

A new method for evaluating forest thinning: growth dominance in managed *Pinus resinosa* stands

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Abstract: Growth dominance is a relatively new, simple, quantitative metric of within-stand individual tree growth patterns, and is defined as positive when larger trees in the stand display proportionally greater growth than smaller trees, and negative when smaller trees display proportionally greater growth than larger trees. We examined long-term silvicultural experiments in red pine (*Pinus resinosa* Ait.) to characterize how stand age, thinning treatments (thinned from above, below, or both), and stocking levels (residual basal area) influence stand-level growth dominance through time. In stands thinned from below or from both above and below, growth dominance was not significantly different from zero at any age or stocking level. Growth dominance in stands thinned from above trended from negative at low stocking levels to positive at high stocking levels and was positive in young stands. Growth dominance in unthinned stands was positive and increased with age. These results suggest that growth dominance provides a useful tool for assessing the efficacy of thinning treatments designed to reduce competition between trees and promote high levels of productivity across a population, particularly among crop trees.

Résumé : La dominance de croissance est une mesure quantitative simple et relativement nouvelle du patron de croissance des arbres individuels dans un peuplement. Elle prend une valeur positive lorsque les plus gros arbres d'un peuplement ont une croissance proportionnellement plus élevée que les plus petits arbres alors qu'elle prend une valeur négative lorsque les plus petits arbres ont une croissance proportionnellement plus élevée que les plus gros arbres. Nous avons étudié des expériences sylvicoles à long terme sur le pin rouge (*Pinus resinosa* Ait.) pour caractériser comment l'âge du peuplement, les traitements d'éclaircie (éclaircies par le bas, par le haut ou par le haut et par le bas) et la densité du peuplement (la surface terrière résiduelle) influencent la dominance de croissance des peuplements en fonction du temps. Dans les peuplements éclaircis par le bas ou par le haut et par le bas, la dominance de croissance n'était pas significativement différente de zéro peu importe l'âge ou la densité du peuplement. La dominance de croissance des peuplements éclaircis par le haut avait tendance à passer de négative à positive lorsque la densité du peuplement passait de faible à forte et était positive dans les jeunes peuplements. La dominance de croissance dans les peuplements non éclaircis était positive et augmentait avec l'âge. Ces résultats indiquent que la dominance de croissance est un outil utile pour évaluer l'efficacité des traitements d'éclaircie visant à réduire la compétition entre les arbres et à obtenir une forte productivité à l'intérieur d'une population, particulièrement dans le cas des arbres d'avenir.

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Introduction

Patterns and processes that occur during forest-stand development reflect the growth of individual trees, which is influenced by resource availability, resource acquisition (as mediated by competitive interactions), and resource-use efficiency. Tree size and age play a crucial role in both resource acquisition and resource-use efficiency. For example, larger trees may have greater access to light and thus higher rates of resource acquisition than smaller trees in the same stand

(Ford 1975; Cannell et al. 1984). However, this advantage may be offset by the countervailing physiological constraints imposed by large size, resulting in lower growth rates. Although the mechanisms driving lower growth rates in larger trees remain unclear (Bond 2000; Peñuelas 2005), observations of size- or age-related growth declines are abundant at both the individual tree (Day et al. 2001; Seymour and Kenefic 2002; Mencuccini et al. 2005) and stand level (Ryan et al. 1997; Smith and Long 2001).

One simple yet quantitative approach to understanding the consequences of resource acquisition and utilization on stand growth is to examine growth dominance (sensu Binkley 2004; Binkley et al. 2006). Growth dominance of an individual tree is determined by the relationship between its growth and biomass, both expressed as a proportion of the whole stand. A tree is considered growth dominant — regardless of its size or crown position — if its growth represents a greater proportion of stand growth than its biomass represents of stand biomass. Thus at the stand level, we may recognize positive growth dominance, in which the larger

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trees account for a greater proportion of stand growth than biomass, or negative growth dominance, in which the smaller trees account for a greater proportion of growth than biomass. Stands in which all trees display growth proportional to their biomass display zero growth dominance (neither positive nor negative).

Based on observations from unmanaged stands, Binkley (2004) and Binkley et al. (2006) developed a hypothesis addressing how growth dominance progresses through stand development. Stands are hypothesized to progress from zero growth dominance at very young ages when competition among seedlings or saplings is minimal, through positive growth dominance as tree canopies compete for light and larger trees obtain more resources, to negative growth dominance when growth of larger trees becomes limited by physiological constraints. However, the hypothesized pattern and magnitude of growth dominance in unmanaged stands may be quite different from managed stands in which resource levels and size structures are deliberately manipulated over time. In managed systems, patterns of resource acquisition and utilization are strongly influenced by silvicultural treatments, such as thinnings, intended to increase levels of resource availability for residual trees through density reductions, as well as to promote higher levels of resource acquisition through increases in leaf area on residual trees (Long et al. 2004). Because thinning treatments typically remove weaker competitors from specified crown classes (Smith et al. 1997), the size and resource-use inequalities observed in unmanaged, even-aged stands may be less pronounced in managed systems. In addition, thinning treatments are generally aimed at promoting individual tree growth versus stand growth (Long et al. 2004), with an emphasis on favoring larger diameter individuals as crop trees during treatment applications. As such, growth dominance may serve as a useful metric for determining the effectiveness of different thinning methods at maintaining high levels of growth among larger trees within a stand over the course of stand development (i.e., positive growth dominance).

Because of the potential differences in growth dominance between self-thinning populations versus those experiencing thinning treatments, an evaluation of the usefulness of this concept in understanding patterns of growth and production in managed stands is warranted. To assess the applicability of growth dominance in managed stands, we applied the growth dominance approach to a long-term thinning experiment in red pine (*Pinus resinosa* Ait.). We characterized how various density reductions and thinning methods influence growth dominance and quantified the influence of growth dominance on long-term stand growth. Specifically, we examined how patterns of growth dominance are influenced by silvicultural treatments (including stocking levels, thinning method, and controls) and stand age. By comparing patterns of growth dominance between different thinning methods and stocking levels, we hoped to gain insight into the stand structures conferring the greatest levels of production on larger trees within the population (cf. O'Hara 1988). In addition, through examining growth-dominance patterns over a 46-year period, we sought to address the interactive effects of age-related trends in stand production (Ryan et al. 1997; Smith and Long 2001) and thinning treatments aimed at promoting individual tree growth.

Materials and methods

Study site and measurements

We examined long-term growth records from the Birch Lake Red Pine Plantation. Located in northeast Minnesota (47°42'N, 91°56'W), the Birch Lake Plantation has a temperate continental climate, with mean annual temperature of 3.2 °C (−14.7 °C in January and 18.8 °C in July) and 716 mm of annual precipitation, occurring primarily between April and October. Soils at the Birch Lake Plantation are well-drained inceptisols (Anderson et al. 2001) with annual nitrogen deposition of approximately 0.15–0.2 kg·ha⁻¹·year⁻¹ (Holland et al. 2005). The Birch Lake Plantation is part of the Superior National Forest; the plantation contains five levels of post-thinning residual basal area and unthinned control blocks, each replicated three times, for a total of 18 blocks. Residual basal areas were 7, 14, 21, 28, and 35 m²·ha⁻¹; the unthinned control had 50 m²·ha⁻¹ basal area at the final sampling (2003). Each block (other than the unthinned blocks) was divided into three stands, which were randomly assigned one of three thinning methods: thinning from above (A), in which dominant and co-dominant trees were removed to favor residual trees within the same crown classes; thinning from below (B), in which the smallest trees were removed; or a combination of thinning from above and below (AB), in which the basal area of removed trees was divided roughly evenly between the largest trees and the smallest trees. Stands were planted at the same initial spacing (2 m) in 1912 and the experiment was installed in 1957, after which stands were thinned at roughly 10-year intervals until 2003. Each stand contains a 0.08 ha circular plot on which diameter at breast height (DBH; outside bark diameter at 1.37 m above ground) and species of all trees larger than 10.2 cm DBH were measured every 5 years starting in 1957. Additional details about the Birch Lake Plantation, plots, and measurements are provided in Bradford and Palik (2009).

Analysis

We combined diameter measurements with allometric equations for stems, branches, and foliage (Table 1) to estimate total aboveground live biomass for every tree at every measurement period. Individual tree growth was calculated for each tree as the change in biomass between measurement periods. Individual tree growth and biomass were used to estimate stand-level growth dominance according to methods detailed in Binkley (2004) and Binkley et al. (2006). Briefly, individual trees were ordered by increasing biomass and cumulative biomass (percentage of total) was compared with cumulative growth (percentage of total) for each tree in that order. Growth dominance for each plot at each measurement period was calculated as the sum of cumulative biomass minus cumulative growth for each tree in the plot. For this coefficient, positive values indicate that larger trees account for a larger proportion of stand growth than biomass (i.e., positive growth dominance); negative values indicate that smaller trees account for a larger proportion of growth than biomass (i.e., negative growth dominance); and values equal to zero indicate conditions in which trees display growth that is proportional to their biomass. Additional description and justification of this

Table 1. Allometric equations for the estimation of stem volume and aboveground biomass from diameter and height measurements of red pine (*Pinus resinosa*).

Component	Equation	Source
Stem volume	$V = 0.003D_{in}^{1.79}H_{ft}^{1.12}$	Fowler 1997
Bole biomass	$\ln(B_{kg}) = -2.84 + 2.39 \cdot \ln(D_{cm})$	Ker 1980; compiled in Jenkins et al. 2004
Branch biomass	$\ln(B_{lb}) = -1.51 + 2.50 \cdot \ln(D_{in})$	Young et al. 1980; compiled in Jenkins et al. 2004
Foliar biomass	$\ln(B_{lb}) = -1.21 + 2.18 \cdot \ln(D_{in})$	Young et al. 1980; compiled in Jenkins et al. 2004

Note: Similar equations for species other than red pine were used and are available in Jenkins et al. (2004). V is stem volume in cubic feet; B_{kg} and B_{lb} are biomass in kilograms and pounds, respectively; D_{cm} and D_{in} are diameter at breast height in centimetres and inches, respectively; and H_{ft} is height in feet. Values were converted to metric units for analysis.

Table 2. ANOVA results for factors influencing stand-level growth dominance of red pine (*Pinus resinosa*), with the dependent variable being the growth-dominance coefficient ($r^2 = 0.47$; this value is for the ANOVA model containing only statistically significant independent variables, not the full model shown).

Source	df	SS	F	Pr >F
Thinning	2	0.000	0.29	0.75
Basal area	4	0.009	1.68	0.23
Thinning × basal area	8	0.012	3.76	0.002
Age	7	0.007	5.38	<0.0001
Thinning × age	14	0.008	2.25	0.01
Basal area × age	28	0.010	1.36	0.13
Thinning × basal area × age	56	0.015	1.09	0.34
Model	127	0.111	3.21	<0.0001
Error	256	0.070		
Total	383	0.181		

Note: Stand age, the interaction between thinning method and stand age, and the interaction between thinning method and relative basal area all significantly influenced growth dominance. SS, sum of squares.

method for estimating stand-level growth dominance and details about the calculations involved are available in Binkley (2004) and Binkley et al. (2006).

To characterize the impact of thinning treatments and stand age on stand-level growth dominance, we used a mixed-model, repeated-measures analysis of variance (ANOVA), with growth-dominance coefficients as the dependent variable. Thinning method, residual basal area, and stand age (plus all possible interactions) were included as independent variables; stand was used as the random effect; and stand age was used as the repeated effect.

Results

Stand-level growth dominance was influenced by stand age, the interaction between residual basal area and thinning method, and the interaction between stand age and thinning method. In combination, this ANOVA model explained 47% of the variability in growth dominance (Table 2). Examining the interaction between residual basal area and thinning method illustrates that growth dominance in unthinned stands differed from that in stands maintained at all other basal areas and thinning methods, with the exception of stands thinned from above at basal area of 34 m²·ha⁻¹, which did not differ from unthinned stands (Fig. 1). Growth dominance in stands thinned from above increased with increasing residual basal area, in contrast to stands thinned from below, and above and below, which showed no pattern across residual basal area (Fig. 1).

Examining the interaction between stand age and thinning method illustrates that growth dominance in unthinned stands was significantly higher than growth dominance in thinned stands at all ages and all thinning methods with the exception of stands thinned from above at age 50 (Fig. 2). Unthinned stands displayed increasing growth dominance with stand age, whereas stands thinned from above displayed decreasing growth dominance with stand age and stands thinned either from below or from a combination of above and below displayed no consistent pattern with stand age. At each individual stand age, thinning method (A vs. AB vs. B) generally did not significantly influence growth dominance, with the exception of age 50, when stands thinned from above displayed higher growth dominance than the other two thinning methods (Fig. 2).

Discussion

Our comparison of the unthinned and thinned stands highlights the value of the growth-dominance approach for quantifying the impact of thinning treatments on intrastand dynamics and competition. Growth dominance in unthinned stands was almost universally higher than that in thinned stands, suggesting that repeated thinning of any kind has a dramatic impact on competitive interactions between individuals by preventing size-related growth dominance from developing. Furthermore, thinned stands displayed extremely small growth-dominance coefficients, regardless of which crown classes were removed or how intensively the stands were thinned. In almost all circumstances, growth dominance in thinned stands did not differ significantly from zero. Interestingly, the growth-dominance coefficients in thinned stands observed in this study, as well as those observed in other, older plantations of red pine in the Lake States (results not shown), were considerably smaller than those found in unmanaged, even-aged stands (Binkley 2004; Binkley et al. 2006; Doi et al. 2010). These differences may result from greater homogeneity of tree sizes and thus greater homogeneity of resource availability created by long-term manipulation of stand density and canopy structure within these plantations. In particular, mean coefficients of variation for stand diameters across thinning treatments were much smaller than those of unthinned stands (Table 3), suggesting a greater potential for size-related resource-use hierarchies in the unthinned populations. Minimal growth dominance in thinned stands may imply that all thinning treatments, even the least severe, have created an environment where competition between individual trees is minimal. Nonetheless, the thinned stands with the greatest level of variation in tree size (i.e., thinning

Fig. 1. Variability in growth-dominance coefficient (unitless) in relation to residual basal area and thinning method, averaged across sampling periods and blocks, of red pine (*Pinus resinosa*). Asterisks indicate where growth dominance differed from zero ($\alpha = 0.05$); error bars are one standard error; and letters indicate significant differences between responses at $\alpha = 0.05$. Unthinned stands displayed higher growth dominance than thinned stands in all cases except for stands thinned from above in the highest basal area. #Thinning from above was the only method to show significant differences across residual basal areas.

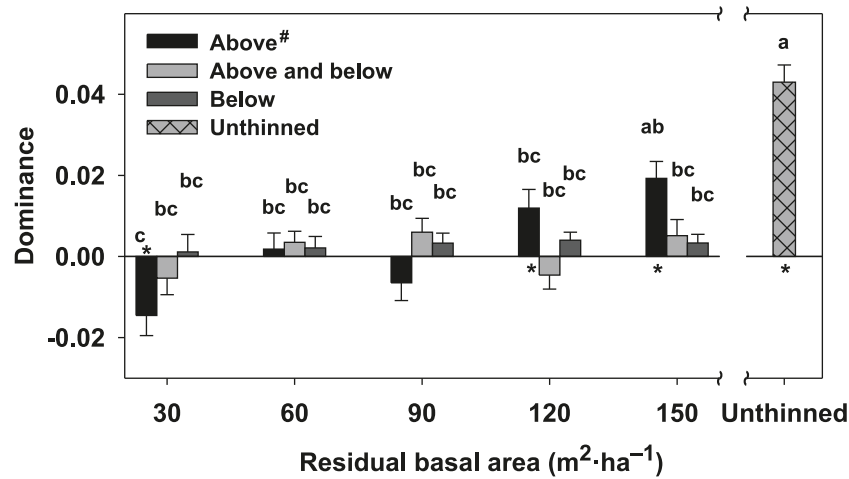


Fig. 2. Variability in growth dominance of red pine (*Pinus resinosa*) in relation to thinning method and stand age, averaged across relative basal-area classes and blocks. Unthinned stands displayed significantly higher growth dominance than thinned stands at all ages except age 50, when growth dominance was not different from stands thinned from above. Letters indicate ages when growth dominance for a given method differed significantly ($\alpha = 0.05$) from zero, and error bars are one standard error. Asterisks indicate ages when thinning methods (above vs. above and below vs. below) resulted in significantly different growth dominance, which occurred only at the youngest age, when stands thinned from above displayed higher growth dominance, and at the oldest age, when stands thinned from below displayed higher growth dominance. #Thinning methods from above and of unthinned stands displayed significant growth dominance trends through time. Growth dominance in unthinned stands increased with age, whereas growth dominance in stands thinned from above decreased with age.

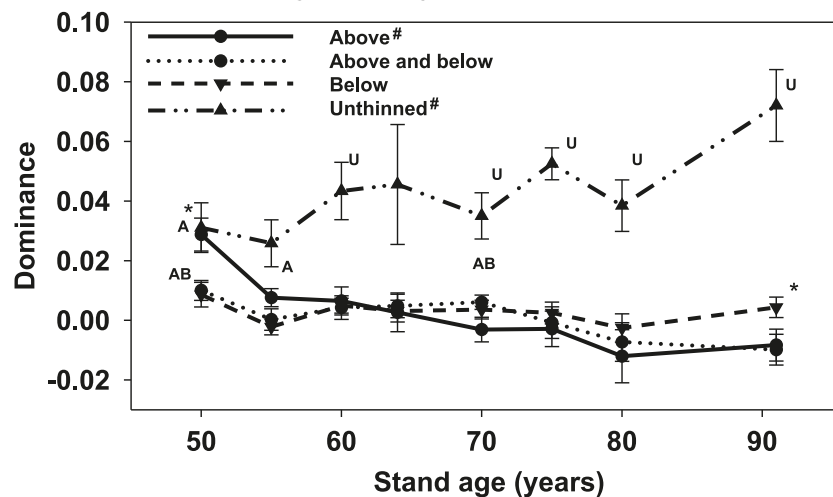


Table 3. Within-plot mean and within-plot coefficient of variation (CV) in individual tree diameters at breast height (DBH) and basal areas averaged across all ages for stands of red pine (*Pinus resinosa*) thinned from above, above and below, below, and unthinned.

Treatment	n	DBH mean (cm)		DBH CV (%)		Basal area mean (cm ²)		Basal area CV (%)	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE
Above	15	25.6	1.1	39	0.8	644	71	36	1.3
Above and below	15	29.9	1.4	20	2.0	680	80	22	3.0
Below	15	31.0	1.6	16	2.6	713	70	20	3.8
Unthinned	9	25.3	0.9	67	0.4	700	83	33	0.7

from above treatment; Table 3) also had the greatest levels of growth dominance. These findings highlight the potential of growth dominance as a tool for evaluating the impact of silvicultural manipulations on size-related resource-use inequalities in managed stands. This is especially relevant considering that one important purpose of thinning is to reduce competition so that limited resources can be spread more evenly among residual trees (Nyland 1996).

Despite the general lack of growth dominance in thinned stands, two significant patterns emerged in stands thinned from above. We speculate that these patterns can be understood by considering how thinning from above and increasing physiological limitation in larger trees interact to influence competition between individuals. First, growth dominance increased with increasing residual basal area in stands thinned from above. At low residual basal area, growth dominance was negative (smaller trees accounting for a larger proportion of growth than biomass) in stands thinned from above, indicating that the openings created by intense thinning were more effectively exploited by smaller trees. At high residual basal area, growth dominance was positive (larger trees accounting for a larger proportion of growth than biomass) in stands thinned from above, perhaps because larger trees typically have greater access to light and a competitive advantage in dense conditions. This may suggest that in conditions of minimal competition (low residual basal area), growth rates are more influenced by inherent physiological limitations of larger trees (Ryan et al. 1997), conferring an advantage on smaller trees. By contrast, in conditions of high competition (high residual basal area), growth is more determined by immediate access to resources, conferring an advantage on larger, more canopy-dominant trees. In addition, the smaller crown sizes of trees within these dense stands likely conferred a higher level of growth efficiency compared with large individuals grown in low-density stands (Long and Smith 1990; Jack and Long 1992). It remains unclear why this pattern of growth dominance as a function of residual basal area was not observed in stands thinned from below or from a combination of above and below. Nonetheless, trends between residual basal area and growth dominance observed in stands thinned from above suggest that the effectiveness of this thinning method at promoting the growth of larger individuals is greatest at higher residual basal areas (i.e., $>21 \text{ m}^2\text{-ha}^{-1}$). This trend is presumably due to the lower levels of production efficiency of dominant and co-dominant individuals within low-density stands managed using this method (Smith and Long 1989, 2001; Long and Smith 1990).

Second, growth dominance in stands thinned from above declined with age from positive at young ages to no different from zero at older ages. Thinning from above in young stands may create positive growth dominance perhaps because the surviving larger trees are still relatively small, not physiologically limited by size, and thus able to efficiently exploit the resources conferred by their social position. Because the stand ages and thinning-from-above treatments are repeatedly applied, the surviving large trees become increasingly physiologically limited by their size and are unable to maintain their growth dominance. In particular, several studies have demonstrated that thinning from above has a greater impact on growth of dominant and co-

dominant individuals relative to thinning from below treatments (Oliver and Murray 1983; Bradford and Palik 2009). The development of physiological constraints, such as an increasing proportion of nonphotosynthetic aboveground biomass and a greater overall tree size (Long and Smith 1992), likely occurs at a much greater rate on dominant individuals in stands thinned from above than in stands treated with low-thinning treatments. Correspondingly, periodic assessments of growth dominance can be applied within managed stands to evaluate if a given thinning method or residual stand structure is effective at promoting high levels of growth on desired crop trees, particularly as stands age and physiological constraints become more pronounced.

Results from our unthinned control stands are consistent with Binkley's hypothesis about how growth dominance progresses during stand development, although growth dominance in all stands was relatively small compared with other studies (Binkley 2004; Binkley et al. 2006; Doi et al. 2010). Because our measurements started at age 50, after stands had achieved canopy closure, we have no insight into the first stage of Binkley's hypothesis — when growth dominance should be negligible. However, we found that growth dominance in unthinned stands increased with age, suggesting that the larger trees within the stand are accounting for an increasingly disproportionate amount of the growth. Binkley (2004) hypothesized that growth dominance would increase from zero in very young stands to a positive phase when large trees dominate. Our temporal trend toward positive growth dominance in unthinned stands between age 50 and age 91 is consistent with this hypothesis, considering that fully stocked red pine stands typically reach canopy closure by roughly 20 years, volume growth culminates at around 25–35 years and begins to decline after 80 years (Buckman et al. 2006), and individual red pine may live as long as 400 years (Benzie 1977).

Conclusions

By quantifying the pervasive impact of thinning treatments on stand-level processes, particularly patterns of growth and resource use across size classes, we found that growth-dominance patterns in unthinned stands increased with age and supported part of Binkley's (2004) hypothesis, whereas growth dominance in thinned stands was generally, but not universally, very minor. Although strong patterns with stocking and age were largely not detected in stands thinned from below and from above and below, the patterns observed in stands thinned from above highlight the interactive effects of increasing size- and age-related physiological constraints to individual tree growth and the structures favored via this particular thinning method (i.e., higher degrees of size inequality and greater levels of growing space allocated to dominant and co-dominants). In particular, our findings suggest that the application of thinning from above is most effective at promoting the growth of dominant individuals at younger stand ages, whereas the other thinning methods maintain similar levels of growth across size classes independent of age. These findings have particular relevance to the effectiveness of thinning from above at promoting the growth of larger diameter trees over time, whether for meeting a particular minimum merchantable

size or restoring late-successional structural elements (Singer and Lorimer 1997). Nonetheless, the positive growth dominance created by thinning from above was restricted to younger stands, suggesting that this thinning method may not be as effective at promoting high levels of growth on large trees in older stands. Further studies should examine these patterns by quantifying growth dominance in either long-term studies or well-controlled chronosequences that include much older stands.

These results suggest three other important foci for future studies. The first involves characterizing the specific physiological processes that limit growth and thus allow the emergence of growth dominance. For example, while the onset of thinnings examined in this study began at a slightly later stage of development than is typical for this and other species, we would expect similar positive growth responses in stands thinned from above at earlier ages owing to the lower degree of physiological constraints on growth in even younger stands. Further study to identify the specific physiological constraints, perhaps water or nutrient acquisition and (or) use efficiency, would strengthen our understanding of the mechanisms behind intrastand competitive interactions. Second, future growth-dominance studies are needed to evaluate the utility of thinning from above within managed stands that contain more diverse age and size structures, as well as greater compositional diversity, than those examined in this study. This is particularly relevant in light of the large degree of variation documented in other studies examining the influence of species composition and stand structure on growth efficiency and age-related trends in production (Ryan et al. 1997; Kollenberg and O'Hara 1999; Seymour and Kenefic 2002). Third, and perhaps most important, these results illustrate the capacity of the growth-dominance metric to characterize subtle differences in intrastand tree growth patterns, and we hope that future studies will continue to utilize the growth-dominance approach as a simple yet quantitative tool for assessing the consequences of forest management practices. This growth-dominance metric can provide a valuable common framework with which to examine and compare patterns of tree growth in thinned stands across forest types and regions.

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