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Patterns of growth dominance in thinned yellow-poplar stands in the southern Appalachian Mountains, USA

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Abstract: Growth dominance provides a quantitative description of the relative contribution of individual trees to stand growth. Positive dominance occurs when the largest individuals account for a greater proportion of growth period increment than total biomass. Conversely, negative dominance occurs when the smallest trees account for a greater proportion of the growth period increment than of total biomass. This study uses the relatively new concept of growth dominance to examine long-term changes in tree growth patterns in thinned yellow-poplar (*Liriodendron tulipifera* L.) in the southern Appalachians. Growth dominance decreased with site index and the interaction between residual relative density and site index but increased with residual relative density and years since thinning. These relationships suggested that discrepancies in growth dominance among varying degrees of residual relative densities, with stands thinned to lower densities displaying negative growth dominance relative to stands receiving less intense thinning treatments, decreased over time. This negative growth dominance indicates that the stand-level growth included a disproportionate increase in growth of nondominant trees. The concept of growth dominance in a management context appears useful for assessing the efficacy of thinning treatments in meeting various management objectives and should be considered a potential tool for quantifying the relative success of management alternatives.

Résumé : La dominance de croissance fournit une description quantitative de la contribution relative des arbres individuels à la croissance d'un peuplement. La dominance est positive lorsque la contribution relative des plus gros individus à l'accroissement périodique est supérieure à leur contribution à la biomasse totale. À l'inverse, la dominance est négative lorsque la contribution relative des plus petits arbres à l'accroissement périodique est supérieure à leur contribution à la biomasse totale. Cette étude utilise le concept relativement nouveau de la dominance de croissance pour examiner les changements à long terme des patrons de croissance de tulipiers de Virginie (*Liriodendron tulipifera* L.) éclaircis dans le sud des Appalaches. La dominance de croissance a diminué avec l'indice de qualité de station et avec l'interaction entre la densité relative résiduelle et l'indice de qualité de station, mais a augmenté avec la densité relative résiduelle et avec le nombre d'années depuis l'application de l'éclaircie. Ces relations indiquent des différences de dominance de croissance entre les différents niveaux de densité relative résiduelle, c'est-à-dire que la dominance de croissance négative des peuplements fortement éclaircis par rapport aux peuplements faiblement éclaircis diminuait avec le temps. Cette dominance de croissance négative indique que la croissance du peuplement est en partie due à une augmentation disproportionnée de la croissance des arbres non dominants. Le concept de la dominance de croissance semble utile dans un contexte d'aménagement pour estimer l'efficacité des traitements d'éclaircie à atteindre différents objectifs d'aménagement et devrait être considéré comme un outil potentiel pour quantifier le succès relatif de diverses options d'aménagement.

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Introduction

The relatively new concept of growth dominance, proposed by Binkley (2004), provides a quantitative measure that describes the relative contribution of individual trees, based on tree size, to stand-level growth. At the stand level, growth dominance occurs when a stand's largest trees account for a greater proportion of growth period increment than stand mass. Conversely, negative, or reverse, dominance occurs when the largest trees within a stand account for a smaller proportion of stand growth increment than of total stand biomass (Binkley et al. 2006). Binkley (2004) hypothesized that growth dominance follows a predictable pattern during stand development, with the periods up until canopy closure dis-

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playing little to no dominance (Phase 1) followed by phases of increasing (Phase 2) and then slowly decreasing (Phase 3) growth dominance and then, finally, a phase of reverse dominance (Phase 4). Testing of this hypothesis has been largely limited to unmanaged stands, and although the proposed pattern of dominance has been documented in a variety of forest types (Binkley et al. 2003, 2006; Binkley 2004; Fernández and Gyenge 2009), others have failed to document phases of both positive and (or) reverse dominance (Binkley et al. 2006; Doi et al. 2010).

Although the vast majority of studies examining growth dominance have been conducted in unmanaged stands for the primary purpose of identifying the mechanisms associated with age-related decline in forest productivity (for a review of the topic, see Ryan et al. 1997; Smith and Long 2001), the concept of growth dominance and how it is affected by forest management may serve as a quantitative measure of whether or not silvicultural activities achieve specific goals and objectives (Bradford et al. 2010). For example, thinning has been customarily used to capture and remove volume that would have been lost due to mortality during stand development as well as increase and concentrate future growth on more economically valuable trees (Nyland 2002). While more traditional objectives associated with thinning are related to timber production, today, thinning treatments are designed and implemented to achieve numerous objectives, including promoting structural characteristics associated with later stages of stand development (e.g., complex, heterogeneous stand structure dominated by large trees). Bradford et al. (2010) is the only study to have examined the effects of active management on growth dominance, and while the authors reported that unthinned red pine plantations (*Pinus resinosa* Ait.) displayed positive growth dominance, repeated thinning lowered growth dominance to near zero, suggesting that thinning creates conditions conducive to tree growth across the diameter distribution. If growth dominance coefficients from these repeatedly thinned stands are compared with the four phases of growth dominance proposed by Binkley et al. (2006), it would appear that repeated thinning treatments promote a competitive environment similar to that prior to canopy closure and may create a more homogenized stand in terms of the distribution of tree sizes. In this paper, I used 35 years of individual tree data to examine patterns of growth dominance in thinned, naturally regenerated yellow-poplar (*Liriodendron tulipifera* L.) stands across a productivity gradient in the southern Appalachian Mountains.

Methods

Experimental design and data collection

This study uses data collected as part of a long-term study examining the growth and yield of yellow-poplar throughout the southern Appalachians in relation to stand age, site index, and post-thinning density. Between 1960 and 1964, one hundred and forty-one 0.1 ha permanent plots were established in yellow-poplar stands throughout the Blue Ridge and northern Ridge and Valley provinces of the southern Appalachian Mountains. Plots were located in northern Georgia, western North Carolina, eastern Tennessee, and southern Virginia. Altitudes of plots range from 340 to 1140 m and are located predominantly on north- and east-facing aspects. Average annual precipitation and temperature range between 960 and 2000 mm and 13 and 15 °C, respectively. All plots were established in even-aged stands dominated by yellow-poplar (>80% of the overstory basal area in yellow-poplar) with no recent evidence of disturbance or harvesting.

At the time of plot establishment and prior to the thinning treatment, all live trees >11.4 cm diameter at breast height (1.37 m above ground line) within each plot were tagged and stem-mapped. For all tagged trees, species, diameter at breast height, and total height were recorded. One increment core at stump height was obtained from five dominant/codominant yellow-poplar trees per plot. Age at stump height was obtained from the increment cores in the laboratory under magnification. Using the age and height data, an estimate of site index (base age 50 years) was calculated using yellow-poplar site index equations developed by Beck (1962) for each of the five trees per plot. Plot-level site index was calculated as the average site index of the five sample trees.

Following plot establishment and the pre-thinning inventory, plots received a low thinning to a residual basal area (square metres per hectare) that was at least one 6 m^2/ha basal area class less than the pre-thinning basal area, where the number of classes that the pre-thinning basal area was reduced to was chosen at random. Species other than yellow-poplar were targeted for removal to obtain the specified residual basal area. The thinning grades ranged from a grade “A” thinning in which only suppressed trees were removed to a grade “D”, or heavy, thinning in which the majority of codominant trees were removed. After the second inventory cycle (1966–1969) was completed, 128 of the 141 permanent plots were thinned from below for a second time to the originally assigned residual basal area. No further management activities occurred. Remeasurement of all plots occurred during the dormant season every 5 years following plot establishment beginning in 1960 up through 1999 for a total of eight inventory cycles including the pre-thinning inventory. During each inventory cycle, the status of all tagged trees was assessed (e.g., live, dead, harvested) and diameter at breast height was recorded on all live trees.

Individual tree biomass (kilograms) at each inventory cycle was estimated using the allometric equations outlined in Jenkins et al. (2003). Biomass increment was calculated as the difference in whole-tree biomass between inventory cycles. Using individual tree biomass, plot-level growth dominance at each inventory cycle was calculated following Binkley et al. (2006). Individual trees were arranged from smallest to largest in terms of biomass at each inventory cycle, and the cumulative distribution of whole-tree increment was plotted as a function of the cumulative distribution of whole-tree biomass (Binkley 2004). A growth dominance coefficient (similar to the Gini coefficient) was then calculated for each plot at each inventory cycle (Binkley et al. 2006; Bradford et al. 2010). A positive growth dominance coefficient signifies positive growth dominance (i.e., growth of the largest trees contributes more percentage-wise to the growth period increment than their percentage contribution to total stand biomass), while negative growth dominance coefficients indicate reverse growth dominance (i.e., growth of the largest trees contributes less percentage-wise to the growth period increment than their percentage contribution to total stand biomass).

Data analysis

Ten of the original 141 plots were lost to harvesting or severe disturbance, leaving 131 plots for this analysis. Linear regressions were used to test the null hypothesis that stand age, years since thinning (YST), site index, and residual post-thinning density had no significant effect on the growth dominance in managed yellow-poplar stands. Therefore, regression analysis was used to assess the significance of these factors in influencing growth dominance as opposed to being used to produce a predictive equation.

A set of four full-rank a priori models were developed that included site index, either residual basal area or residual relative density, either stand age or YST, and, because of evidence suggesting growth dominance changes over time (e.g., Binkley et al. 2006) as well as with stand density (Bradford et al. 2010), the interaction between the measures of stand density and either YST or age. Residual relative density was calculated based on stand density index (SDI) where residual relative density is equal to $\mathrm{SDI}_{\mathrm{observed}}/\mathrm{SDI}_{\mathrm{max}}$ ($\mathrm{SDI}_{\mathrm{max}}$ for yellow-poplar = 1140). All four models were compared using the Akaike information criterion (AIC), with the model with the lowest AIC value considered the best model. Autocorrelation among repeated measurements that occurred on each independent plot was modeled using an unstructured covariance structure, as this covariance structure produced models with the lowest AIC values. Analyses were conducted using SAS/STAT software (version 9.2) and were performed with a significance level of 0.05.

Results

All plots were located on productive sites with site index ranging from 22.9 to 40.2 m. Prior to the 1961 thinning, basal area, density, and quadratic mean diameter of the 131 plots ranged from 10.9 to 48.2 m^2/ha, from 270 to 1080 trees/ha, and from 15.5 to 44.8 cm, respectively (Table 1). After the initial thinning, basal area and density ranged from 8.8 to 35.0 m^2/ha and from 80 to 800 trees/ha, respectively, which equated to relative densities between 15% and 56%. Because low thinning was used, the quadratic mean diameter increased in all plots and ranged from 15.9 to 51.4 cm immediately following the thinning. By the end of the last inventory cycle, a limited amount of mortality was observed with relative density approaching 75% in some of the plots.

Across all inventory periods, growth dominance coefficients varied between –0.28 and 0.29, with 75% of dominance coefficients between –0.06 and 0.03. Models that incorporated measures of residual relative density performed significantly better than those that incorporated measures of absolute post-thinning density (i.e., residual basal area), indicating that post-thinning relative density explained a greater proportion of the variance in growth dominance than residual basal area (Table 2). Similarly, models substituting stand age for YST increased AIC values, indicating a poorer fit, regardless of whether residual or absolute measures of post-thinning density were used. Of the four a priori full-rank models examined, the model that related growth dominance to site index, YST, residual relative density, and the interaction between residual relative density explained the greatest variability in growth dominance (i.e., produced the lowest AIC value). Parameter estimates associated with residual relative density and YST suggested a positive relationship with growth dominance, while a negative relationship was observed between growth dominance and the interaction between YST and residual relative density (Fig. 1) as well as between growth dominance and site index (Fig. 2). Although all model coefficients associated were significantly different from zero, relationships between growth dominance and variables of interest were relatively weak, suggesting that other stand or site variables influence patterns of tree growth in these thinned yellow-poplar stands. Although weak, the significant relationships among residual relative density, YST, and growth dominance suggest that while growth dominance is negatively affected by progressively lower levels of residual relative density, the observed differences in growth dominance associated with residual relative density decreases as YST increases (Fig. 1). Regardless of YST and residual relative density, stands of lower site quality (i.e., lower site index) possessed greater growth dominance coefficients than stands of progressively higher site quality (Fig. 2).

Discussion

Growth dominance coefficients reported in this study varied between –0.28 and 0.29; however, 75% of the dominance coefficients fell between –0.06 and 0.03. These values are of substantially smaller magnitude than reported by Binkley et al. (2006) for lodgepole pine (*Pinus contorta* Douglas ex Loudon) (range 0.0–0.23), old-growth ponderosa pine (*Pinus ponderosa* Dougl.as ex P. Lawson & C. Lawson) (range –0.22 to –0.25), and Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) – subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (average –0.33) forest types in the interior west but are comparable with values reported by Bradford et al. (2010) and Binkley et al. (2006) for red pine and trembling aspen (*Populus tremuloides* Michx.) forests, respectively.

This study provides evidence that post-thinning density, site quality, and time since thinning significantly exert some level of influence on the patterns of growth dominance in managed yellow-poplar stands throughout the southern Appalachian Mountains. Parameter estimates from the regression analysis suggest that growth dominance coefficients increase as the time since thinning and residual relative density increase but are reduced with increases in site index, although variability in the data set was substantial (Table 2). Although residual relative density had a positive effect on growth dominance, the influence of residual relative density diminished as the time since thinning increased. Within the range of residual relative densities examined in this study, during the immediate years following thinning, growth dominance coefficients were generally negative, indicating that the relative contribution of smaller trees to stand growth was greater than the relative contribution of smaller trees to overall stand biomass. Thinning operations that retained a relatively high proportion of the original number of stems (i.e., a higher residual relative density) possessed growth dominance coefficients near zero. As the time since thinning elapsed, low-density stands progressed from periods of negative dominance to neutral or positive growth dominance. The positive

Table 1. Stand attributes prior to and immediately following the initial thinning ($n = 131$).

Stand attribute	Mean	Minimum	Maximum	Standard deviation
Pre-thinning				
Site index (m)	32	22.9	40.2	3.3
Age (years)	48	18	76	14
Basal area (m^2/ha)	31.3	10.9	48.2	7.0
Density (trees/ha)	572	270	1080	176
Relative density (%)	54	23	71	10
Quadratic mean diameter (cm)	27.4	15.5	44.8	5.8
Immediately post-thinning				
Site index (base age 50 years) (m)	32	22.9	40.2	3.3
Age (years)	48	18	76	14
Basal area (m^2/ha)	19.7	8.8	35.0	6.8
Density (trees/ha)	252	80	800	143
Residual relative density (%)	32	15	56	10
Quadratic mean diameter (cm)	34.0	15.9	51.4	8.3

Note: Relative density = $SDI_{observed}/SDI_{max}$; SDI_{max} = 1 140.

Table 2. Comparison of the four a priori full-rank models relating growth dominance in thinned yellow-poplar (*Liriodendron tulipifera*) stands to site index, either residual basal area or residual relative density, and either years since the first thinning (YST) or stand age.

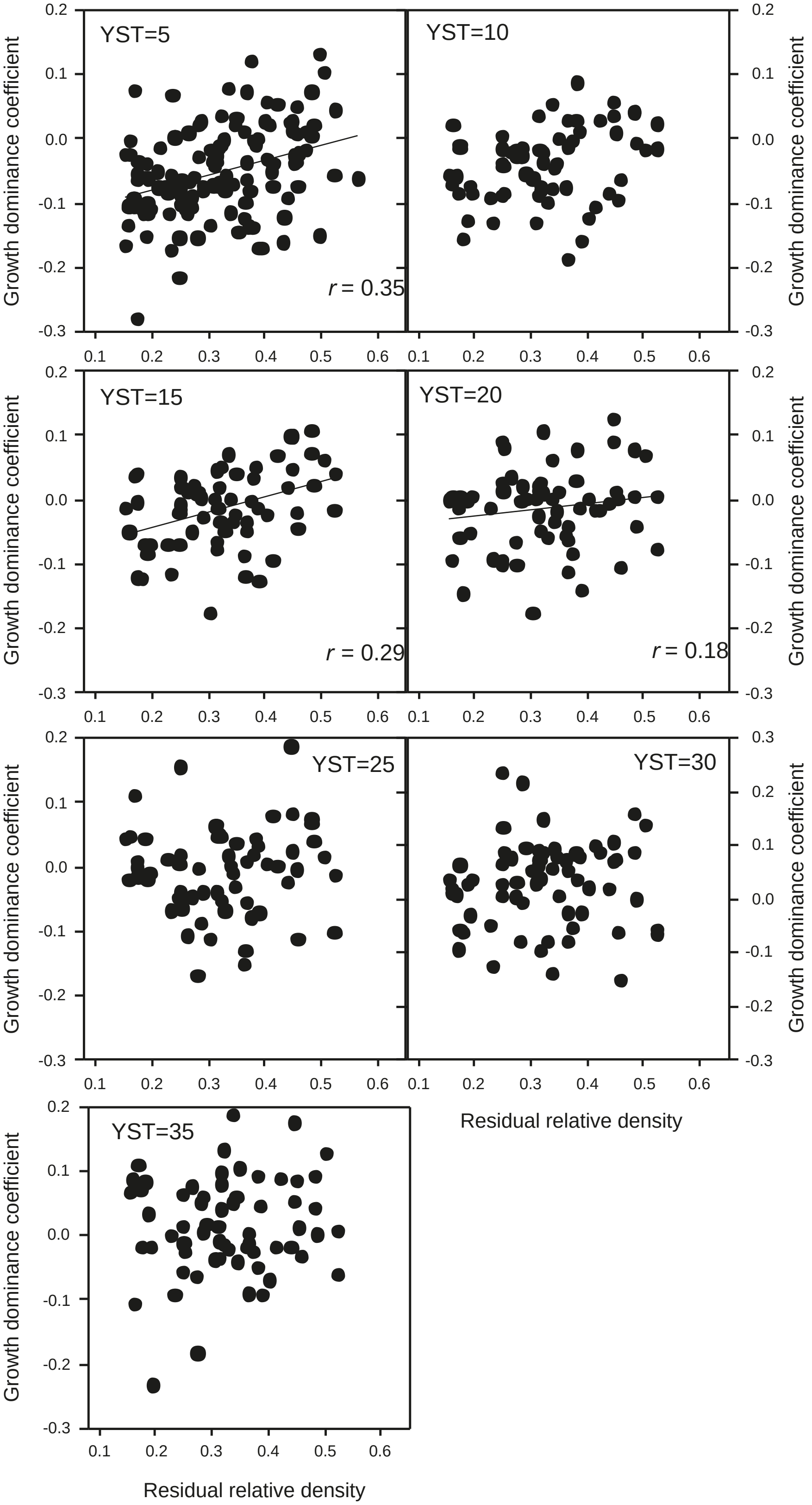
Parameter	Estimate	Standard error	*t*	*P*
Model 1 (AIC = –2651.9)				
Intercept	–0.0233	0.0412	–0.56	0.5730
Site index	–0.0032	0.0013	–2.44	0.0159
Residual basal area	0.0030	0.0009	3.47	0.0007
YST	0.0041	0.0007	6.29	<0.0001
YST × residual basal area	–0.0001	<0.0001	–2.77	0.0065
Model 2 (AIC = –2670.2)				
Intercept	–0.0293	0.0408	–0.72	0.4747
Site index	–0.0031	0.0012	–2.54	0.0123
Residual relative density	0.0254	0.0555	3.70	0.0003
YST	0.0039	0.0007	5.60	<0.0001
YST × residual relative density	–0.0046	0.0021	–2.21	0.0291
Model 3 (AIC = –2594.3)				
Intercept	–0.1034	0.0551	–1.88	0.0622
Site index	–0.0026	0.0015	–1.70	0.0919
Residual basal area	0.0042	0.0019	2.25	0.0259
Age	0.0027	0.0006	4.62	<0.0001
Age × residual basal area	–0.0001	<0.0001	–2.33	0.0206
Model 4 (AIC = –2615.0)				
Intercept	–0.1075	0.0544	–1.98	0.0499
Site index	–0.0031	0.0014	–2.19	0.0308
Residual relative density	0.3400	0.1168	2.91	0.0040
Age	0.0026	0.0006	4.33	<0.0001
Age × residual relative density	–0.0041	0.0018	–2.24	0.0259

Note: *P* values pertain to the null hypothesis that variables are not significantly different from zero.

effect of density on growth dominance observed in this study is consistent, in part, with studies in managed red pine and unmanaged ponderosa pine plantations where high-density stands experienced a significant, albeit small, increase in growth dominance over that in lower density stands (Fernández and Gyenge 2009; Bradford et al. 2010). In a highly competitive environment (e.g., high-density stand), large dominant and codominant canopy trees are able to capture resources at the expense of smaller trees in subordinate canopy positions. This differential access to resources in higher versus lower density stands promotes the growth of dominant individuals and advances the development of size inequalities and negatively skewed diameter distributions within stands (Palahí et al. 2006).

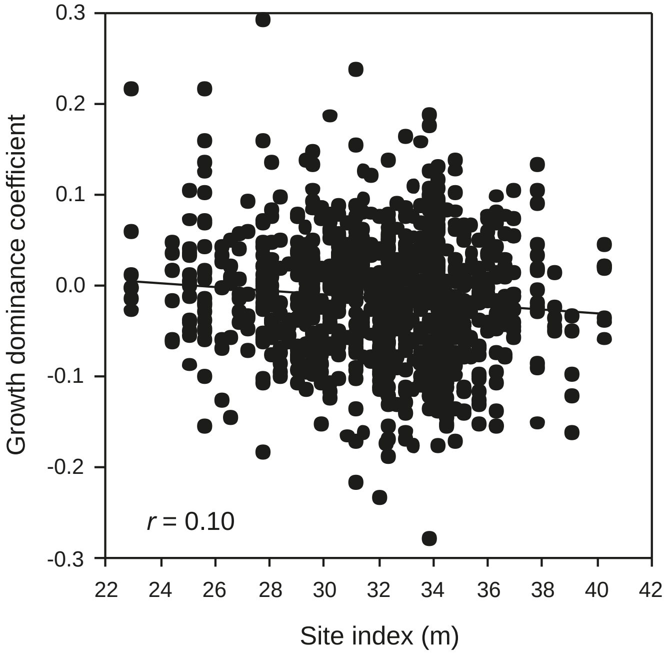
Bradford et al. (2010) suggested that the concept of growth dominance may be useful in assessing the efficacy of thinning treatments in meeting specific management objectives, including creating structural characteristics associated with the later stages of stand development and continued growth of large-diameter crop trees. Because the data set used here did not contain unthinned controls, this study is unable to address the effects of thinning on patterns of growth dominance

Fig. 1. Relationship between growth dominance coefficients and residual relative density by years since the first thinning (YST). Pearson's correlation coefficients (*r*) are reported for inventory periods when significant relationships were observed ($P < 0.05$).



relative to unmanaged conditions. Within a managed stand context, results from this study suggest that low thinning to progressively lower relative densities does not immediately translate into positive growth dominance. Rather, low-density conditions during the immediate years following thinning promoted a competitive environment that favored the growth

Fig. 2. Relationship between growth dominance coefficients and site index. The Pearson correlation coefficient (*r*) was significant at $\alpha = 0.05$.



of smaller rather than larger individuals (i.e., negative growth dominance), but this trend lessened as the time since thinning elapsed. By the end of the study period, no differences in growth dominance were present in stands thinned to some of the highest (55%) and lowest (15%) relative densities (Fig. 1). If managing for increased growth of a select few large crop trees, thinning to extremely low residual densities appears to concentrate growth across the broad range of residual diameter classes, as opposed to on the largest individuals within a stand, which may cause a decrease in the variability in tree sizes within a stand in the short term while still stimulating overall diameter growth in these stands (Beck and Della-Bianca 1975). In the context of this study, management goals that include a more complex structure characteristic of the later stages of stand development may be achieved by implementing low thinnings to higher residual relative densities which stimulates diameter growth across the range of tree sizes (Beck and Della-Bianca 1975) but ultimately creates an environment where increment is disproportionally greater among the largest individuals. Regardless of the objectives of thinning, these data suggest that repeated thinnings may be required to meet long-term structural objectives as the growth effect associated with residual density is diminished over time.

Despite the weak relationship between site quality and growth dominance (Fig. 2), this study does suggest that future tests of Binkley's growth dominance hypothesis (Binkley 2004; Binkley et al. 2006) take into account variation in site productivity as a possible factor in explaining variation in growth dominance in both managed and unmanaged forest conditions. The data presented here show that the influence of thinning on growth dominance was stronger on low site index stands than on more productive sites, suggesting that thinning on lower quality sites is more productive at creating an environment conducive to positive growth dominance. High-quality sites in the southern Appalachians are characterized by abundant nutrient and moisture availability throughout the growing season, supporting greater leaf area than found on low-quality sites (Bolstad et al. 2001). Although these high-quality sites are conducive to rapid stand growth and development, resource availability and (or) the efficiency of resource utilization (DeRose and Seymour 2010) in subordinate canopy positions (Gilmore and Seymour 1996; Reid et al. 2004; Gersonde and O'Hara 2005) on high-quality sites may not be as limiting as in low-quality stands, promoting disproportionally greater growth of the smaller individuals regardless of post-thinning structure.

Conclusions

Binkley et al. (2006) proposed that stands possess zero growth dominance up until canopy closure, as trees of all sizes grow in direct proportion to their sizes. After canopy closure, positive growth dominance might occur for an extended period of time as dominant trees contribute disproportionately larger amounts of stand growth than nondominant trees. Although stands utilized in this study were well beyond the point of canopy closure at the time of thinning (Beck and Della-Bianca 1981), growth dominance coefficients were substantially less than those reported for other forest types in unmanaged conditions at similar points in stand development (e.g., Binkley et al. 2006; Doi et al. 2010). A comparison of the patterns of growth dominance in managed versus unmanaged yellow-poplar stands was not possible in this study. However, the relationships presented here, coupled with results from other thinning studies (Bradford et al. 2010), suggest that intermediate stand management activities alter the patterns of growth dominance outlined by Binkley (2004) and Binkley et al. (2006). Furthermore, although the relationships presented here were generally weak, this study suggests that future studies using the concept of growth dominance to describe stand dynamics and patterns of tree growth in both managed and unmanaged conditions should account for the possible effects of site quality and structural attributes, such as stand density (Fernández and Gyenge 2009; Bradford et al. 2010), on patterns of growth dominance. Site quality may be of particular importance in explaining patterns of growth and biomass accumulation over time in locations where the productivity gradient is steeper than the productivity gradient inherent to this data set (e.g., Coomes and Allen 2007).

It should be mentioned that land-use history of the study sites is relatively similar, with the yellow-poplar stands sampled originating after a period of widespread exploitive logging in the southern Appalachians during the late 19th and early 20th centuries. Prior to logging, the majority of these stands were likely of mixed-species composition (e.g., mixed-oak), with the conversion to yellow-poplar occurring as a result of the ability of yellow-poplar from seedling origin to outcompete many species, including oak, on these high-quality sites following substantial overstory removal (Loftis 1990). On some of the less severe slopes, past land use may have included agricultural activities and grazing. Given that past land use can affect the interpretation of the results of ecological studies (e.g., Foster et al. 2003), it should be clarified that the results presented here are not designed to be a predictive model of growth dominance over time; rather, this study was designed to examine a suite of stand and site variables that may account for variability in growth dominance beyond the variable of stand age proposed by Binkley (2004) and Binkley et al. (2006). Although management activities have been restricted on the study sites over the course of this study, land-use history has been demonstrated to influence ecosystem processes and functioning, including tree growth (e.g., Comita et al. 2010), which may be of some significance when considering the applicability of the results presented here to other systems and (or) within similar systems with vastly different land-use histories.

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