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ARTICLE

The impact of overstory density on sapling height growth in the Missouri Ozarks: implications for interspecific differentiation during canopy recruitment

Lance A. Vickers, David R. Larsen, Benjamin O. Knapp, John M. Kabrick, and Daniel C. Dey

Abstract: Successful canopy recruitment is one of the most important components of sustainable forestry practices. For many desirable species in oak-dominated forests, insufficient sapling growth is a common limitation to successful recruitment. The objectives of this study were to (*i*) examine the impact of overstory density on sapling growth in the Missouri Ozarks, (*ii*) investigate the potential for overstory retention to promote compositional shifts via interspecific differences in sapling height growth, and (*iii*) compare the use of mean and near-maximum growth rates to quantify the impact of overstory density on sapling growth and height differentiation among species. We found that the periodic annual height increment of saplings decreased with increasing overstory density for all species groups in this study (red oaks (*Quercus* spp.), white oaks (*Quercus* spp.), hickories (*Carya* spp.), sassafras (*Sassafras* spp.), blackgum (*Nyssa* spp.), dogwood (*Cornus* spp.), red maple (*Acer* spp.), ashes (*Fraxinus* spp.), and elms (*Ulmus* spp.)). There was evidence of interspecific differentiation in growth rates during the sapling stage, and the observed differences were more pronounced at low overstory densities. Increasing overstory densities either reduced or eliminated the differences in growth among species. Although red oaks displayed the greatest maximum growth rates of all species under low overstory densities (<5 $m^2 \cdot ha^{-1}$), the growth advantage of red oaks was reduced with increasing overstory density. This may provide opportunities to shift species composition toward white oaks using partial harvesting regimes in the Missouri Ozarks. However, white oaks had little to no advantage in height growth over many competing species when overstory density exceeded about 10 $m^2 \cdot ha^{-1}$. This implies that the probability of recruitment under overstory densities greater than about 10 $m^2 \cdot ha^{-1}$ is likely to decline for all oaks in the Missouri Ozarks. We found that using the 90th quantile of height growth rates to evaluate the impact of overstory density on sapling growth had two potential advantages over using the mean growth rate: (*i*) it provided better models of the limiting effects of overstory density on sapling height growth, and (*ii*) the focus was on the growth rates of stems that were most likely to recruit into the canopy.

Key words: silviculture, regeneration, recruitment, differentiation, quantile.

Résumé : Le succès du recrutement dans le couvert dominant est une des plus importantes composantes des pratiques de foresterie durable. Dans le cas de plusieurs espèces désirées des forêts dominées par le chêne, la croissance insuffisante des gaules est le facteur qui limite couramment la réussite du recrutement. Les objectifs de cette étude consistaient à (*i*) examiner l'impact de la densité du couvert dominant sur la croissance des gaules dans les monts Ozarks du Missouri, (*ii*) évaluer le potentiel de mesures de rétention du couvert dominant pour favoriser des changements de composition induits par des différences interspécifiques de croissance en hauteur des gaules et (*iii*) comparer l'utilisation des taux de croissance moyen et près du maximum pour quantifier l'impact de la densité du couvert dominant sur la croissance des gaules et sur les différences de croissance entre les espèces. Nous avons trouvé que l'accroissement annuel périodique en hauteur des gaules diminuait avec l'augmentation de la densité du couvert dominant pour tous les groupes d'espèces dans cette étude (chênes rouge et blanc, caryers, sassafras, nyssa, cornouiller, érable rouge, frênes et ormes). Il y avait des signes de différences interspécifiques du taux de croissance des gaules et les différences observées étaient plus prononcées lorsque la densité du couvert dominant était faible. L'augmentation de la densité du couvert dominant réduisait ou éliminait les différences de croissance entre les espèces. Bien que le chêne rouge ait montré le taux maximal de croissance le plus élevé parmi toutes les espèces lorsque la densité du couvert dominant était faible (<5 $m^2 \cdot ha^{-1}$), cet avantage diminuait avec l'augmentation de la densité du couvert dominant. Ceci peut offrir des possibilités de changer la composition des espèces en faveur du chêne blanc à l'aide de coupes partielles dans les monts Ozarks du Missouri. Toutefois, l'avantage de croissance en hauteur du chêne blanc était faible ou nul par rapport à plusieurs espèces concurrentes lorsque la densité du couvert dominant dépassait environ 10 $m^2 \cdot ha^{-1}$. Ceci implique que la probabilité de recrutement de tous les chênes des monts Ozarks du Missouri va probablement diminuer sous des couverts dominants de densité supérieure à 10 $m^2 \cdot ha^{-1}$. Nous avons trouvé que l'utilisation du 90^e quantile du taux de croissance en hauteur pour évaluer l'impact de la densité du couvert dominant sur la croissance des gaules avait deux avantages potentiels par rapport à l'utilisation du taux de croissance moyen: (*i*) meilleurs modèles des effets limitatifs de la densité du couvert dominant sur la croissance en hauteur des gaules, et (*ii*) emphase placée sur le taux de croissance des tiges les plus susceptibles d'atteindre le couvert dominant. [Traduit par la Rédaction]

Mots-clés : sylviculture, régénération, recrutement, différentiation, quantile.

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Introduction

Regeneration and canopy recruitment are two vital ecosystem processes necessary for sustainable forestry (Dey 2014). Unfortunately, difficulties and failures to regenerate either economically or ecologically important species are common in many forest ecosystems. Although these regeneration failures can result from inadequacies in seed production or poor seedling establishment, insufficient sapling recruitment into the canopy is also a major cause (Clark et al. 1999; Coates 2002; Peet and Christensen 1987).

Saplings compete with the overstory for space and resources both above and below the ground (Horn 1985). The density, structure, and composition of the overstory has an influence on the quantity and quality of light reaching the forest floor (Canham et al. 1994; Larsen and Kershaw 1996) and also on the availability of water and nutrients (Coomes and Grubb 2000). In turn, resource availability affects the abundance, survival, and growth of saplings (e.g., Kneeshaw et al. 2006; Kobe et al. 1995; Pacala et al. 1994). Consequently, the density of the regeneration layer is often reduced as resource competition intensifies among saplings, but the cohort may be eliminated altogether depending on the magnitude of release provided by canopy disturbance (Oliver and Larson 1996).

Successful canopy recruitment is largely disturbance driven, and there have been several efforts to organize disturbance response patterns into a framework that offers insight into the suitability of a species to certain environmental conditions (e.g., MacArthur and Wilson 1967; Noble and Slatyer 1980; Grime 2006). Yet, despite numerous investigations into the impacts of resource limitation on canopy recruitment, consensus is lacking on the relative importance of the underlying physiological mechanisms involved (Coomes and Grubb 2000; Valladares and Niinemets 2008). Stem analyses suggest that successful recruits typically do not experience suppression during their ascent into the canopy (Landis and Peart 2005). Faster growing saplings generally have a lower risk of mortality (Kobe et al. 1995) and are more likely to capture available growing space (Loftis 1990*a*; Dey et al. 1996). Individuals that successfully differentiate from their peers in stature often benefit from the advantages of asymmetric competition (Schwinning and Weiner 1998; Weiner 1990).

However, rate of growth, per se, may not be an entirely sufficient predictor of successful recruitment unless it provides a lasting advantage in relative stature among co-occurring species with differences in life histories (Clatterbuck and Hodges 1988). Moreover, growth is only beneficial to the extent that resource availability and (or) efficiency exceed respiration costs (Givnish 1988; Messier et al. 1999). For many species, trade-offs between rapid growth with abundant resources and survival with scarce resources suggest that efficiency and persistence should be favored as delays in recruitment extend exposure to suppression (Tilman 1982; Walters and Reich 2000). Thus, shade-intolerant species are likely to exhibit growth reduction, carbon imbalance, frequent dieback, and increased mortality when recruitment is delayed due to insufficient release (Kobe et al. 1995; Poorter et al. 2005).

Increasingly, regeneration methods that leave a partial overstory are being favored throughout the United States. Concurrently, there has been increasing concern that widespread recruitment problems are leading to compositional shifts and reductions in oak importance across much of the eastern United States (e.g., Fei and Steiner 2007; Nowacki and Abrams 2008; Oliver et al. 2005). Because oak species (*Quercus* spp.) have historically been an important, and often dominant, component of these forests, this concern has prompted extensive research into the regeneration niche of many oak species (Johnson et al. 2009).

At one time, clear-cutting followed by intermediate thinnings was advocated as the optimal method for maintaining oak-dominated forests in the Central Hardwood Forest Region (Roach and Gingrich 1968). However, clear-cutting has led to oak recruitment failures at highly productive sites where intense and sustained competition from shade-intolerant species excludes oak saplings (Beck and Hooper 1986). Consequently, variations of shelterwood methods were developed to increase the relative performance of oak saplings by reducing the abundance and (or) growth of competitors (e.g., Loftis 1990*b*; Brose et al. 1999). However, partial harvesting of oak-dominated forests has allowed for the proliferation of shade-tolerant species in some cases (e.g., Schuler 2004). This suggests that successful oak recruitment is a complex process that is dependent, in part, on stand structure and composition in addition to local site conditions.

Tree recruitment dynamics in the Missouri Ozarks may be rather unique compared with much of the eastern United States. The soils, climate, and flora throughout much of the Missouri Ozarks favor an oak–hickory (*Carya* spp.) forest type by limiting the composition, stature, and (or) longevity of potential competitors (Johnson et al. 2009). While there are few long-lived, shade-intolerant species, and most shade-tolerant species are not capable of persisting through stand development to ascend into the canopy of mature forests (Dey et al. 1996). This phenomenon is believed to be due, in part, to the relatively xeric conditions that provide opportunities for oaks to persist where less drought-tolerant species cannot (Larsen and Johnson 1998). Consequently, several silvicultural systems may be appropriate to sustain the oak–hickory forests in the Missouri Ozarks, including single-tree selection (Loewenstein et al. 2000). However, partial harvesting likely delays recruitment and may promote a successional shift from mixed oaks to predominantly white oaks in the Missouri Ozarks (Kabrick et al. 2008*b*).

To date, results from longitudinal studies suggest that the effects of varying levels of residual overstory density on recruitment dynamics in oak-dominated forests are not yet fully understood (Kabrick et al. 2008*b*; Atwood et al. 2011; Schweitzer and Dey 2011). Moreover, there is some uncertainty regarding how the effects of overstory density on recruitment should be quantified (Oliver et al. 2005). Overstory density is highly influential on sapling populations, but growth can be constrained by several limiting factors (Canham et al. 1996; Niinemets and Valladares 2006). Because of this complexity, when growth is plotted as a function of a single limiting factor, the resulting graph is often a scatter of points with increasing or decreasing variance (heteroscedasticity) with a conspicuous upper boundary (Cade et al. 1999; Kaiser et al. 1994). Although the means of such distributions are informative, an alternative approach is to use the maxima, which may provide a more ecologically meaningful description of the effect of a single limiting factor in the presence of many factors (Cade et al. 1999). In addition, individuals that are most likely to be lasting participants in the recruitment process often exhibit above-average growth (Landis and Peart 2005; Oliver et al. 2005). This provides opportunities for differentiation in stature, domination of neighbors, and continued ascent towards the canopy (Oliver and Larson 1996; Schwinning and Weiner 1998; Weiner 1990). Thus, the maxima of growth–resource relationships are likely to better represent the growth displayed by successful canopy recruits.

Applying knowledge of physiological and ecological principles to simultaneously meet regeneration and multiple-use objectives is a hallmark of scientific forest management, but changes in community composition, structure, and function should be intentional and well reasoned. The ability to quantify and understand the competitive dynamics that result in the successful recruitment and dominance of desired species is essential to prevent unintended shifts in forest composition and ecosystem function. Therefore, the objectives of this study are as follows: (*i*) to examine the effect of overstory density on sapling growth in the Missouri Ozarks, (*ii*) to investigate the potential for overstory retention to promote shifts in composition via interspecific differences in sapling height growth, and (*iii*) to compare the use of mean and near-maximum growth rates to quantify the impact of overstory

density on sapling growth and height differentiation among species.

Materials and methods

The data used in this study were collected from the Missouri Ozark Forest Ecosystem Project (MOFEP), which encompasses more than 3700 ha within the Current River watershed in the Carter, Reynolds, and Shannon counties of southeastern Missouri. The study region is an unglaciated, deeply dissected plateau primarily comprised of Ordovician and Cambrian dolomites and sandstones (Kabrick et al. 2000). Average annual precipitation is 115 cm and average annual temperature is 13.5 °C (Kabrick et al. 2008*b*). Slope aspect and slope position are important characteristics used for site classification in the region (Nigh et al. 2000). The sites used in this study were on exposed (aspect 135–315°) and protected (aspect 315–135°) backslopes with an average site index (*Quercus velutina* Lam., base age 50) of 21.0 ± 1.3 m and 22.0 ± 1.1 m, respectively (McQuilkin 1974). Overstory species composition for the two site classes was heavily dominated (>70% basal area) by oak species (primarily *Q. velutina*, *Q. alba* L., *Q. coccinea* Münchh., and *Q. stellata* Wangenh.), and compositional differences between the two site classes were subtle (Kabrick et al. 2004). Protected backslopes usually have a slightly higher *Q. alba* component than exposed backslopes, whereas *Q. stellata* and *Pinus echinata* Mill. are more common on exposed backslopes (Kabrick et al. 2004). Shifley and Brookshire (2000) provide a detailed documentation of the abundance and diversity of species found on MOFEP.

MOFEP is a long-term, landscape-scale experiment initiated in 1989 by the Missouri Department of Conservation (MDC) to evaluate the effects of forest management on ecosystem composition, structure, and function within the Missouri Ozark Highlands (Brookshire and Shifley 1997). The forest management systems under evaluation at MOFEP include even-aged, uneven-aged, and no-harvest management regimes. The even-aged management regime included clearcutting with reserves ($\sim$5 $m^2 \cdot ha^{-1}$) for stands to be regenerated and intermediate thinning elsewhere, as prescribed by Roach and Gingrich (1968). In the clear-cut stands, all live trees either >3 m in total height or >4 cm in diameter at breast height (dbh, 1.37 m) were felled, with the exception of trees left as reserves (Missouri Department of Conservation 1986). The uneven-aged management regime consisted of single-tree selection on a 15-year harvest cycle with group openings that ranged from one to two tree heights (0.03–0.15 ha) interspersed throughout and summed to 5% of the harvested land area, as prescribed by Law and Lorimer (1989). Areas designated for a no-harvest management regime were maintained as experimental controls. In 1996, stands were harvested and MDC Forest Land Management Guidelines (1986) were followed. For additional information on MOFEP, including study rationale, experimental design, site conditions, inventory methods, and early findings, see Brookshire and Shifley (1997), Shifley and Brookshire (2000), and Shifley and Kabrick (2002).

Woody overstory vegetation on MOFEP was sampled via 648 circular 0.2 ha permanent plots that were randomly located throughout the study area with the constraint that each stand must have at least one plot located therein. On these 0.2 ha plots, the dbh and the species of trees with a dbh ≥11 cm were recorded. The dbh and the species of woody understory vegetation with a dbh of 4–11 cm was sampled on four 0.02 ha subplots nested within each 0.2 ha plot. A stratified random sample of eighty-eight 0.02 ha understory subplots (17 clearcut, 23 thinned, 16 harvested with single-tree selection, 8 in group openings, and 24 in stands that were not harvested), equally allocated to exposed and protected backslopes, received measurements additional to those described above. Due to the random determination of plot locations, the proportion of a subplot occupied by a group opening or single-tree gap varied. At the 88 subplots, the species, dbh, and total height were recorded for all stems ≥1 m in 1999 (3 years after treatment) and again in 2004 (8 years after treatment). Other variables, including the apparent origin of stems (seed or sprout), were recorded but these largely categorical data were not included in the analyses that follow.

Given the number of species included in this dataset, some species were grouped for analyses at the genera or subgenera level. All species, genera, or subgenera that had ≥100 trees in the dataset were included in our analyses. The nine species groups used in this study were as follows: red oaks (*Quercus rubra* L., *Q. velutina* Lam., *Q. coccinea* Münchh., *Q. marilandica* Münchh.), white oaks (*Q. alba* L., *Q. stellata* Wangenh., *Q. muehlenbergii* Engelm.), hickories (*Carya tomentosa* (Lam. ex Poir.) Nutt., *C. glabra* (Mill.) Sweet, *C. ovata* (Mill.) K. Koch., *C. texana* Buckley, *C. cordiformis* (Wangenh.) K. Koch.), sassafras (*Sassafras albidum* (Nutt.) Nees), blackgum (*Nyssa sylvatica* Marshall), dogwood (*Cornus florida* L.), red maple (*Acer rubrum* L.), ashes (*Fraxinus americana* L., *F. pennsylvanica* Marsh.), and elms (*Ulmus alata* Michx., *U. rubra* Muhl., *U. americana* L.). Within the red oaks group, *Q. velutina* (75%) and *Q. coccinea* (23%) were the most common species. *Quercus alba* (86%) and *Q. stellata* (12%) were the most common species in the white oaks group. *Carya texana* (45%), *C. tomentosa* (34%), and *C. glabra* (20%) were the major components of the hickories group. *Fraxinus americana* (94%) was the most common species in the ashes group, and *U. alata* (58%) and *U. rubra* (34%) were the most common elm species.

The response variable analyzed in this study was periodic annual height increment (PAI_{HT}) of saplings (trees >1 m tall, ≤5 cm dbh). PAI_{HT} was calculated as the mean annual height increment between the 1999 and 2004 measurements. Only stems that were alive at both measurement intervals and had a $PAI_{HT} \geq 0$ were included in our analyses. The random location of the study plots and the variability in post-treatment overstory densities offered a gradient to estimate the effects of overstory density on sapling PAI_{HT} (Table 1; Fig. 1). PAI_{HT} was calculated from the trees within the 0.02 ha understory subplots, whereas overstory density (basal area per hectare of stems ≥11.5 cm dbh) was calculated from the 0.2 ha overstory plot that each understory subplot was nested within. Although overstory basal area is an imperfect descriptor of stand density, it is widely used in silvicultural prescriptions because it is simple to measure. Overstory basal area is strongly correlated with canopy openness in the Missouri Ozarks (Blizzard et al. 2013) and has proven to be a useful indicator of the competitive pressure exerted by overstory trees in other locales (Biging and Dobbertin 1995; Lorimer 1983).

Plots of PAI_{HT} vs overstory basal area suggested that there was an exponential decline in growth with increasing overstory basal area (Fig. 1). Eight variants of a negative exponential function were used as candidate models to describe this relationship (Table 2). Model I was a basic negative exponential model with only an intercept (a) and decay parameter (b) used to estimate the reduction in sapling growth (PAI_{HT}) as a function of increasing overstory basal area (x_1). It was expected that site differences between exposed and protected backslopes would impact sapling growth, thus models II, III, and IV incorporated site effects in different ways. Model II posits that site differences have the greatest influence on sapling growth in the absence of overstory competition and includes a parameter (s_1) and indicator variable (x_2) for site class (0 for exposed backslopes, 1 for protected backslopes) with the intercept parameter of the basic model. Model III posits that site differences have the greatest influence on the rate that sapling growth declines with increasing overstory competition and includes a parameter (s_2) and indicator variable (x_2) for site class with the decay parameter of the basic model. Model IV posits that site differences influence growth through both of the mechanisms described in models II and III and, therefore, includes site parameters and indicator variables with both the intercept and decay parameters of the basic model.

Table 1. Mean initial conditions of the 5-year measurement period.

Management regime	Harvest type	*n*	Overstory density		Saplings	
			Trees per hectare	Basal area ($m^2 \cdot ha^{-1}$)	Trees per hectare	Initial height (m)
Even-aged	Clearcut	17	36.8 (15.5)	2.2 (0.8)	10 635.8 (676.6)	1.6 (0.1)
	Thinned	23	324.1 (15.2)	14.0 (0.6)	2 276.5 (234.1)	2.2 (0.3)
Uneven-aged	Single-tree	16	299.8 (16.6)	15.0 (0.9)	2 476.2 (331.5)	2.1 (0.2)
	Group opening	8	233.4 (25.7)	12.1 (1.3)	2 914.6 (329.4)	1.9 (0.2)
None	No-harvest	24	366.8 (18.7)	21.0 (0.7)	2 511.2 (373.4)	2.6 (0.3)

Note: The number of subplots in each harvest type is denoted by *n*. Sapling (>1 m height, ≤5 cm dbh) characteristics were calculated from 88 subplots (0.02 ha). Overstory density (≥11.5 cm dbh) characteristics were calculated from the overstory plots (0.2 ha) that each subplot was nested within. Values in parentheses are standard errors. Harvest treatments were implemented in 1996; the measurement period analyzed in this study began in 1999 and ended in 2004. The initial conditions described in this table are from the measurements taken in 1999.

Fig. 1. Periodic annual height increment ($m \cdot year^{-1}$) of saplings along a gradient of overstory density (residual basal area; $m^2 \cdot ha^{-1}$).

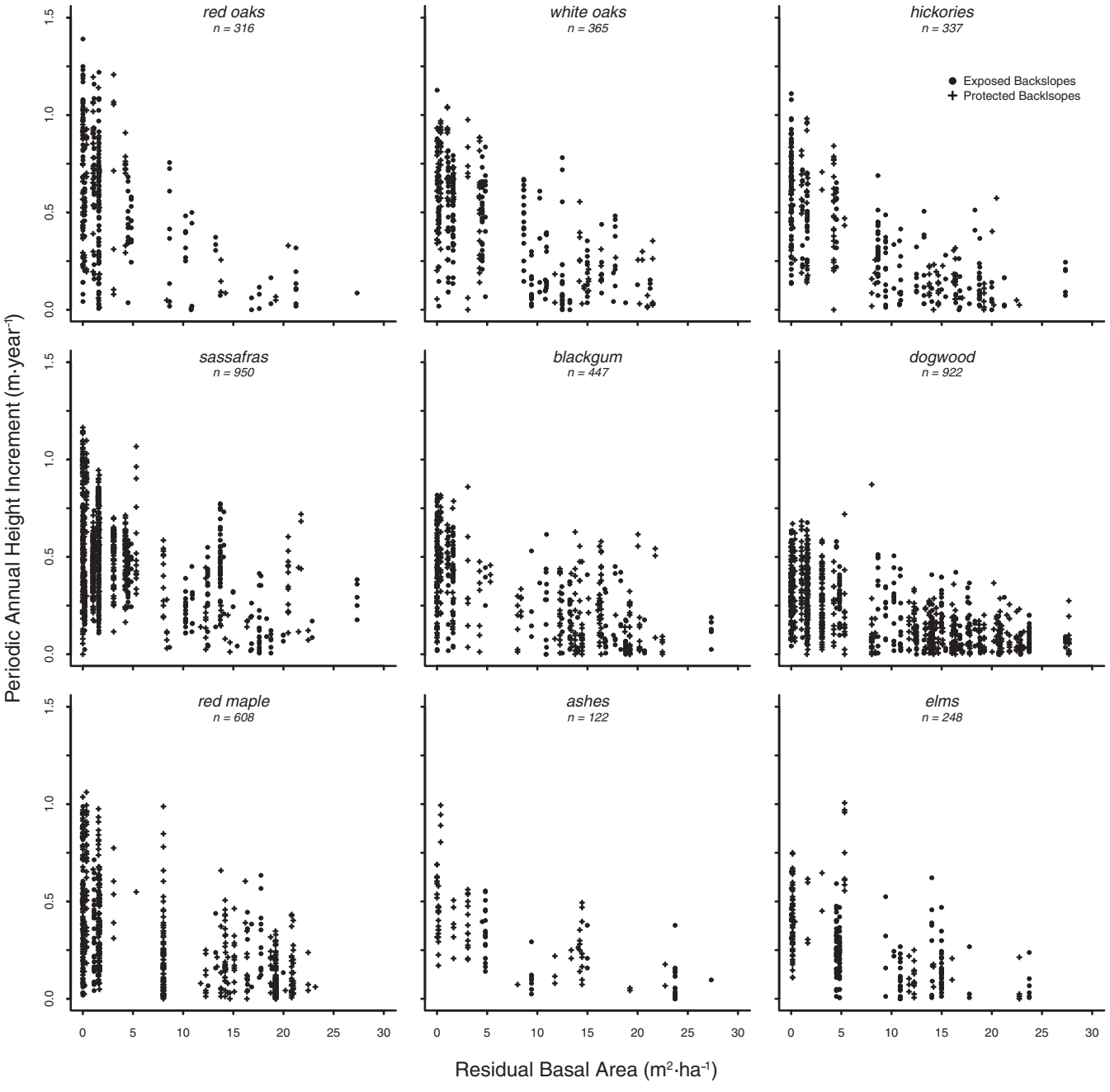


Table 2. Candidate models for estimating PAI_{HT} of saplings as a function of residual overstory density and other covariates.

Model	df	Form
I	3	$PAI_{HT} = ae^{x_1/b}$
i	4	$PAI_{HT} = [ae^{x_1/b}]x_3^{\theta}$
II	4	$PAI_{HT} = (a + s_1x_2)e^{x_1/b}$
ii	5	$PAI_{HT} = [(a + s_1x_2)e^{x_1/b}]x_3^{\theta}$
III	4	$PAI_{HT} = ae^{x_1/(b+s_2x_2)}$
iii	5	$PAI_{HT} = [ae^{x_1/(b+s_2x_2)}]x_3^{\theta}$
IV	5	$PAI_{HT} = (a + s_1x_2)e^{x_1/(b+s_2x_2)}$
iv	6	$PAI_{HT} = [(a + s_1x_2)e^{x_1/(b+s_2x_2)}]x_3^{\theta}$

Note: The parameters estimated from the data are as follows: x_1, overstory basal area ($m^2 \cdot ha^{-1}$); x_2, site class (0 if exposed backslopes, 1 if protected backslopes); x_3, initial sapling height (m); a, intercept; b, decay; s_1, site class modifier to intercept; s_2, site class modifier to decay; θ, initial sapling height modifier. Parameter estimates for the mean were fit using GNLS with the variance modeled as a power function of the conditional mean and a compound symmetric error correlation structure. These additional parameters are not included in the reported degrees of freedom (df). Parameter estimates for the near maxima were fit using nonlinear quantile regression, which does not account for variance heterogeneity or error correlation.

There was evidence of a nonlinear relationship between the initial sapling height and the PAI_{HT} in this dataset. Although there is clear biological precedent for such a relationship (Weiner and Thomas 2001), differences in sapling establishment dates between clear-cut subplots and partial- or no-harvest subplots also likely contributed to perceived "size" effects on PAI_{HT}. At the beginning of the study period, the maximum initial height of saplings in the clear-cut subplots, which were 3 years after harvest at the start of the study period, was about 4.5 m. Saplings in the partial- and no-harvest subplots may have established several years earlier than the study period and, therefore, had a broader range of initial heights. Models of periodic growth (absolute or relative) that do not appropriately account for initial size may be subject to bias (MacFarlane and Kobe 2006). Thus, the effect of initial height was parameterized by adding an initial height covariate (x_3) and exponent (θ) parameter (Pacala et al. 1994; MacFarlane and Kobe 2006) to all models described above, resulting in models *i*, *ii*, *iii*, and *iv* listed in Table 2.

Parameter estimates for mean PAI_{HT} were obtained via the generalized nonlinear least squares (GNLS) function within the NLME package (Pinheiro et al. 2011) in R version 2.13.0 (R Core Team 2013). GNLS extend nonlinear regression by allowing for correlated errors and (or) nonconstant variance (Pinheiro and Bates 2000). In this dataset, variance was clearly nonconstant and was modeled as a power function of the conditional mean. The data were structured as repeated measurements (trees) in space (subplot), making it likely that trees on the same subplot had correlated errors. Thus, a compound symmetric covariance structure was incorporated to account for within-subplot error correlation.

Nonlinear quantile regression (Koenker 2005) was used to model the near maxima of the growth–resource distributions in this study (Cade and Noon 2003). Quantile regression allows for the estimation of conditional quantiles (e.g., 25th, 50th, 75th, etc.) instead of the conditional mean of a response variable as a function of covariates (Koenker 2005). The maximum quantile that can be precisely estimated varies with sample size and data distribution; thus, estimates of the absolute maxima (e.g., 99th quantile) may not be reliable without very large samples due to potential for bias from measurement error and other sources (Cade et al. 1999). To avoid limitations due to sample size, the 90th quantile was chosen to represent the near-maxima of the growth–resource distributions ($PAI_{HT\text{-}Q90}$). Parameter estimates for the quantile regression analyses were obtained via the nonlinear quantile regression function within the QUANTREG package (Koenker 2012) in R version 2.13.0 (R Core Team 2013).

The candidate models were compared using Akaike's information criterion corrected for small sample sizes (AIC_c) (Burnham and Anderson 1998). For a species group, the model with the lowest AIC_c value was selected as the "best" model among all those considered (Burnham and Anderson 1998). Goodness-of-fit for the best models was calculated using the square of Pearson's correlation coefficient (r^2) of predicted values against observed values. Paired bootstrapping (2000 iterations, percentile method) was used to construct pointwise 95% confidence bands (Harrell 2001) for the best models of both mean and near-maximum PAI_{HT}. These confidence bands were used for visual statistical inference among groups. Nonoverlapping confidence bands indicate statistical differences among groups at a significance level of $\alpha \leq 0.05$, although statistical differences may also exist where confidence bands overlap slightly.

Results

The best models (according to the lowest AIC_c value) explained between 28% and 55% of the variation in mean PAI_{HT} (r^2, Table 3). Initial sapling height was a significant predictor of mean PAI_{HT} for all species groups. There was considerable uncertainty in parameter estimates for some species, particularly for the parameters associated with site productivity. The best models of mean PAI_{HT} for all species groups included one or more parameter(s) to account for differences between the exposed and protected backslopes. Sassafras, blackgum, red maple, and elms were best represented by model *iv*, which included a site modifier for both the intercept and decay parameters. Red oaks, white oaks, hickories, and dogwood were best represented by model *ii*, which included a site modifier for only the intercept parameter. Ashes were best represented by model *iii* which included a site modifier for the decay parameter only.

The parameter estimate for initial sapling height (θ) varied among species (Table 3). For all species, θ was positive but <1, which indicated that larger stems had an advantage over smaller stems (Fig. 2), but the magnitude per unit size diminished with increasing size (MacFarlane and Kobe 2006). The growth advantage exhibited by larger saplings was greatest at low overstory densities and diminished considerably with increasing overstory density (Fig. 2).

The mean PAI_{HT} of saplings decreased with increasing overstory density for all species groups (Fig. 3). As overstory density increased, decreases in mean PAI_{HT} were similar among most species except for sassafras and red maple on exposed backslopes, which declined less in growth rate than the other species. Few changes in rank occurred among species as mean PAI_{HT} converged with increasing overstory density. The range of separation in mean PAI_{HT} among all species groups was about 50 $cm \cdot year^{-1}$ with no residual overstory and was reduced to about 25 $cm \cdot year^{-1}$ at the highest densities in this study (30 $m^2 \cdot ha^{-1}$). There was evidence of differentiation among species groups in mean PAI_{HT} at the lowest levels of overstory density and on exposed backslopes, particularly for those that occupied different strata in mature forests in the Missouri Ozarks. Oaks exhibited an advantage over many species at low overstory densities, but the advantage decreased with an increasing overstory density.

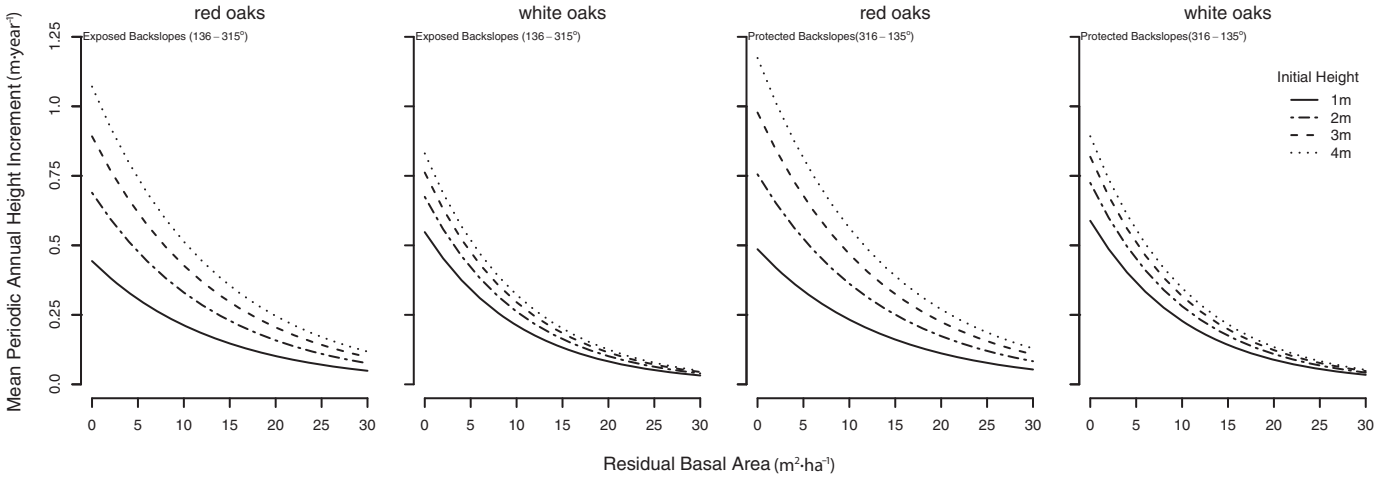
In general, mean PAI_{HT} was somewhat greater on protected backslopes than on exposed backslopes for most species groups (Fig. 2). However, the increases in mean PAI_{HT} related to slope aspect were only statistically significant for sassafras (s_1, Table 3). Red maple and elms exhibited considerable but nominal increases in mean PAI_{HT} at low overstory densities as site quality increased. In contrast, blackgum and dogwood were much less competitive on

Table 3. Parameter estimates for best models of mean PAI_{HT} of saplings as a function of overstory density and other covariates.

Species	*N*/*n*	Model	*a*	*b*	s_1	s_2	θ	Power	Rho	RSE	r^2	Akaike weights
Red oaks	320/35	*ii*	0.443 (0.03)	−13.591 (1.70)	**0.043 (0.03)**	—	0.636 (0.08)	0.492	**0.039**	0.343	0.39	0.60
White oaks	365/48	*ii*	0.547 (0.05)	−10.552 (1.12)	**0.041 (0.05)**	—	0.301 (0.07)	0.141	0.217	0.227	0.46	0.59
Hickories	343/61	*ii*	0.497 (0.08)	−12.198 (1.74)	**0.096 (0.09)**	—	0.169 (0.08)	0.612	0.514	0.459	0.48	0.33
Sassafras	968/58	*iv*	0.446 (0.06)	−21.762 (6.33)	0.176 (0.08)	**6.922 (7.14)**	0.109 (0.04)	0.032	0.608	0.199	0.26	0.57
Blackgum	455/62	*iv*	0.422 (0.05)	−12.612 (1.81)	**−0.062 (0.06)**	**−6.964 (3.83)**	0.392 (0.08)	0.369	0.213	0.274	0.42	0.93
Dogwood	455/81	*ii*	0.347 (0.03)	−12.418 (0.85)	−0.054 (0.02)	—	0.339 (0.06)	0.588	0.162	0.325	0.41	0.54
Red maple	646/44	*iv*	0.289 (0.06)	−29.076 (13.15)	**0.133 (0.07)**	**15.921 (13.24)**	0.409 (0.06)	0.742	0.205	0.472	0.38	0.99
Ashes	122/20	*iii*	0.414 (0.05)	−13.493 (3.11)	—	**−2.060 (4.43)**	0.397 (0.13)	0.346	0.387	0.223	0.55	0.65
Elms	249/24	*iv*	0.351 (0.09)	−16.767 (6.61)	**0.158 (0.12)**	**5.496 (7.25)**	0.169 (0.08)	0.461	0.411	0.297	0.34	0.74

Note: *N*/*n* is the total number of trees in the understory subplots and total number of overstory plots in which a species was measured, respectively. The model listed is the best model for a species, according to the AIC_c value found from the candidate models described in Table 2. The model parameters estimated from the data are as follows: *a*, intercept; *b*, decay; s_1, site class modifier to intercept; s_2, site class modifier to decay; θ, initial sapling height modifier. Parameter estimates were fit using GNLS with the variance modeled as a power function of the conditional mean (power) and a compound symmetric error correlation structure at the overstory plot level (rho). RSE is the residual standard error of the model. Goodness-of-fit was assessed using the square of Pearson's correlation coefficient (r^2) of predicted values against observed values. The Akaike weights indicate the proportional weight of evidence for the best model relative to the other candidate models in Table 2. Values in parentheses are standard errors. Bold text indicates parameters included in a model that were not statistically significant (α = 0.05).

Fig. 2. Impact of initial height on sapling mean periodic annual height increment (m·year^{-1}) for red and white oaks along a gradient of overstory density (residual basal area; m^2·ha^{-1}). Graphs are shown for exposed backslopes (left two graphs) and protected backslopes (right two graphs).



protected backslopes, particularly at low overstory densities. According to the site parameter estimates, mean PAI_{HT} for blackgum and dogwood was lower (nominally for blackgum) on protected than exposed backslopes, but the rank changes across site classes was driven more by greater mean PAI_{HT} for sassafras, red maple, and elm than by lower mean PAI_{HT} for blackgum and dogwood (s_1, Table 3). Ashes and blackgum exhibited nominally lower reductions in mean PAI_{HT} as the overstory density increased on protected backslopes than on exposed backslopes (s_2, Table 3). Hickories exhibited modest but nominal increases in mean PAI_{HT} at low overstory densities on protected backslopes. Both red oaks and white oaks exhibited only slight nominal increases in mean PAI_{HT} at low overstory densities on protected backslopes.

The best models of near-maximum growth rates using $PAI_{HT\text{-}Q90}$ were more parsimonious than the models of mean PAI_{HT} (Table 4). Except for sassafras, the best model of $PAI_{HT\text{-}Q90}$ was model I, which included only the intercept and scale parameters. The best model for sassafras (model II) included a site modifier for the intercept. The interval estimates for the decay parameter (*b*, Table 4) largely overlapped across species groups and provided little evidence of species segregating into distinct tolerance classes related to growth decline at the sapling stage. The $PAI_{HT\text{-}Q90}$ of most species was reduced by half [ln(2)·*b*] between 10 m^2·ha^{-1} and 15 m^2·ha^{-1}. Sassafras exhibited the greatest tolerance in growth to overstory density, reducing in growth by half at about 28 m^2·ha^{-1}.

Quantile regression analyses of $PAI_{HT\text{-}Q90}$ provided evidence of greater interspecific differentiation in sapling growth than was suggested by mean PAI_{HT}. Among species groups in this study, $PAI_{HT\text{-}Q90}$ suggested a four-tiered growth hierarchy at low overstory densities. Red oaks were the fastest growing species and exhibited significantly greater growth than all other species in the absence of an overstory (Fig. 4). The difference in $PAI_{HT\text{-}Q90}$ between red oaks and the second tier, which included white oaks, hickories, red maple, and sassafras (protected aspects), was approximately 15 cm·year^{-1}. Red oaks were able to maintain a statistical advantage over the second tier only when overstory densities were <~5 m^2·ha^{-1}. At low overstory densities, $PAI_{HT\text{-}Q90}$ for red oaks was approximately 40 cm·year^{-1} greater than blackgum, ashes, elms, and sassafras (exposed aspects), which comprised the third tier of growth. Red oaks were statistically indistinguishable from the third tier once overstory density reached about 10 m^2·ha^{-1}. The difference in $PAI_{HT\text{-}Q90}$ between red oak and dogwood (fourth tier) was greatest in the absence of an overstory (≈50 cm·year^{-1}), but the difference decreased as overstory density increased and was only statistically significant below about 18 m^2·ha^{-1}.

$PAI_{HT\text{-}Q90}$ was significantly greater (≈15 cm·year^{-1}) for the second tier than for the third tier without a residual overstory, but the two tiers were largely indistinguishable once overstory density exceeded about 5 m^2·ha^{-1}. $PAI_{HT\text{-}Q90}$ was significantly lower for dogwood than for all other species when overstory density was

Fig. 3. Mean regression curves and confidence bands for sapling periodic annual height increment (m·year^{-1}) along a gradient of overstory density (residual basal area; m^2·ha^{-1}) for both exposed and protected backslopes. Figure adjusted to represent an initial sapling height of 2 m, which was approximately average across the study. Regression curves are depicted for hickories, sassafras, red maple, and ashes. Confidence bands are depicted for red oaks, white oaks, blackgum, elms, and dogwood. Nonoverlapping confidence bands indicate differences among groups at a significance level $\alpha \leq 0.05$. Statistically significant differences among groups may also exist in areas where their confidence bands slightly overlap.

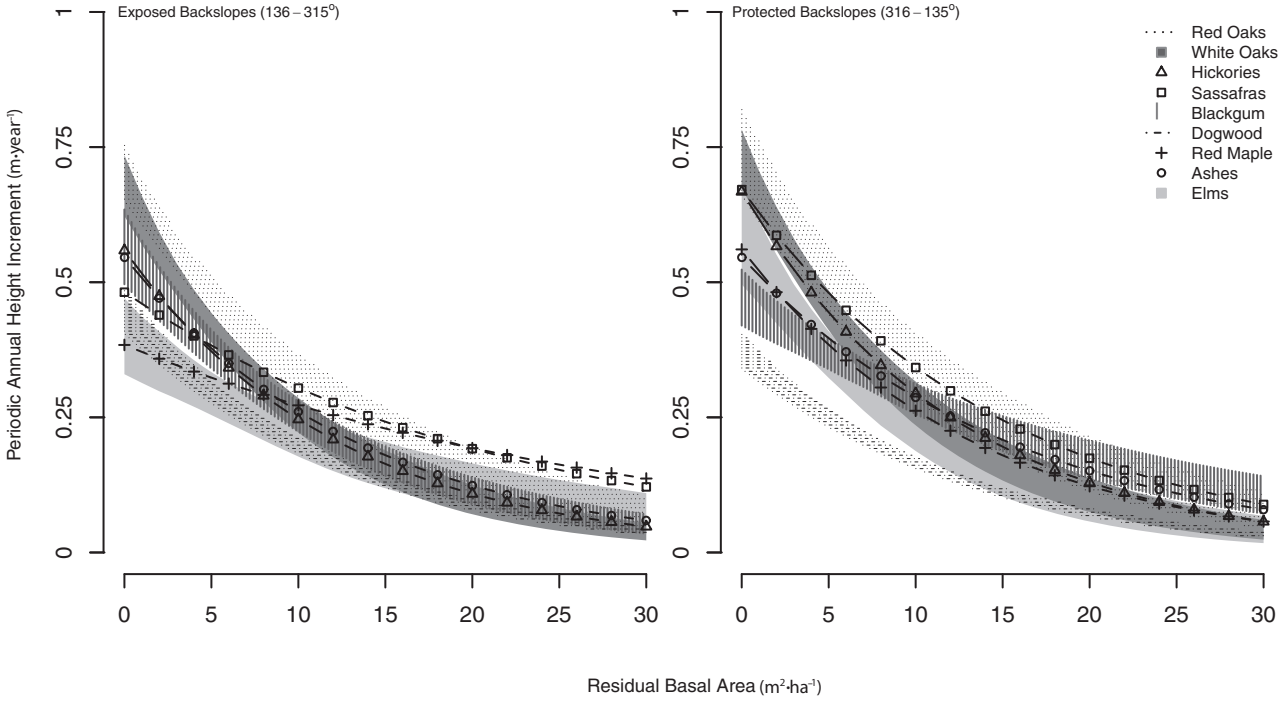


Table 4. Parameter estimates for best models of $PAI_{HT\text{-}Q90}$ of saplings.

		a		*b*		s_1		
Species	Model	Mean (SE)	CI	Mean (SE)	CI	Mean (SE)	CI	Akaike weights
Red oaks	I	1.066 (0.04)	1.00, 1.16	−14.371 (2.02)	−18.13, −11.29	—		0.29
White oaks	I	0.907 (0.03)	0.85, 0.96	−22.282 (2.82)	−27.67, −16.75	—		0.34
Hickories	I	0.878 (0.03)	0.84, 0.91	−15.315 (1.70)	−18.93, −13.23	—		0.41
Sassafras	II	0.658 (0.01)	0.63, 0.69	−40.927 (5.77)	−54.3, −30.45	0.271 (0.02)	0.21, 0.31	0.38
Blackgum	I	0.707 (0.02)	0.68, 0.74	−26.117 (2.92)	−35.59, −21.82	—		0.36
Dogwood	I	0.567 (0.01)	0.54, 0.58	−18.488 (1.05)	−21.12, −16.44	—		0.39
Red maple	I	0.859 (0.02)	0.82, 0.89	−18.195 (1.32)	−20.49, −15.23	—		0.31
Ashes	I	0.646 (0.08)	0.60, 0.91	−20.826 (6.01)	−39.53, −13.08	—		0.39
Elms	I	0.657 (0.02)	0.60, 0.72	−20.227 (3.91)	−28.34, −14.85	—		0.41

Note: The model listed is the best model for a species selected by the AIC_c value found from the candidate models described in Table 2. The model parameters estimated from the data are as follows: *a*, intercept; *b*, decay; s_1, site class modifier to intercept. Parameter estimates were fit using nonlinear quantile regression of 0.9 conditional quantile of the response distribution. The Akaike weights indicate the proportional weight of evidence for the best model relative to the other candidate models in Table 2. SE estimates are from the nonlinear quantile regression. CI values are bootstrapped confidence intervals for parameter estimates ($\alpha = 0.05$). All parameters were statistically significant.

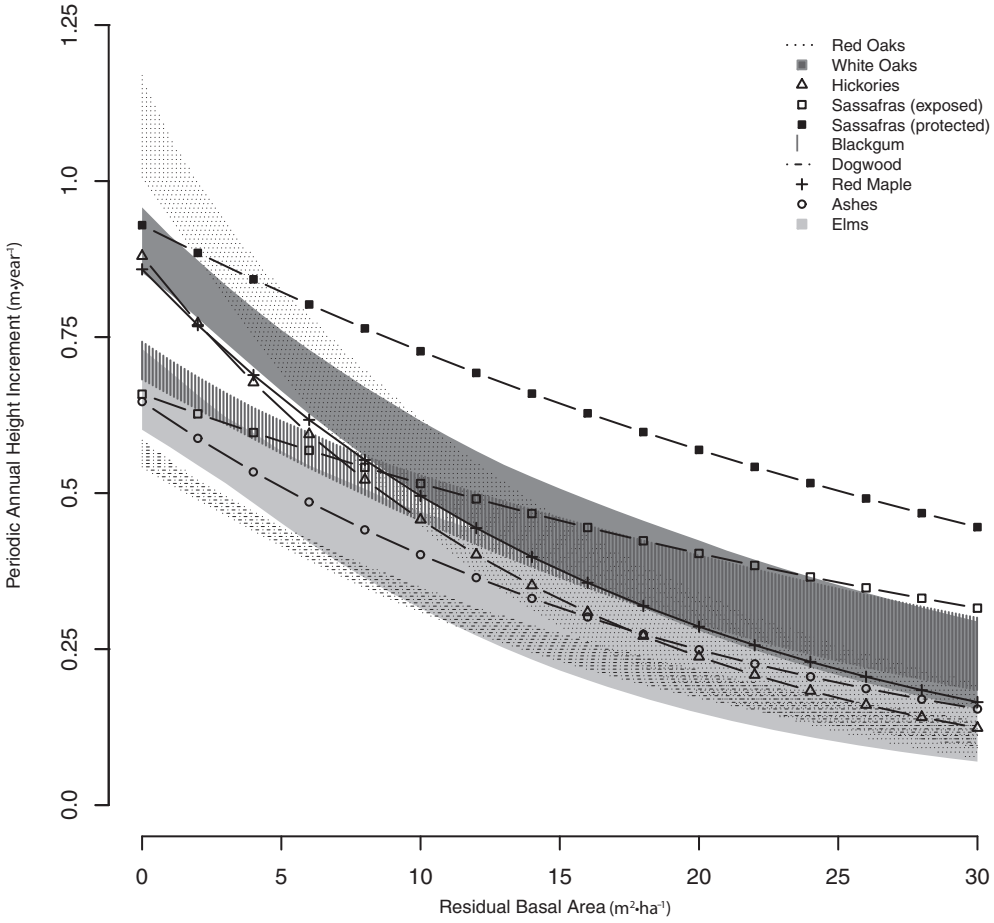
less than about 5 m^2·ha^{-1}. Beyond that threshold, dogwood and elms were statistically indistinguishable, and at overstory densities greater than about 20 m^2·ha^{-1}, dogwood was only significantly different from sassafras, blackgum, and white oak.

Discussion

The influence of overstory density on recruitment is a critical component of community dynamics (Oliver and Larson 1996). We found that the method of statistical analysis was an important factor in quantifying and interpreting these dynamics. By placing greater emphasis on saplings with the best intraspecific growth rates, quantile regression analyses of $PAI_{HT\text{-}Q90}$ provided evidence of greater interspecific differentiation in sapling growth than was suggested by mean PAI_{HT}. Moreover, AIC_c scores ranked the basic negative exponential models for $PAI_{HT\text{-}Q90}$ better than the more complex models using quantile regression. In contrast, AIC_c scores ranked the more complex models better for the mean, supporting the notion that the maxima of growth–resource distributions provide more ecologically meaningful estimates of the effect of a single limiting factor in the presence of multiple limiting factors (Cade et al. 1999; Cade and Guo 2000). Growth differentiation is often difficult to quantify with traditional statistical procedures (e.g., Oliver et al. 2005); our results support the use of quantile regression to quantify a more meaningful response by targeting the population of above-average performers that are most successful.

The species analyzed in this study span a range of reported shade tolerance (Baker 1949; Burns and Honkala 1990; Niinemets

Fig. 4. Quantile regression curves and confidence bands for the 90th quantile of sapling periodic annual height increment (m·year^{-1}) along a gradient of overstory density (residual basal area; m^2·ha^{-1}). Regression curves are depicted for hickories, sassafras, red maple, and ashes. Confidence bands are depicted for red oaks, white oaks, blackgum, elms, and dogwood. Nonoverlapping confidence bands indicate differences among groups at a significance level $\alpha \leq 0.05$. Statistically significant differences among groups may also exist in areas where their confidence bands slightly overlap.



and Valladares 2006). The growth of all species declined as the overstory density increased, and the rate of decline differed among some species (parameter *b*, Table 4). Thus, there was some evidence of rank changes among species in the magnitude of growth along the gradient of overstory density analyzed in this study (Fig. 4). We found that the overstory density affected the growth of sassafras the least. In fact, the overstory density at which growth was reduced by half for sassafras was almost double that of all other species (Table 4). Moreover, the magnitude of growth for sassafras became greater than most other species as overstory density increased, especially on protected backslopes (Fig. 4). Although sassafras is generally considered intolerant of shade, Bazzaz et al. (1972) reported that sassafras was able to photosynthesize efficiently at low light intensities. However, reliable recruitment of sassafras via small openings in the canopy of mature forests in the Missouri Ozarks has not been reported.

Interpreting the observed differences among species in the magnitude of growth, albeit statistically significant, as ecologically meaningful may be premature. We do not yet know if there are threshold rates of growth for a species to successfully recruit into the canopy or how such thresholds might vary with ontogeny or other factors such as site, overstory composition and structure, and disturbance regime (Poorter et al. 2005; Wright et al. 2000). Nonetheless, canopy recruitment is a process rather than an event; thus, the cumulative effects of even minor sustained advantages could prove influential.

Previous studies in the Missouri Ozarks have suggested that interspecific differences in reproduction abundance are related to site quality and residual overstory density (Green 2008; Kabrick et al. 2008*b*; Larsen et al. 1997). Our results showed that species also exhibited differentiated growth rates during the sapling stage and that differences were most pronounced at relatively low overstory densities (<10 m^2·ha^{-1}). Residual overstory densities >5 m^2·ha^{-1} eliminated the growth advantage of red oaks over white oaks. In the Missouri Ozarks, susceptibility to episodic red oak decline events may be a catalyst for foresters to favor white oaks over red oaks (Shifley et al. 2006; Kabrick et al. 2008*a*). Our results suggest that there is potential for partial harvesting methods to reach such an objective. However, the growth advantage exhibited by white oaks over competing species also decreased with increasing overstory density. White oaks had little to no advantage in height growth over many competing species when the overstory density exceeded about 10 m^2·ha^{-1}. Moreover, the sprouting probabilities and subsequent growth rates of oaks have also been reported to decrease with increasing overstory density (Dey et al. 2008; Atwood et al. 2009). This implies that the probability of recruitment under overstory densities greater than about 10 m^2·ha^{-1} is likely to decline for all oaks in the Missouri Ozarks, which is consistent with the residual overstory densities recommended to sustain oak recruitment by Larsen et al. (1997, 1999). Oliver et al. (2005) reported similar recruitment dynamics with increasing overstory density in the bottomland forests of the southern United States, but the

threshold densities recommended for oak recruitment were lower.

Many of the species analyzed in this study rarely (ashes, blackgum, elms, red maple, sassafras) or never (dogwood) attain overstory stature in the mature forests of the Missouri Ozarks (Burns and Honkala 1990; Johnson et al. 2009). However, these species groups are often among the most abundant members of the seedling and sapling layer during stand development (Dey 1991; Johnson et al. 2009; Schlesinger et al. 1993). Because of this, these common associates in oak–hickory forests play an influential, albeit temporally constrained, role in the canopy recruitment process by limiting spatial opportunities for recruitment and delaying or, perhaps, eliminating the release of neighboring oaks and hickories from the sapling strata by exhibiting increasingly comparable growth under increasing overstory density. The temporal importance of this limiting influence is likely more constrained in the Missouri Ozarks than in the more mesic parts of the eastern United States, where many of the competing species that we analyzed and several others have greater potential to reach the overstory and are a more lasting source of competition (Atwood et al. 2011; Loftis 1990*b*; Nowacki and Abrams 2008; Oliver et al. 2005; Schuler 2004). As increasing overstory density progressively reduces both sapling abundance and differences in growth rates, repeated disturbance, stochasticity, and differentiation along other gradients may become more important determinants of recruitment success (Beckage and Clark 2003; Grubb 1977). In general, oaks and hickories are thought to predominately utilize persistence strategies for regeneration and recruitment and exhibit various degrees of tolerance to both drought and fire (Arthur et al. 2012; Brose et al. 2013; Burns and Honkala 1990). The ability to persist in temporarily unfavorable conditions via dieback, vegetative reproduction, and seedling storage increases longevity (Bond and Midgley 2003; Warner and Chesson 1985). It is likely that differential mortality plays an important role in recruitment dynamics (Coates 2002; Pacala et al. 1996; Wright et al. 1998). Given the relatively xeric conditions of the Missouri Ozarks, differences in mortality rates among species may provide additional opportunities for differentiation during the sapling stage; however, this is an area in need of quantitative research.

Undoubtedly, other factors, in addition to overstory density, affect sapling growth as evidenced by the spread of response in Fig. 1. One likely source of the variation in growth that we observed was an inability of the overstory metric used in this study to capture the spatial heterogeneity of resource availability. Varying spatial arrangement while maintaining the same stand-level basal area can substantially alter competitive neighborhoods and influence regeneration and other ecosystem processes (Boyden et al. 2012; Palik et al. 2003). The models of mean PAI_{HT} suggest that another source of the observed variation in growth was site quality. Despite many nonsignificant site parameters (Table 3), models of mean PAI_{HT} that included site differences were ranked better by AIC_c for all species groups. It is possible that the nonsignificance of site parameters was due to inherent variation, model misspecification, and (or) the coarse-scaled site delineation used in these analyses. Another possible explanation is the limited observation period of this study, although greenhouse studies have found site effects on tree seedling growth after a single growing season (Latham 1992).

The influence of site was greatest for the four species that were best described by model *iv*. We observed a relatively large increase in growth on protected backslopes compared with exposed backslopes for sassafras, red maple, and elms in this study. This is consistent with several other studies that reported an increased importance of these species on more productive sites (e.g., Kabrick et al. 2008*b*; Schlesinger et al. 1993). However, the increase in mean PAI_{HT} from exposed to protected backslopes was accompanied by nominal increases in the rate that growth declined with increasing overstory density (s_2, Table 3). This suggests that growth and (or) tolerance trade-offs may exist for these species (Kaelke et al. 2001; Niinemets and Valladares 2006; Walters and Reich 2000) but is inconclusive because overstory composition, structural arrangement, and other potentially confounding differences among plots were not accounted for.

Increases in mean PAI_{HT} from exposed to protected backslopes were expected and observed (sometimes nominally) for most species but not all (s_1, Table 3). Blackgum showed evidence of having reduced growth at better sites with low overstory densities but had a nominal reduction in the rate that growth declined with increasing overstory density. This is consistent with Abrams' (2007) suggestion that blackgum should be most successful in xeric upland forests. There, the disadvantages of relatively slow inherent growth rates may be somewhat mitigated by considerable stress tolerance and a reduction in the number and competitive capacity of associated species (Abrams 2007). Our results suggest that the species that were best described by model *iii* (oaks, hickories, and dogwood) were also influenced by differences in site class; however, the relationship between site class and overstory density on mean PAI_{HT} was not as dynamic as the species described by model *iv*. Mean PAI_{HT} of oaks and hickories at low overstory densities was nominally greater on protected backslopes than on exposed backslopes. However, we observed a significant reduction in mean PAI_{HT} on protected backslopes compared with exposed backslopes for dogwood. Given the reported shade tolerance and drought intolerance of this understory species (Horn 1985; McLemore 1990), this result was not expected.

It has long been known that a seedling bank of large advance reproduction is often vital to successful canopy recruitment of oaks due to the inherently slow growth of seedlings that lack well-developed root systems (Johnson et al. 2009). Due to frequent dieback and resprouting of upland oaks, root-collar diameter is a better predictor of root biomass than height (Knapp et al. 2006). Nonetheless, we found that initially taller oak saplings exhibited a growth advantage in mean PAI_{HT} over shorter saplings (Fig. 2). The magnitude of the initial height effect on mean PAI_{HT} was much more pronounced for red oaks ($\theta = 0.64$, Table 3) than for white oaks ($\theta = 0.30$, Table 3), which is consistent with previous estimates of the relative impact of size on reproduction growth among oak species (Dey 1991). In fact, an initial height effect on mean PAI_{HT} was significant for all species in this study (θ, Table 3). However, the effect of size on competitive capacity under a dense overstory was limited due to the intrinsically low growth for all saplings in that setting (Fig. 2).

Our results provide insight into how overstory density manipulation alters the composition and structure of the regeneration layer in Missouri Ozark forests. This information could be valuable to foresters considering regeneration techniques that utilize partial cutting and multiple entries. Although we have not yet established longitudinal growth thresholds for successful canopy recruitment across a range of overstory density, the models of mean PAI_{HT} presented herein should provide inferences into the timing required to attain recommended size thresholds for advance reproduction prior to a planned harvest (e.g., Brose et al. 2008; Sander et al. 1984). This potentially extends the application of existing regeneration simulators (e.g., Dey et al. 1996) by providing insight into how preparatory partial harvesting might alter the structure of the regeneration layer prior to a clear-cut harvest. Of course, this potential is constrained by the species and sizes reported in this study and the inherent assumptions of existing regeneration simulators.

Conclusion

PAI_{HT} of saplings decreased within increasing overstory density for all species groups (objective *i*). Secondly, species differentiation in growth rates occurred during the sapling stage, but differences were most pronounced at lower overstory densities. We

identified thresholds in overstory densities that are related to possible shifts in species composition on certain sites in the Missouri Ozarks (objective *ii*). This information should be valuable to foresters and improve the likelihood of achieving regeneration objectives. Finally, we suggest that the near-maxima of growth–resource distributions have two potential advantages over the mean: (1) better models of the limiting effects of overstory density on sapling height growth were provided, and (2) the focus was on the growth rates of stems that were most likely to recruit into the canopy (objective *iii*). Additional research into the role of recruitment fluctuation is certainly warranted. Longitudinal monitoring of individuals in addition to populations on established studies like MOFEP will be essential to better understand the biology and ecology of forest dynamics and provide science-based management guidelines.

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References

Abrams, M.D. 2007. Tales from the blackgum, a consummate subordinate tree. Bioscience, **57**(4): 347–359. doi:10.1641/B570409.

Arthur, M.A., Alexander, H.D., Dey, D.C., Schweitzer, C.J., and Loftis, D.L. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. J. For. **110**: 257–266.

Atwood, C.J., Fox, T.R., and Loftis, D.L. 2009. Effects of alternative silviculture on stump sprouting in the southern Appalachians. For. Ecol. Manage. **257**: 1305–1313. doi:10.1016/j.foreco.2008.11.028.

Atwood, C.J., Fox, T.R., and Loftis, D.L. 2011. Effects of various silvicultural systems on regeneration in mixed hardwood stands of the southern Appalachians. J. Sust. For. **30**: 419–440. doi:10.1080/10549811.2011.541020.

Baker, F.S. 1949. A revised tolerance table. J. For. **47**: 179–181.

Bazzaz, F.A., Paape, V., and Boggess, W.R. 1972. Photosynthetic and respiratory rates of *Sassafras albidum*. For. Sci. **18**: 218–222.

Beck, D.E., and Hooper, R.M. 1986. Development of a southern Appalachian hardwood stand after clearcutting. South. J. Appl. For. **10**: 168–172.

Beckage, B., and Clark, J.S. 2003. Seedling survival and growth of three forest tree species: the role of spatial heterogeneity. Ecology, **84**(7): 1849–1861. doi:10.1890/0012-9658(2003)084[1849:SSAGOT]2.0.CO;2.

Biging, G.S., and Dobbertin, M. 1995. Evaluation of competition indices in individual tree growth models. For. Sci. **41**(2): 360–377.

Blizzard, E.M., Kabrick, J.M., Dey, D.C., Larsen, D.R., Pallardy, S.G., and Gwaze, D.P. 2013. Light, canopy closure, and overstory retention in upland Ozark forests. *In* Proceedings of the 15th Biennial Southern Silvicultural Research Conference. *Edited by* J.M. Guldin. USDA Forest Service, Southern Research Station, Asheville, North Carolina, Gen. Tech. Rep. SRS-GTR-175. pp. 73–79.

Bond, W.J., and Midgley, J.J. 2003. The evolutionary ecology of sprouting in woody plants. Int. J. Plant. Sci. **164**(S3): S103–S114. doi:10.1086/374191.

Boyden, S., Montgomery, R., Reich, P.B., and Palik, B. 2012. Seeing the forest for the heterogeneous trees: stand-scale resource distributions emerge from tree-scale structure. Ecol. Appl. **22**(5): 1578–1588. doi:10.1890/11-1469.1. PMID: 22908715.

Brookshire, B.L., and Shifley, S.R. (*Editors*). 1997. Proceedings of the Missouri Ozark Forest Ecosystem Project Symposium: An Experimental Approach to Landscape Research. 3–5 June 1997. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, Gen. Tech. Rep. NC-193.

Brose, P.H., Van Lear, D.H., and Keyser, P.D. 1999. A shelterwood-burn technique for regenerating productive upland oak sites in the Piedmont region. South. J. Appl. For. **23**: 158–163.

Brose, P.H., Gottschalk, K.W., Horsley, S.B., Knopp, P.D., Kochenderfer, J.N., McGuinness, B.J., Miller, G.W., Ristau, T.E., Stoleson, S.H., and Stout, S.L. 2008. Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic Region. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, Gen. Tech. Rep. NRS-33.

Brose, P.H., Dey, D.C., Phillips, R.J., and Waldrop, T.A. 2013. A meta-analysis of the fire-oak hypothesis: does prescribed burning promote oak reproduction in eastern North America? For. Sci. **59**(3): 322–334. doi:10.5849/forsci.12-039.

Burnham, K.P., and Anderson, D.R. 1998. Model selection and inference. A practical information-theoretic approach. Springer.

Burns, R.M., and Honkala, B.H. (*Editors*). 1990. Silvics of North America. Vol. 2. Hardwoods. USDA Forest Service Agriculture Handbook 654, Washington, D.C.

Cade, B.S., and Guo, Q. 2000. Estimating effects of constraints on plant performance with regression quantiles. Oikos, **91**: 245–254. doi:10.1034/j.1600-0706.2000.910205.x.

Cade, B.S., and Noon, B.R. 2003. A gentle introduction to quantile regression for ecologists. Front. Ecol. Environ. **1**(8): 412–420. doi:10.1890/1540-9295(2003)001[0412:AGITQR]2.0.CO;2.

Cade, B.S., Terrell, J.W., and Schroeder, R.L. 1999. Estimating effects of limiting factors with regression quantiles. Ecology, **80**(1): 311–323. doi:10.1890/0012-9658(1999)080[0311:EEOLFW]2.0.CO;2.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. **24**(2): 337–349. doi:10.1139/x94-046.

Canham, C.D., Berkowitz, A.R., Kelly, V.R., Lovett, G.M., Ollinger, S.V., and Schnurr, J. 1996. Biomass allocation and multiple resource limitation in tree seedlings. Can. J. For. Res. **26**(9): 1521–1530. doi:10.1139/x26-171.

Clark, J.S., Beckage, B., Camill, P., Cleveland, B., HilleRisLambers, J., Lichter, J., McLachlan, J., Mohan, J., and Wyckoff, P. 1999. Interpreting recruitment limitation in forests. Am. J. Bot. **86**(1): 1–16. doi:10.2307/2656950. PMID: 21680341.

Clatterbuck, W.K., and Hodges, J.D. 1988. Development of cherrybark oak and sweet gum in mixed, even-aged bottomland stands in central Mississippi, U.S.A. Can. J. For. Res. **18**(1): 12–18. doi:10.1139/x88-003.

Coates, K.D. 2002. Tree recruitment in gaps of various size, clearcuts and undisturbed mixed forest of interior British Columbia, Canada. For. Ecol. Manage. **155**: 387–398. doi:10.1016/S0378-1127(01)00574-6.

Coomes, D.A., and Grubb, P.J. 2000. Impacts of root competition in forests and woodlands: a theoretical framework and review of experiments. Ecol. Monogr. **70**(2): 171–207. doi:10.1890/0012-9615(2000)070[0171:IORCIF]2.0.CO;2.

Dey, D.C. 1991. A comprehensive Ozark regenerator. Ph.D. dissertation, University of Missouri, Columbia, Missouri.

Dey, D.C. 2014. Sustaining oak forests in eastern North America: regeneration and recruitment, the pillars of sustainability. For. Sci. [In press]. doi:10.5849/forsci.13-114.

Dey, D.C., Johnson, P.S., and Garrett, H.E. 1996. Modeling the regeneration of oak stands in the Missouri Ozark Highlands. Can. J. For. Res. **26**(4): 573–583. doi:10.1139/x26-066.

Dey, D.C., Jensen, R.G., and Wallendorf, M.J. 2008. Single-tree harvesting reduces survival and growth of oak stump sprouts in the Missouri Ozark Highlands. *In* Proceedings of the 16th Central Hardwood Forest Conference. *Edited by* D.F. Jacobs and C.H. Michler. USDA Forest Service, Northern Research Station, Newtown Square, Pennsylvania, Gen. Tech. Rep. NRS-P-24. pp. 26–37.

Fei, S., and Steiner, K.C. 2007. Evidence for increasing red maple abundance in the eastern United States. For. Sci. **53**(4): 473–477.

Givnish, T.J. 1988. Adaptation to sun and shade: a whole plant perspective. Aust. J. Plant. Physiol. **15**: 63–92. doi:10.1071/PP9880063.

Green, J.L. 2008. Overstory density and its effect on oak regeneration abundance and oak understory height growth in the Missouri Ozark Highlands. M.Sc. thesis, University of Missouri, Columbia, Missouri.

Grime, J.P. 2006. Plant strategies, vegetation processes, and ecosystem properties. John Wiley & Sons.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biol. Rev. **52**: 107–145. doi:10.1111/j.1469-185X.1977.tb01347.x.

Harrell, F.E. 2001. Regression modeling strategies with applications to linear models, logistic regression, and survival analysis. Springer.

Horn, J.C. 1985. Responses of understory tree seedlings to trenching. Am. Midl. Nat. **114**(2): 252–258. doi:10.2307/2425600.

Johnson, P.S., Shifley, S.R., and Rogers, R. 2009. The ecology and silviculture of oaks. CABI Publishing, CAB International, Wallingford, UK.

Kabrick, J.M., Meinert, D., Nigh, T., and Gorlinsky, B.J. 2000. Physical environment of the Missouri Ozark forest ecosystem project sites. *In* Missouri Ozark Forest Ecosystem Project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the landscape experiment. *Edited by* S.R. Shifley and B.L. Brookshire. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, Gen. Tech. Rep. NC-208. pp. 41–70.

Kabrick, J.M., Shifley, S.R., Jensen, R.G., Larsen, D.R., and Grabner, J.K. 2004. Oak forest composition, site quality, and dynamics in relation to site factors in the southeastern Missouri Ozarks. *In* Upland oak ecology symposium: history, current conditions, and sustainability. *Edited by* M.A. Spetich. USDA Forest Service, Southern Research Station, Asheville, North Carolina, Gen. Tech. Rep. SRS-73. pp. 94–101.

Kabrick, J.M., Dey, D.C., Jensen, R.G., and Wallendorf, M. 2008*a*. The role of environmental factors in oak decline and mortality in the Ozark Highlands. For. Ecol. Manage. **255**: 1409–1417. doi:10.1016/j.foreco.2007.10.054.

Kabrick, J.M., Zenner, E.K., Dey, D.C., Gwaze, D., and Jensen, R.G. 2008*b*. Using ecological land types to examine landscape-scale oak regeneration dynamics. For. Ecol. Manage. **255**: 3051–3062. doi:10.1016/j.foreco.2007.09.068.

Kaelke, C.M., Kruger, E.L., and Reich, P.B. 2001. Trade-offs in seedling survival,

growth, and physiology among hardwood species of contrasting successional status along a light-availability gradient. Can. J. For. Res. **31**(9): 1602–1616. doi:10.1139/x01-090.

Kaiser, M.S., Speckman, P.L., and Jones, J.R. 1994. Statistical models for limiting nutrient relations in inland waters. J. Am. Stat. Assoc. **89**: 410–423. doi:10.1080/01621459.1994.10476763.

Knapp, B.O., Wang, G.G., Van Lear, D.H., and Walker, J.L. 2006. Predicting root biomass of burned and unburned white oak advance reproduction from diameter and height. South. J. Appl. For. **30**(1): 40–45.

Kneeshaw, D.D., Kobe, R.K., Coates, K.D., and Messier, C. 2006. Sapling size influences shade tolerance ranking among southern boreal tree species. J. Ecol. **94**: 471–480. doi:10.1111/j.1365-2745.2005.01070.x.

Kobe, R.K., Pacala, S.W., Silander, J.A., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. **5**: 517–532. doi:10.2307/1942040.

Koenker, R. 2005. Quantile regression. Cambridge University Press.

Koenker, R. 2012. Quantreg: quantile regression. R package version 4.91. http://CRAN.R-project.org/package=quantreg.

Landis, R.M., and Peart, D.R. 2005. Early performance predicts canopy attainment across life histories in subalpine forest trees. Ecology, **86**(1): 63–72. doi:10.1890/03-0848.

Larsen, D.R., and Johnson, P.S. 1998. Linking the ecology of natural oak regeneration to silviculture. For. Ecol. Manage. **106**: 1–7. doi:10.1016/S0378-1127(97)00233-8.

Larsen, D.R., and Kershaw, J.A. 1996. Influence of canopy structure assumptions on predictions form Beer's law. A comparison of deterministic and stochastic simulations. Agr. For. Meteorol. **81**: 61–77.

Larsen, D.R., Metzger, M.A., and Johnson, P.S. 1997. Oak regeneration and overstory density in the Missouri Ozarks. Can. J. For. Res. **27**(6): 869–875. doi:10.1139/x97-010.

Larsen, D.R., Loewenstein, E.F., and Johnson, P.S. 1999. Sustaining recruitment of oak reproduction in uneven-aged stands in the Ozark Highlands. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, Gen. Tech. Rep. NC-203.

Latham, R.E. 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology, **73**: 2129–2144. doi:10.2307/1941461.

Law, J.R., and Lorimer, C.G. 1989. Managing uneven-aged stands. *Edited by* F.B. Clark and J.G. Hutchinson. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, Central Hardwood Note 6.08.

Loewenstein, E.F., Johnson, P.S., and Garrett, H.E. 2000. Age and diameter structure of a managed uneven-aged oak forest. Can. J. For. Res. **30**(7): 1060–1070. doi:10.1139/x00-036.

Loftis, D.L. 1990*a*. Predicting post-harvest performance of advance red oak reproduction in the southern Appalachians. For. Sci. **36**(4): 908–916.

Loftis, D.L. 1990*b*. A shelterwood method for regenerating red oak in the southern Appalachians. For. Sci. **36**(4): 917–929.

Lorimer, C.G. 1983. Tests of age-independent competition indices for individual trees in natural hardwood stands. For. Ecol. Manage. **6**: 343–360. doi:10.1016/0378-1127(83)90042-7.

MacArthur, R.H., and Wilson, E.O. 1967. The theory of island biogeography. Princeton University Press.

MacFarlane, D.W., and Kobe, R.K. 2006. Selecting models for capturing tree-size effects on growth–resource relationships. Can. J. For. Res. **36**(7): 1695–1704. doi:10.1139/x06-054.

McLemore, B.F. 1990. *Cornus florida* L. flowering dogwood. *In* Silvics of North America. Vol. 2. Hardwoods. *Edited by* R.M. Burns and B.H. Honkala. USDA Forest Service Agriculture Handbook 654, Washington, D.C.

McQuilkin, R.A. 1974. Site index prediction tables for black, scarlet, and white oaks in southeastern Missouri. USDA Forest Service, North Central Forest Experimental Station, St. Paul, Minnisota, Res. Pap. NC-108.

Messier, C., Doucet, R., Ruel, J.-C., Claveau, Y., Kelly, C., and Lechowicz, M.J. 1999. Functional ecology of advance regeneration in relation to light in boreal forests. Can. J. For. Res. **29**(6): 812–823. doi:10.1139/x99-070.

Missouri Department of Conservation. 1986. Forest land management guidelines. Missouri Department of Conservation, Jefferson City, Missouri.

Nigh, T., Buck, C., Grabner, J., Kabrick, J., and Meinert, D. 2000. Ecological classification system for the Current River Hills subsection. Missouri Department of Conservation Publication, Jefferson City, Missouri.

Niinemets, Ü., and Valladares, F. 2006. Tolerance to shade, drought, and waterlogging of temperate northern hemisphere trees and shrubs. Ecol. Monogr. **76**(4): 521–547. doi:10.1890/0012-9615(2006)076[0521:TTSDAW]2.0.CO;2.

Noble, I.R., and Slatyer, R.O. 1980. The use of vital attributes to predict successional changes in plant communities subject to recurrent disturbances. Vegetatio, **43**: 5–21. doi:10.1007/BF00121013.

Nowacki, G.J., and Abrams, M.D. 2008. The demise of fire and "mesophication" of forests in the eastern United States. Bioscience, **58**(2): 123–138. doi:10.1641/B580207.

Oliver, C.D., and Larson, B.C. 1996. Forest stand dynamics. John Wiley & Sons, New York.

Oliver, C.D., Burkhardt, E.C., and Skojac, D.A. 2005. The increasing scarcity of red oaks in Mississippi River floodplain forests: influence of the residual overstory. For. Ecol. Manage. **210**: 393–414. doi:10.1016/j.foreco.2005.02.036.

Pacala, S.W., Canham, C.D., Silander, J.A., and Kobe, R.K. 1994. Sapling growth as a function of resources in a north temperate forest. Can. J. For. Res. **24**(11): 2172–2183. doi:10.1139/x94-280.

Pacala, S.W., Canham, C.D., Saponara, J., Silander, J.A., Kobe, R.K., and Ribbens, E. 1996. Forest models defined by field measurements: estimation, error analysis, and dynamics. Ecol. Monogr. **66**: 1–43. doi:10.2307/2963479.

Palik, B., Mitchell, R.J., Pecot, S., Battaglia, M., and Pu, M. 2003. Spatial distribution of overstory retention influences resources and growth of longleaf pine seedlings. Ecol. Appl. **13**: 674–686. doi:10.1890/1051-0761(2003)013[0674:SDOORI]2.0.CO;2.

Peet, R.K., and Christensen, N.L. 1987. Competition and tree death. Bioscience, **37**(8): 586–595. doi:10.2307/1310669.

Pinheiro, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-PLUS. Springer-Verlag New York, Inc.

Pinheiro, J.C., Bates, D.M., Debroy, S., Sarkar, D., and the R Core Team. 2011. NLME: linear and nonlinear mixed effects models. R package version 3.1-100.

Poorter, L., Bongers, F., Sterck, F.J., and Woll, H. 2005. Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. J. Ecol. **93**: 256–267. doi:10.1111/j.1365-2745.2004.00956.x.

R Core Team. 2013. R: a language environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://R-project.org/.

Roach, B.A., and Gingrich, S.F. 1968. Even-aged silviculture for upland central hardwoods. USDA Forest Service Agriculture Handbook 355.

Sander, I.L., Johnson, P.S., and Rogers, R. 1984. Evaluating oak advance reproduction in the Missouri Ozarks. USDA Forest Service, North Central Forest Experimental Station, St. Paul, Minnisota, Res. Pap. NC-251.

Schlesinger, R.C., Sander, I.L., and Davidson, K.R. 1993. Oak regeneration potential increased by shelterwood treatments. North. J. Appl. For. **10**(4): 149–153.

Schuler, T.M. 2004. Fifty years of partial harvesting in a mixed mesophytic forest: composition and productivity. Can. J. For. Res. **34**(5): 985–997. doi:10.1139/x03-262.

Schweitzer, C.J., and Dey, D.C. 2011. Forest structure, composition, and tree diversity response to a gradient of regeneration harvests in the mid-Cumberland Plateau escarpment region, USA. For. Ecol. Manage. **262**: 1729–1741. doi:10.1016/j.foreco.2011.07.020.

Schwinning, S., and Weiner, J. 1998. Mechanisms determining the degree of size asymmetry in competition among plants. Oecologia, **113**: 447–455. doi:10.1007/s004420050397.

Shifley, S.R., and Brookshire, B.L. (*Editors*). 2000. Missouri Ozark Forest Ecosystem Project: site history, soils, landforms, woody and herbaceous vegetation, down wood, and inventory methods for the Landscape Experiment. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, Gen. Tech. Rep. NC-208.

Shifley, S.R., and Kabrick, J.M. (*Editors*). 2002. Proceedings of the Second Missouri Ozark Forest Ecosystem Project Symposium. 17–18 October 2000. USDA Forest Service, North Central Forest Experiment Station, St. Paul, Minnesota, Gen. Tech. Rep. NC-227.

Shifley, S.R., Fan, Z., Kabrick, J.M., and Jensen, R.G. 2006. Oak mortality risk factors and mortality estimation. For. Ecol. Manage. **229**: 16–26. doi:10.1016/j.foreco.2006.03.033.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press.

Valladares, F., and Niinemets, U. 2008. Shade tolerance, a key plant feature of complex nature and consequences. Annu. Rev. Ecol. Evol. Syst. **39**: 237–257. doi:10.1146/annurev.ecolsys.39.110707.173506.

Walters, M.B., and Reich, P.B. 2000. Trade-offs in low-light CO_2 exchange: a component of variation in shade tolerance among cold temperate tree seedlings. Funct. Ecol. **14**: 155–165. doi:10.1046/j.1365-2435.2000.00415.x.

Warner, R.R., and Chesson, P.L. 1985. Coexistence mediated by recruitment fluctuations: a field guide to the storage effect. Am. Nat. **125**(6): 769–787. doi:10.1086/284379.

Weiner, J. 1990. Asymmetric competition in plant populations. Trends Ecol. Evol. **5**: 360–364. doi:10.1016/0169-5347(90)90095-U. PMID:21232393.

Weiner, J., and Thomas, S.C. 2001. The nature of tree growth and the "age-related decline in forest productivity". Oikos, **94**: 374–376. doi:10.1034/j.1600-0706.2001.940219.x.

Wright, E.F., Coates, K.D., Canham, C.D., and Bartemucci, P. 1998. Species variability in growth response to light across climatic regions in northwestern British Columbia. Can. J. For. Res. **28**(6): 871–886. 10.1139/x98-055.

Wright, E.F., Canham, C.D., and Coates, K.D. 2000. Effects of suppression and release on sapling growth for 11 tree species of northern, interior British Columbia. Can. J. For. Res. **30**(10): 1571–1580. doi:10.1139/x00-089.