Effects of Fertilization On The Growth Dominance of Inland Northwest Forests of The United States

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Abstract

Large trees have disproportionately large competitive advantage in access to light, which has been proposed to increase growth dominance of large trees (e.g., accounting for a larger proportion of growth than volume of a stand). Tree growth may also be limited by the availability of other resources besides light. Nutrient deficiency, especially of nitrogen, is considered common among temperate forests, including mixed-conifer forests of the Inland Northwest of the United States. Data from a long-term forest nutrition study across four Inland Northwest states were analyzed to evaluate nitrogen × potassium fertilization's effects on growth dominance over an eight-year period following treatment in a region of complex forest vegetation types and site conditions. Our results show that growth dominance varied substantially across similar plots in each fertilization treatment, and its mean values generally were at minuscule magnitudes, negative, and not significantly different from zero. We propose that this lack of a clear pattern in growth dominance was the result of the mixed-species composition where shade-tolerant species remained in lower crown positions, yet their relative growth kept pace with large trees. Limited moisture availability at dry sites may have hampered the development of growth dominance. Growth dominance also was lowered by mortality observed among relatively large trees. The largely negative growth dominance across fertilization treatments indicates that small trees maintained higher relative growth rates than large trees, even if absolute growth and size was concentrated in large trees. In the case fertilization does improve stand growth, a significant part of this improved growth will be lost in density-dependent mortality over time if not captured through biomass removals.

1. Introduction

Forest growth usually peaks and declines around the time of canopy closure (Ryan et al. 1997). This pattern is related to changes in forest structure driven by resource supply, demand, competition, and use efficiency (Perry 1985, Binkley 2004). Light supply generally is consistent and limited over the course of forest development. Competition for light among trees is considered size-asymmetric such that large trees have access to a disproportionately larger amount of light than small trees (Weiner 1990). This is proposed to result in increasing growth dominance of large trees (e.g., accounting for a larger proportion of growth than volume of a stand) and declining resource use efficiency of small trees (Binkley 2004).

Light often is not the only resource limiting forest growth. Tree growth processes are halted when tissue water-potential decreases below thresholds under moisture stress (Cole et al. 1990). Stomata are closed to prevent moisture loss, which prevents carbon uptake and photosynthesis, when moisture stress persists (McDowell et al. 2008). Growing season drought, as is common in the Inland Northwest of the United States (Jain and Graham 2015), further worsens moisture stress due to high vapor pressure deficits and limits tree growth as high incident radiation is not utilized (Runyon et al. 1994). The ability of trees to compete for moisture is thought to be proportional to their sizes, which gives no competitive advantage to large trees (Lieffers and Titus 1989, Weiner et al. 1997). The proposed increases in growth dominance related to large trees’ disproportionate access to light will be compromised if they have no commensurate access to moisture.

Growth of temperate forests has long been viewed to be limited by nutrient availability (Tamm 1995). Nitrogen (N) deficiency is considered common among many forest types, including mixed-conifer forests of the Inland Northwest (Coleman et al. 2014). Previous studies, e.g., Shafii et al. (1989) and Moore et al. (1991), have reported positive responses of foliar N concentration and stand growth to N fertilization in this region. However, effects of fertilization on growth dominance likely are more complex as nutrient availability and demand both vary greatly through stand development and across different sized trees. Nutrient uptake from fertilization of young forests is low since tree size is small, and the rapid decomposition of organic materials accumulated on the forest floor and in the upper soil horizons provides nutrients sufficient to meet tree demand (Vitousek and Matson 1985). Available nutrients are gradually captured by trees and decline over time, but demands increase as trees grow larger (Fox et al. 2007). The relationships between forest structure, growth, and growth dominance likely are complicated by changes in nutrient availability (Ryan et al. 1997).

Effects of resource availability, forest composition, and structure on forest growth and hence growth dominance are intertwined. Moisture is more difficult to manipulate than nutrients, yet the efficacy of fertilization interacts with moisture availability (Gessel et al. 1990). For example, Rothstein (2018) proposed that trees had constrained responses to fertilization when moisture was also limited during the growing season, and Maggard et al. (2017) found that fertilization can compensate for decreased moisture availability by increasing water use efficiency of trees. Inland Northwest forests present a complex array of forest vegetation types, which are concomitant with the highly variable moisture regimes (Cooper et al. 1991). Light interception and use efficiency likely increase in mixed stands owning to more shade-tolerant understory trees (Binkley et al. 2006). Tolerance to drought differs across species in addition to tolerance to shade (Niinemets and Valladares 2006). Trees’ adaptive abilities to moisture and light availability may result in differentiated growth and growth dominance. For example, Douglas-fir (Pseudotsuga menziesii var. glauca [Mirb.] Franco) is a major component across vegetation types common in this region, and its competitiveness for growth dominance likely varies across vegetation types owning to varying moisture availability, its crown position, and the relative competitiveness of the other trees.

Fertilization potentially affects not only forest growth but also mortality. Fertilization increases nutrient availability and potentially reduces mortality by alleviating the competition for nutrients (Newton and Amponsah 2006). Fertilization may also intensify size-asymmetric competition...
where large trees capture a greater proportion of light and prevent light from reaching small trees (Schwinning and Weiner 1998). In addition, fertilization may cause nutrient imbalances in the soil that influence tree physiology and production of defensive compounds (Mandzak and Moore 1994), which may increase density-independent mortality from insect attacks and diseases (Filip et al. 2002). Mortality directly affects growth dominance. For example, in a stand where large trees have growth dominance (e.g., in terms of volume), the death of a large tree will reduce this growth dominance as a larger proportion of potential growth than volume will be eliminated (i.e., the ratio between growth and volume of large trees will be reduced), and vice versa.

The Intermountain Forestry Cooperative at the University of Idaho carried out a long-term forest health and nutrition study across four states of the Inland Northwest of the United States (Shaw et al. 2014). The study provides repeated tree measurements covering major forest types in the region and offers an opportunity to evaluate N × potassium (K) fertilization's effects on forest growth and growth dominance. This evaluation helps understand how availabilities of various resources affect trajectories of forest development in a region of complex forest vegetation types and site conditions. The objectives of this study were to 1) examine changes in growth dominance following one-time N × K fertilization treatments over an eight-year period across various naturally regenerated Inland Northwest forests and 2) assess how changes in growth dominance were related to growth, mortality, species composition classified by shade tolerance, and vegetation series as a surrogate of moisture availability and hence site quality.

2. Material And Methods

2.1. Study sites

Data used in this study were collected at 27 sites across the Inland Northwest of the United States as a part of the Intermountain Forestry Cooperative's forest health and nutrition study established between 1994 and 1996 (Figure 1; Shaw et al. 2014). These sites of naturally regenerated forests cover four soil parent materials of granitic, basaltic, metamorphic, and mixed (alluvium and glacial sedimentary deposits), as well as three forest vegetation series. Vegetation series range from dry/low productivity Douglas-fir series to moderate grand fir (Abies grandis [Douglas] Lindley) series and to moist/high productivity western redcedar (Thuja plicata Donn)/western hemlock (Tsuga heterophylla [Raf.] Sarg.) series (Cooper et al. 1991). Parent materials and vegetation series are representative of the region (Shaw et al. 2014). The most abundant species, by stem count, were Douglas-fir (48%), ponderosa pine (Pinus ponderosa Douglas; 39%), and lodgepole pine (Pinus contorta var. latifolia Engelm.; 9%) at Douglas-fir series sites; Douglas-fir (42%), ponderosa pine (29%), and lodgepole pine (11%) at grand fir series sites; and grand fir (38%), Douglas-fir (35%), and western redcedar (17%) at western redcedar/western hemlock series sites. Site elevation ranged from 671 to 1,737 m.

At each site, plots receiving different fertilization treatments were established within a single stand to ensure similarities in stand structure, species composition, and stand history. Treatment plots were 0.2-ha squares with a 6.1 m buffer on all four sides. A 0.04-ha growth plot, from where tree measurements were taken, was nested within the center of each treatment plot. A total of 164 plots with initial stand ages between 15 and 74 years were available in this study (some sites had multiple plots of the same treatment), and stand attributes from these plots are summarized by fertilization treatment and vegetation series in Table 1.
Table 1
Means of pre-treatment stand attributes by fertilization treatment and vegetation series.

| treatment | attribute         | western redcedar | grand fir | Douglas-fir |
|-----------|-------------------|------------------|-----------|-------------|
|           | No. of plots      | 12               | 8         | 7           |
|           | age (year)        | 36               | 36        | 55          |
| control   | trees ha⁻¹         | 1,246            | 571       | 568         |
|           | volume (m³ ha⁻¹)   | 177              | 99        | 139         |
|           | elevation (m)      | 998              | 997       | 1,137       |
|           | No. of plots      | 14               | 8         | 8           |
|           | age (year)        | 38               | 36        | 56          |
| N         | trees ha⁻¹         | 1,158            | 534       | 568         |
|           | volume (m³ ha⁻¹)   | 200              | 103       | 145         |
|           | elevation (m)      | 991              | 997       | 1,124       |
|           | No. of plots      | 11               | 8         | 7           |
|           | age (year)        | 36               | 36        | 55          |
| K         | trees ha⁻¹         | 1,094            | 541       | 547         |
|           | volume (m³ ha⁻¹)   | 144              | 100       | 140         |
|           | elevation (m)      | 995              | 997       | 1,137       |
|           | No. of plots      | 33               | 31        | 17          |
|           | age (year)        | 35               | 33        | 60          |
| N + K     | trees ha⁻¹         | 1,022            | 638       | 427         |
|           | volume (m³ ha⁻¹)   | 203              | 92        | 150         |
|           | elevation (m)      | 1,028            | 1,034     | 1,239       |

2.2. Fertilization treatments and tree measurements

Four one-time fertilization treatments of control (no fertilization), N only at 336 kg ha⁻¹, K only at 191 kg ha⁻¹, and N + K (same rates as in N and K only plots) were applied to the plots. Fertilization occurred in the fall of the year that the sites were established. N was added as urea (CO(NH₂)₂), while K was added as potassium chloride (KCl). Fertilizer was applied evenly across the plots using a hand spreader.

Tree measurements were collected in the fall starting with pre-treatment measurements. Trees were identified to species. DBH (diameter at 1.37 m above the ground) was measured on every tree in the growth plots every two years, and total height was measured at four-year intervals. Mortality of individual trees was recorded every two years. A total of eight years of data were available in this study.

2.3. Data preparation and analysis

Height was not measured in the second- and sixth-year measurements, so it was predicted for those years using the height-diameter equations from the Inland Empire Variant of the Forest Vegetation Simulator (FVS-IE; Keyser 2008). Height and DBH were used to predict tree volumes using Flewelling’s two-point profile models contained in the National Volume Estimator Library maintained by the Forest Products Measurement Group in the Forest Service Forest Management Service Center (Wykoff et al. 1982). Individual-tree volumes in each plot were summed and converted to per-hectare values (m³ ha⁻¹). Trees were characterized as tolerant, mid-tolerant, and intolerant to shade. The most common tolerant species were grand fir and western redcedar (shade tolerance index of 4.0 and 4.7, respectively (Niinemets and Valladares 2006)), the most common mid-tolerant species were Douglas-fir and western white pine (Pinus monticola Douglas; shade tolerance index of 2.8 and 3.0, respectively), and the most common intolerant species were ponderosa pine and lodgepole pine (shade tolerance index of 1.6 and 1.5, respectively).
For each plot and measurement period, coefficient of variation (CV) of DBH was computed as \( \text{standard deviation} / \text{mean} \times 100\% \). CV is a metric used to summarize size inequality such that a larger value indicates higher size inequality, e.g., wider DBH distribution. CV is unitless and can be viewed as standard deviation normalized by the mean, which makes it comparable across samples of trees of varying sizes and/or trees measured using different units (e.g., cm vs. inch).

Growth dominance (G), a relative measure of how stand growth is distributed among trees of different sizes (Binkley 2004), was computed using the procedure presented by West (2014):

\[
G = 1 - \sum_{i=1}^{n-1} \left( \frac{S_i}{S_j} - 1 \right) \left( \frac{d_i}{d_j} + 1 \right)
\]

Where \( S_i = \sum_{j=1}^{n} D_j / \sum_{j=1}^{n} S_j \) and \( S_j \) is the volume of the \( j \)th tree such that \( S_j \leq S_j \), and \( d_j = \sum_{j=1}^{n} D_j / \sum_{j=1}^{n} d_j \) and \( D_j \) is the volume growth of the \( j \)th tree in a plot of \( n \) trees. \( G \) is unitless and falls within a range from -1 to 1. \( G = 0 \) when every tree grows at the same proportion to their initial volumes, \( G > 0 \) when large trees account for a larger proportion of stand growth than volume, and \( G < 0 \) when small trees account for a larger proportion of stand growth than volume. \( G \) was computed for each plot and measurement period. Obviously, other measures of tree sizes and growth can also be used to compute growth dominance despite the use of volume in this study.

3. Results

3.1. Changes in growth dominance

Growth dominance varied considerably across plots in the same vegetation series that received the same fertilization treatment (Figure 2). Both decreases and increases in growth dominance were observed in each occasion shown in Figure 2 and appeared not to be related to stand age. Mean growth dominance was at small magnitudes ranging from -0.06 to 0.01 and mostly negative over time and across fertilization treatments (Figure 3). Most of these statistics including all of the positive ones were not significantly different from zero at the 0.05 significance level (Figure 3). Multivariate analysis of variance showed that mean growth dominance generally was not significantly separated by vegetation series, fertilization treatments, or their interactions (Supplemental material Figure S1). Nevertheless, fertilized plots had consistently higher mean growth dominance than control plots, and growth dominance generally increased over time in all treatments in western redcedar/western hemlock series, where forests were relatively young and dense (Table 1, Figure 3).

3.2. Effects of growth and mortality on growth dominance

Observed initial and eighth-year mean DBH showed that DBH increments were higher in both absolute and relative terms in western redcedar/western hemlock series than in the other vegetation series (Table 2). Both the largest and smallest 25% of trees by volume generally accounted for higher percentages of growth than intermediate trees across fertilization treatments and vegetation series (Table 3), which had a neutralizing effect on growth dominance (Figure 3). Dead trees were smaller in western redcedar/western hemlock series (mean DBH of 5.7 cm, 41% of that of living trees) compared to grand fir (mean DBH of 11.0 cm, 73% of that of living trees) and Douglas-fir series (mean DBH of 17.6 cm, 81% of that of living trees; Figure 4). Mortality of smaller trees resulted in increases in the initially negative growth dominance and simultaneously larger decreases in CV and hence size inequality in western redcedar/western hemlock series compared to the other vegetation series (Table 2, Figure 3). No clear effect of growth and mortality on growth dominance across fertilization treatments was found.

| treatment | western redcedar/western hemlock | grand fir | Douglas-fir |
|-----------|---------------------------------|-----------|-------------|
|           | initial mean DBH (cm) | initial CV of DBH | 8th year mean DBH (cm) | initial CV of DBH | 8th year mean DBH (cm) | initial CV of DBH |
| control   | 10.8                      | 88        | 14.4        | 77         | 16.1                   | 57       | 19.0       | 55         | 18.6                   | 58       | 20.6       | 56         |
| N         | 11.9                      | 83        | 15.2        | 80         | 15.8                   | 65       | 18.9       | 63         | 19.2                   | 54       | 22.3       | 49         |
| K         | 11.1                      | 83        | 14.6        | 73         | 15.9                   | 58       | 19.6       | 54         | 19.3                   | 49       | 20.9       | 49         |
| N + K     | 12.7                      | 78        | 17.2        | 69         | 13.4                   | 75       | 14.3       | 85         | 22.7                   | 43       | 25.8       | 42         |

Table 2: Observed pre-treatment and eight years after treatment mean DBH (diameter at 1.37 m above the ground) and its coefficient of variation (CV) by fertilization treatment and vegetation series.
Table 3
Observed mean percentages of total stand volume growth in each quartile of stand volume (with first and fourth quartiles being the smallest and largest trees, respectively) by fertilization treatment and vegetation series.

| treatment | western redcedar/western hemlock | grand fir | Douglas-fir |
|-----------|----------------------------------|-----------|-------------|
|           | mean % of total growth | mean % of total growth | mean % of total growth |
|           | attributed to trees of | attributed to trees of | attributed to trees of |
|           | 1st quartile | 2nd quartile | 3rd quartile | 4th quartile | 1st quartile | 2nd quartile | 3rd quartile | 4th quartile | 1st quartile | 2nd quartile | 3rd quartile | 4th quartile |
| control   | 27 | 25 | 23 | 25 | 25 | 23 | 25 | 27 | 25 | 21 | 25 | 28 |
| N         | 26 | 24 | 25 | 25 | 28 | 24 | 21 | 27 | 23 | 25 | 23 | 28 |
| K         | 25 | 26 | 23 | 26 | 28 | 23 | 22 | 27 | 29 | 24 | 19 | 29 |
| N + K     | 25 | 25 | 24 | 26 | 28 | 24 | 22 | 26 | 25 | 25 | 23 | 27 |

3.3. Species composition and growth dominance

Changes in compositions of trees of varying shade tolerance were highly consistent across fertilization treatments in each vegetation series over the eight-year period (Figure 5). In terms of volume, percentages of shade-tolerant and -intolerant trees decreased with increases of mid-tolerant trees ranging from 2.9–4.7% over the eight-year period in western redcedar/western hemlock series, where shade-tolerant and -intolerant trees were the smallest and largest trees, respectively (Table 4, Figure 5). Their simultaneous declines neutralized growth dominance. Both grand fir and Douglas-fir series shifted towards shade-intolerant species (volumes increased by 6.9-8.7% and 2.8-3.3%, respectively, over eight years; Figure 5). Intolerant species were larger and faster-growing than the others in grand fir series, but the potential positive effect on growth dominance was offset by larger dead trees of tolerant and mid-tolerant species (Table 4, Figure 5). Intolerant species were smaller but grew faster than the others in Douglas-fir series, but the consequent decreasing effect on growth dominance was countered by mortality of smaller trees of the larger mid-tolerant species (Table 4, Figure 5).

Table 4
Observed mean DBH (diameter at 1.37 m above the ground) of living and dead trees by shade tolerance and vegetation series.

| shade tolerance | western redcedar/western hemlock | grand fir | Douglas-fir |
|-----------------|----------------------------------|-----------|-------------|
|                 | initial mean DBH living trees (cm) | 8th year mean DBH living trees (cm) | mean DBH dead trees (cm) | initial mean DBH living trees (cm) | 8th year mean DBH living trees (cm) | mean DBH dead trees (cm) | initial mean DBH living trees (cm) | 8th year mean DBH living trees (cm) | mean DBH dead trees (cm) |
| tolerant        | 10.1 | 13.0 | 4.9 | 8.0 | 8.8 | 11.0 | 23.0 | 24.5 | -- |
| mid-tolerant    | 14.5 | 20.0 | 7.5 | 14.8 | 15.2 | 11.7 | 23.7 | 26.7 | 17.1 |
| intolerant      | 17.0 | 21.0 | 11.4 | 15.8 | 20.2 | 9.6 | 17.5 | 20.0 | 18.9 |

4. Discussion

Growth dominance varied substantially across similar plots in each treatment, and its mean values generally were at minuscule magnitudes and not significantly different from zero. This lack of a clear pattern in growth dominance does not agree with the hypothesis of Binkley (2004), who suggested that positive growth dominance occurs between canopy closure and old growth. The initially 15 to 74 years old stands in this study were expected to exhibit strong positive growth dominance as that reported in the mixed stands in coastal Oregon (Binkley 2004). Growth dominance generally increased, albeit remained largely negative, in relatively moist and dense western redcedar/western hemlock series but not in relatively dry grand fir and Douglas-fir series following fertilization in this study. Pronounced increases in growth dominance following fertilization and vegetation control have been reported in loblolly pine (Pinus taeda L.) stands in Florida (Martin and Jokela 2004). However, Tschieder et al. (2012) inferred that growth dominance should decrease in fertilized and irrigated young loblolly pine stands because the size-related differences in relative growth were diminished by higher resource availability for small trees.
The two types of young stands evaluated in Binkley et al. (2006) that were intended to support the hypothesis of Binkley (2004) also did not show significant positive growth dominance. Binkley et al. (2006) speculated that photosynthates shared through grafted roots of lodgepole pine and among ramets of aspen (Populus tremuloides Michx.) clones moderated potentially significant growth dominance. Natural root grafts occur in many tree species including most of those in this study (Graham and Bormann 1966). If this was the actual driving factor, it could be a cause of the lack of growth dominance observed in this study.

Alternative theories related the lack of growth dominance to wind stresses encountered by large lodgepole pine trees or their low growth efficiency (Binkley et al. 2006, Binkley and Kashian 2015), but mixed species in stands may have also played a role. Aspen stands mixed with understory conifers were found to have growth dominance around zero in pure aspen stands to negative values in mixed stands, where understory conifers kept high relative growth rates likely because of improved light interception and/or use efficiency (Binkley et al. 2006). Similarly in this study, shade-tolerant species generally started in lower crown positions with initial mean height at 8.8 m, while initial mean height for other species was 11.1 m. Shade-tolerant species remained in lower crown positions over the eight-year study period, and their relative growth apparently kept pace with large trees (Table 4, Figure 4). This may be a result of the large pine trees typically having clumped foliage arrangements that allow increased light to reach lower strata trees (Stenberg et al. 1994).

There may be species-specific disparities in developing growth dominance. For example, growth dominance was absent in lodgepole pine stands but accentuated in Eucalyptus saligna stands both across a wide range of stand ages (Binkley et al. 2006, Doi et al. 2010). McGown et al. (2015) found practically no growth dominance over a 35-year period in initially 40-70 years old ponderosa pine stands. Tschiefer et al. (2012) concluded that competition generally is symmetrical in pine stands based on 21 years of observations on initially five years old loblolly pine stands, which resulted in null growth dominance. The abilities of species to develop growth dominance may also interact with site quality. The relatively small mid-tolerant Douglas-fir established growth dominance with improved proportions of stand volumes in moist western redcedar/western hemlock series but did not gain competitive advantages against intolerant pines in dry grand fir and Douglas-fir series (Table 4, Figure 5).

The phase of increasing growth dominance by large trees proposed by Binkley (2004) may apply to situations where light is the most limiting resource in tree growth, and large trees capture an increasingly larger proportion of light than small trees (Weiner 1990). Consequently, growth of large trees is sustained and accounts for an increasingly larger proportion of stand growth at the cost of the suppressed growth of small trees. This disproportionate growth of large trees will result in commensurate increases in transpiration and moisture demand (Maggard et al. 2017), but trees' abilities to compete for moisture are considered proportional to their sizes (Lieffers and Titus 1989, Weiner et al. 1997). In situations of limited moisture availability as may occur in grand fir and Douglas-fir series in this study, large trees would face relatively as much moisture deficiency as small trees, which would hamper the development of disproportionately large crowns and improved light interception. Competition for nutrients also is size-symmetric (Weiner et al. 1997, Nilsson et al. 2002), and nutrient deficiency is common in the Inland Northwest (Coleman et al. 2014). The alleviation of nutrient deficiency by fertilization generally did not improve growth dominance, especially in dry grand fir and Douglas-fir series. This may be an indication of the limiting role of soil moisture on mineralization of soil organic matter, release of nutrients, and nutrient transport in the soil-plant continuum (Cole et al. 1990).

Increased mortality following fertilization in Inland Northwest has been reported (e.g., Shen et al. 2001), although this mortality occurs more often among small trees mainly because improved stand growth following fertilization intensifies self-thinning (Barclay and Brix 1985, Elfving 2010). As a result, tree size distribution narrowed (CV decreased) following fertilization especially in western redcedar/western hemlock series of relatively high initial density (Table 1). Mortality noticeably increased among relatively large trees in dry grand fir and Douglas-fir series likely because of large trees facing similar moisture deficiency in the size-symmetric competition with small trees (Table 4, Figure 4; Weiner et al. 1997). This mortality had a potential effect to extend DBH distribution of remaining trees. Consequently, CV of DBH showed more decreases in western redcedar/western hemlock series than in the other series (Table 2). This observed pattern in CV followed its general trend during stand development (McGown et al. 2016), but Harrington and Devine (2011) found that fertilization broadened tree size distribution in western redcedar dominated stands. Harrington and Devine (2011) considered the cause to be the greatly improved growth of dominant trees and some small redcedar trees having survived the intensified competition but had stagnated growth. Both of these effects were not observed in this study.

Growth dominance does not only result from changes in relative growth of various-sized trees (Binkley et al. 2006). Since it is a statistic computed on survivor trees over a period (e.g., West 2014), mortality during this period directly affects growth dominance. For example, in a stand where large trees have initial growth dominance (i.e., account for a larger proportion of growth than volume), the death of a large tree will remove relatively more growth than volume and hence reduce the growth dominance of large trees. The lack of positive growth dominance in grand fir and Douglas-fir series may partly result from mortality observed among relatively large trees. This pattern occurred across all treatments including the control. The minuscule and not significant growth dominance may also be a result of the distribution of growth. It clearly differed between large and small trees in some previous studies (e.g., Martin and Jokela 2004, Fernández et al. 2011), but both the largest and smallest 25% trees generally accounted for ≥25% of stand growth in this study (Table 3), which had a neutralizing effect on growth dominance. This pattern was consistent across fertilization treatments and vegetation series where site quality and stand age clearly differed.
Improved nutrient availability may not be the sole cause since this pattern also was observed in unfertilized plots (Tschieder et al. 2012). Species-specific potentials in developing growth dominance and limited moisture availability may also be contributing factors.

The metric of growth dominance has been considered a useful tool to quantitatively assess the effectiveness of silvicultural treatments such as thinning (Bradford et al. 2010, Keyser 2012). It was found that thinning eased competition and favored growth of small rather than large trees, although the goal of thinning often is to concentrate growth on large crop trees (Nyland 2016). The general effect of fertilization found in this study is similar to that of thinning. The largely negative growth dominance across fertilization treatments indicates that small trees maintained higher relative growth rates than large trees, even if absolute growth and size was concentrated in large trees. In the case fertilization does improve stand growth, a significant part of this improved growth will be lost in density-dependent mortality over time if not captured through biomass removals.

A caveat is that growth dominance found in this study and some previous studies (e.g., Binkley et al. 2006, Bradford et al. 2010, Tschieder et al. 2012, McGown et al. 2015) is of very small magnitudes. Growth dominance is computed based on volume, biomass, or other dimensions of trees, which generally are not directly measurable and are predicted using various empirical models. The minuscule growth dominance, regardless positive or negative, likely falls within the uncertainties of these models, and may not be able to provide quantitative and even qualitative information to assess the efficacy of silvicultural treatments as proposed by Bradford et al. (2010). In the case of patterns existing in these uncertainties across, e.g., stand structure, composition, and site quality, growth dominance statistics may also be biased according to these patterns, and silvicultural prescriptions based on growth dominance statistics may be misguided. Finally, growth dominance may be evaluated with improved accuracy using data from large sample plots. Otherwise, growth dominance may be overly affected by rare mortality observations. The relatively small plots with an average of ~30 trees likely caused growth dominance to vary in wide ranges across plots in this study.

**Declarations**

**Ethics approval and consent to participate**

Not applicable.

**Consent for publication**

Not applicable.

**Availability of data and materials**

Data are available upon requests sent to cen.chen@maine.edu.

**Competing interests**

No.

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**Authors’ contributions**

Conceptualization: AN; Methodology: AN, CC; Software: CC; Validation: CC; Formal Analysis: CC; Investigation: CC; Resources: AN, MK, TS; Data curation: TS; Writing – original draft: CC; Writing – review & editing: AN, CC, MK, TS; Visualisation: CC; Supervision: AN; Project Administration: AN; Funding acquisition: AN, MK.

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Figures
Figure 1

The study area and its location in the United States, where black dots are study sites.
Figure 2

Observed growth dominance two years and eight years after fertilization treatment (left and right ends of the lines, respectively) at corresponding stand ages by vegetation series and fertilization treatment.

Figure 3

Observed mean of growth dominance and its 95% confidence interval over time by fertilization treatment and vegetation series.
Figure 4

Observed mean DBH (diameter at 1.37 m above the ground) of living and dead trees by shade tolerance, fertilization treatment, and vegetation series.

Figure 5

Observed mean percentages of varying shade tolerance trees by volume pre-treatment and eight years after treatment by fertilization treatment and vegetation series.
Supplementary Files

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- FigureS1.jpeg