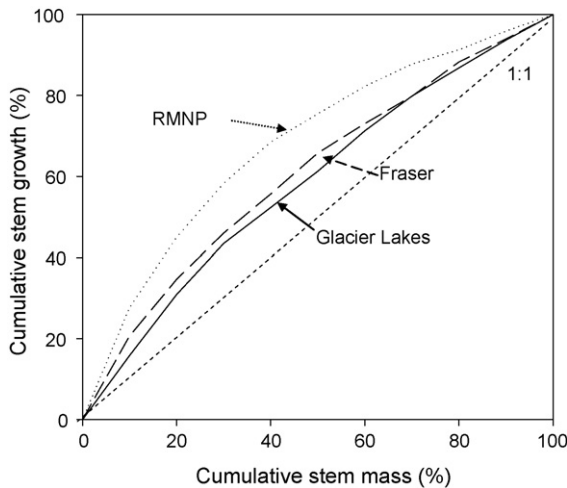


Fig. 4. The growth dominance coefficients for old-growth stands of spruce-fir (some including lodgepole pine) differed from 0 at all three locations, and the Rocky Mountain National Park stands showed significantly stronger reverse growth dominance than the Glacier Lakes stands ( $P = 0.02$ ).

The growth dominance coefficient for the younger aspen stand in the Medicine Bow Mountains of Wyoming (0.01) did not differ from 0; the proportional contribution of trees of all sizes was the same for increment as for mass (Fig. 5). The growth dominance coefficient for the adjacent older stand (−0.03) did not differ significantly from that of the younger stand, but it was significantly lower than 0. This unreplicated pair of stands provided moderate support for expectations of reverse growth dominance in old stands, but there was no sign of a strong-dominance Phase 2.

The growth dominance coefficients for the old, pure-aspen stands in Rocky Mountain National Park (−0.01) did not differ from 0, and showed relatively high variability (S.D. 0.23; Fig. 5). The average growth dominance coefficient for the old aspen stands with conifer encroachment (−0.11, S.D. 0.08) did not differ from that of the pure-aspen stands, but did fall below 0. The mixed aspen/conifer stands matched expectations of Phase 4 reverse growth dominance, but either the pure aspen stands were not old enough to have shifted to reverse growth

dominance, or the expectation that aspen stands should progress to Phase 4 was wrong.

The older lodgepole pine stands in Yellowstone National Park showed the expected trend of reverse growth dominance, but surprisingly no age group showed evidence of a Phase 2 period of strong growth dominance (Fig. 6). The growth dominance coefficients declined linearly with increasing stand age ( $r^2 = 0.28$ ,  $P < 0.0001$ ), dropping from 0 for stands less than 40 years old to −0.23 for stands over 250 years. Reverse growth dominance was stronger in stands with multiple cohorts than in single-cohort stands.

### 5. Discussion

The expected Phase 4 reverse growth dominance was strongly apparent in old (>150 year) forests of ponderosa pine, spruce/fir and lodgepole pine. The larger trees in these stands comprised a larger percentage of stand mass than of stand growth, and this reverse growth dominance would lead to a decrease in the relative distribution of tree sizes over time. For example, a tree at the 50th percentile for stem mass in a stand might have 50% of the mass of a tree at the 80th percentile at the beginning of Phase 4. This two-fold difference in tree sizes would narrow, even if the absolute growth rate of the larger tree remained higher than that of the smaller tree.

Reverse growth dominance could result from accelerating growth of the non-dominant trees, from declining growth of the dominant trees, or a combination of both. We expect that declining growth of the dominant trees is the major factor, but long-term data would be needed on individual trees within stands for a complete story. The factors responsible for slower growth in larger trees remain unclear, despite substantial research over the past decade on the possible influence of increasing woody respiration, belowground carbohydrate allocation, nutrient limitation, hydraulic limitation, stand structure, and canopy abrasion from wind (cf. Ryan et al., 1997, 2004, in press; Binkley et al., 2002; Rudnicki et al., 2003). The present study would be consistent with the pattern of reduced growth in larger trees, but does not provide insights on

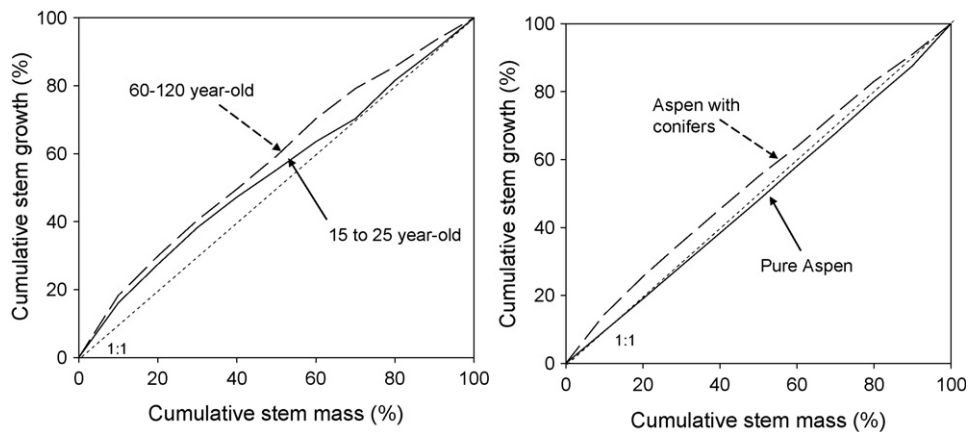


Fig. 5. The growth dominance coefficients for the aspen stands in the Medicine Bow Mountains did not differ from each other, but the older stand differed from 0 (left). The growth dominance coefficients in old aspen stands in Rocky Mountain National Park did not differ between pure aspen and aspen/conifer classes, though the aspen/conifer stands differed from 0 (right).

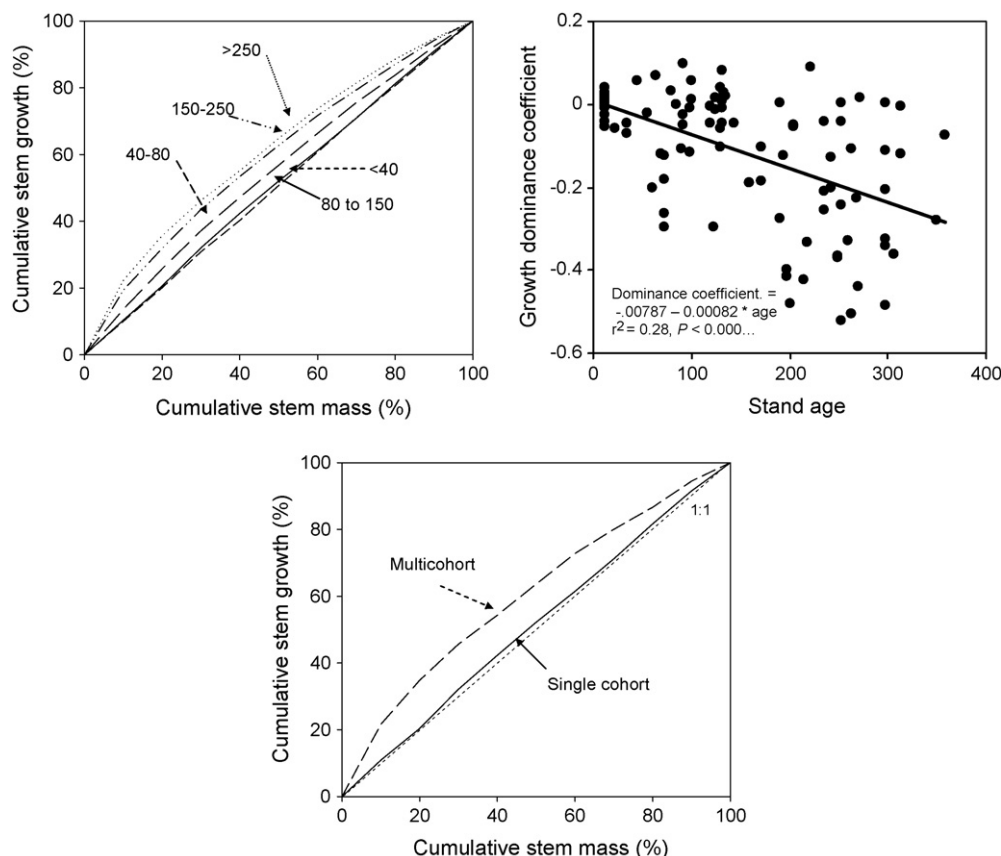


Fig. 6. No growth dominance was evident in lodgepole stands <40 years and between 80 and 150 years in Yellowstone National Park (left), moderate reverse growth dominance was apparent in 40–80-year-old stands, and strong reverse growth dominance in stands older than 150 years. Growth dominance coefficients decreased with increasing age (right). Reverse growth dominance was stronger ( $P = 0.02$ ) in stands with multiple cohorts (bottom).

processes. The stronger reverse growth dominance (more negative coefficient) in the Rocky Mountain National Park stands than in Fraser and Glacier Lakes stands could also be examined in detail to see if differences in factors such as species composition (and dominance), and environmental factors (such as wind exposure) could account for the difference.

Reverse growth dominance was not evident in the replicated old stands of aspen in Rocky Mountain National Park, except for the stands with conifer encroachment. The one old stand of aspen in the Medicine Bow Mountains showed slight reverse growth dominance. Individual aspen trees may live to be over 200 years, but stands typically are expected not to last longer than 110–120 years in Colorado and Wyoming (Perala, 1990), so our stands (100–140 years old) would be within the common upper age group for aspen stands found across most Rocky Mountain landscapes. Stands older than 140 years might develop reverse growth dominance (we have no data), but most stands would not last long enough to spend much time in Phase 4 of Fig. 2.

What factors might account for the sustained “evenness” in the relationship between tree size and growth in aspen? Most aspen stands in this region originate as sprouts from roots of the previous generation of trees. Root connections among ramets within a clone may or may not remain important for more than a century (Lieffers et al., 2001). Substantial interactions among neighboring trees could influence dom-

inance within a stand; too much differentiation among stems within an interconnected clone could lower the total growth of the clone. Conclusive answers to this question would likely require a combination of long-term growth records for individual (tagged) trees, and experimental manipulations of resource supplies.

More surprising than the lack of reverse growth dominance in the old aspen stands was the complete absence of strong, positive growth dominance at any age in the lodgepole pine stands. All of the growth dominance curves for more than 96 stands in Yellowstone National Park were on or above the 1:1 line, indicating no Phase 2 period. The young aspen stand also failed to show strong growth dominance, but with only one stand of this age class, we do not know if would be a general pattern. The lack of a clear Phase 2 period means, for example, that the larger trees comprising 20% of stem mass never contributed more than about 20% of the stand increment. Early relative differences in tree sizes (which might arise from differences in age, microsite fertility or competition with other plants) simply appeared to be sustained and not amplified through stand development.

This lack of strong growth dominance for lodgepole pine stands contrasts sharply with the dominance pattern in three earlier studies. Mixed stands with Douglas-fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), and red alder (*Alnus rubra*) in coastal Oregon, showed increasing

growth dominance coefficients from near 0 at age 25, to a maximum of 0.26 at age 75, declining again to 0 by 140 years (Binkley, 2004). Martin and Jokela (2004) found that dominance increased with stand age in the first 18 years of development of slash pine (*P. elliottii*) stands in Florida, and that fertilization accentuated dominance. The trees accounting for the top 20% of stand mass contributed 25–30% of stand growth between age 13 and 18 years in the fertilized treatment; the trees comprising the smallest 20% of stem mass accounted for just 12–15% of stand growth. Martin and Jokela (2004) found that growth dominance was less pronounced in loblolly pine (*P. taeda*) stands, unless fertilizer was added. The final study included a monoculture plantation of *Eucalyptus saligna* in Hawaii, where growth dominance coefficients rose from 0 at age 2 to a peak of 0.48 at age 11, and declined to 0.40 at age 20 (Binkley et al., 2003b). Monocultures of *Falcataria moluccana* in the same study showed a continual increase in growth dominance coefficients throughout the first 20 years of stand development, reaching 0.46. The growth dominance coefficients in mixed stands of *Eucalyptus* and *Falcataria* also increased through 20 years, reaching 0.32. The productivities of all of these previous studies were much greater than in the lodgepole pine stands, so the difference in development of growth dominance could result from either species-related effects or environment/productivity effects.

The high wind environment of lodgepole pine stands may play a role in limiting the dominance of larger trees. Lodgepole pine is noted for its limited taper (Lotan and Critchfield, 1990), which may relate to growth responses to high stand densities. The taper of stems relates to the wind stresses encountered by canopies (and the heights of the canopies above the ground; Dean and Long, 1986; Dean et al., 2002), and stand structure strongly influences crown collisions and damage (Long and Smith, 1992; Rudnicki et al., 2003). Trees that gain dominance over neighbors may have the opportunity for deploying larger canopies to intercept more light, leading to increased growth of dominant trees and a positive feedback that further differentiates tree sizes. We speculate that the advantage of lodgepole pine trees gaining dominance over neighbors may be offset by exposure to more severe wind stress that reduces the opportunity for large increases in tree leaf area and light interception. A corollary would be that wind stresses play a notably smaller role in restricting dominance in situations where Phase 2 growth dominance develops.

An alternative explanation for limited dominance in lodgepole pine stands would involve sharing of photosynthate among trees (as with aspen ramets). The ability of a dominant tree to outpace neighbors might be impeded if neighboring trees had access to a portion of the carbohydrates of dominant trees. Such a connection is possible through a grafted root system (Fraser et al., 2005), or through a common mycorrhizal network among trees (Newman, 1988; Taylor, 2006). A substantial net flow of photosynthate between trees via root grafts or a common mycorrhizal network would be required to moderate the development of growth dominance among trees, and we expect a large net flow is unlikely (Robinson and Fitter, 1999; Kytöviita et al., 2003).

More analyses of dominance patterns in relation to stand age are needed to determine whether an absence of strong growth dominance (Phase 2) is rare, and to verify that a reverse growth dominance pattern (Phase 4) is common in old forests. This pattern-focused approach to examining the distribution of growth among trees within stands needs to be combined with process-focused studies and experiments to provide more insight on stand development (Binkley et al., 2002). For example, consider two trees in a 5-year-old plantation of *Eucalyptus saligna* in Hawaii. A 19-cm diameter tree (50 percentile in size) had a mass of 125 kg, and a 24-cm diameter tree (85 percentile in size) had a mass of 190 kg, or 1.5 times the mass of the smaller tree. The smaller tree had 50 m<sup>2</sup> of leaf area, intercepting 55 MJ of photosynthetically active radiation (PAR) per day (calculated from data from Binkley et al., 2002). The larger tree had 65 m<sup>2</sup> leaf area and intercepted 90 MJ of PAR per day. The larger tree not only intercepted 60% more light, but it also grew 47% more wood per unit of light intercepted, supporting a 2.5-fold difference in current stem growth. The current difference in stem sizes was 1.5-fold, so the combined effect of greater light interception and higher efficiency of light use led to an increasing differentiation of tree sizes in this Phase 2 (strong growth dominance) stand.

We speculate that the lack of strongly developed growth dominance in lodgepole pine stands should relate to smaller differences among trees in light interception and use efficiency than in the *Eucalyptus* example. The distribution of tree sizes in lodgepole pine stands might be similar to the *Eucalyptus* example; a 1.5-fold difference between the size of a median tree and an 85th percentile tree might be common. However, we expect that the difference in light interception and efficiency of light use would be much smaller for lodgepole pine trees than for *Eucalyptus* trees. This line of reasoning could also be tested in old forests showing reverse growth dominance, with the expectation that larger trees would either not have much more leaf area than median-sized trees, or that the efficiency of using light (and other resources) was lower for larger trees.

A process-focused approach would also be useful in evaluating the causes of growth dominance patterns in mixed-species stands. The net effect of species composition on growth dominance should relate to the proportion of stand light interception (or gain of other limiting resources) attained by each species, coupled with the efficiency of using light (or other resources). The aspen stands in this paper with encroaching conifers showed reverse growth dominance, in contrast to near 0 growth dominance for pure aspen stands. We speculate that the understory conifers substantially increased the stand's light interception, or increased the average efficiency of light use for the stand. Process-focused studies could also examine environmental factors other than resource supply, such as guying trees to reduce swaying in the wind (V.J. Lieffers, M. Rudnicki, pers. commun.). These speculations are all testable, and the combination of analyzing patterns of stand growth dominance and processes of forest productivity may lead to useful insights about scaling forest dynamics from the level of trees to stands, across decades of stand development.



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