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ORIGINAL PAPER

Comparing individual-tree approaches for predicting height growth of underplanted seedlings

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Abstract
• **Key message Individual-tree seeding height growth models developed using tree inventory data were comparable to those requiring the unique observation of point-based canopy structure data at each seedling.**
• *Context* Quantitative approaches describing the relationship between canopy structure and seedling growth can inform silvicultural decision making regarding the development of tree reproduction beneath a dominant forest canopy.
• *Aims* Individual-tree seedling growth models with canopy structure predictors derived from tree inventory data have not been well-explored. This study compared a model framework fit using point-based measures of canopy structure observed at the seedling level to one fit using area-wide canopy structure variables derived from standard inventory plot data.
• *Methods* Species-specific models predicting 5-year height growth were fit for cherrybark oak (*Quercus pagoda* Raf.), water oak (*Quercus nigra* L.), and yellow-poplar (*Liriodendron tulipifera* L.) underplanted within a canopy structure gradient created by silvicultural manipulation of a closed-canopy forest in Georgia, USA.
• *Results* Though the species varied in shade tolerance and growth rates, the general relationship between the predictor variables and height growth was similar among species and model type. Models highlight the importance of including predictor variables that describe seedling size along with openness and vertical structure of the forest canopy.
• *Conclusion* While the two model frameworks had comparable fit statistics, the one with predictors derived from tree inventory data may have enhanced utility as it can be directly integrated into existing individual-tree forest growth simulators.

Keywords Forest structure · Seedling growth · Mixed-model · *Quercus* · *Liriodendron tulipifera*

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Contribution of the co-authors John Lhotka and Edward Loewenstein were each responsible for study design and manuscript preparation. John Lhotka was responsible for developing the model framework and completing the statistical analysis.

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1 Introduction

Forest canopy structure varies in complexity among forest types. However, a fundamental relationship exists between canopy structure and the environmental factors influencing growth of understory trees (Parker 1995; Aussenac 2000; Wagner et al. 2011). Interactions between the horizontal and vertical distribution of foliage can considerably alter the understory growth environment (Valladares 1999) and, therefore, the development of tree seedlings beneath a dominant canopy. Knowledge of these relationships gives practitioners the ability to formulate and evaluate silvicultural practices that manipulate forest structure with the intent of affecting the growth and mortality of natural advance reproduction or underplanted seedlings.

In order to describe how seedling reproduction responds to conditions created by silvicultural practices, a number of approaches have been used to quantify the empirical relationship between canopy structure and seedling development. Much of this research has focused on measures of canopy structure that are correlated with understory light availability, and seedling growth is often predicted using variables such as canopy closure (Brandeis et al. 2001; Jain et al. 2004; Chrimes and Nilson 2005; Angell et al. 2014) and basal area (Mitchell 2001; Krueger et al. 2007; Angell et al. 2014). Because vertical structure has also been found to influence the understory growth environment (Valladares 1999; Parker et al. 2002; Comeau and Heineman 2003; Comeau et al. 2006), it might reasonably be expected that seedling growth and mortality would also be related to the vertical distance from the ground to the forest canopy overhead. Additional research identifies seedling size (Loftis 1990; Dey and Parker 1997; Spetich et al. 2002) and understory competition (Collet and Chenost 2006; Krueger et al. 2007; Ligot et al. 2013) as other important factors controlling seedling development following partial or complete canopy removal.

Existing frameworks for predicting seedling growth dynamics can generally be characterized as stand-level models that use area-wide measures of canopy structure or individual-tree models incorporating point-based metrics of structure observed at each seedling. However, few studies have explored the utility of an individual-tree approach where predictors representing canopy openness and vertical structure are derived from tree inventory data. This alternative approach would be analogous to the many large-tree diameter growth equations used in forest growth simulators where tree-level parameters are directly measured and canopy structure characteristics are generated from the list of individual tree data (i.e., species, dbh, total height, crown ratio).

In work related to Forest Vegetation Simulator (FVS) (USDA Forest Service, Fort Collins, CO), Crookston and Stage (1999) provide an overview of how inventory data and crown width equations can be used to generate horizontal and vertical canopy structure variables similar to those directly measured in many seedling growth studies. Therefore, if successfully developed and validated, seedling growth models that utilize tree inventory data for the quantification of canopy structure could be integrated into forest growth software like FVS. Another benefit of these models is that they are based upon variables commonly collected by practitioners under standard forest inventory protocols. In contrast, many seedling growth equations developed using canopy closure data require specialized devices such as densiometers or hemispherical photography equipment for the collection of model inputs. The point-based nature of canopy closure data (Jennings et al. 1999) also makes it difficult to incorporate these models into tree list-based forest growth simulators.

We hypothesize that the growth of tree reproduction developing beneath a forest canopy can be predicted as a function of the variables: canopy openness, vertical canopy structure, seedling size, and seedling competitive position. Our goal is to predict the height growth of individual seedlings with this hypothesized model framework using two distinct approaches to the measurement of canopy structure: (1) direct observation at the seedling level and (2) metrics derived from standard tree inventory data. For this work, we focused on the empirical relationships that describe height growth of three deciduous broadleaf species, cherrybark oak (*Quercus pagoda* Raf.), water oak (*Quercus nigra* L.), and yellow-poplar (*Liriodendron tulipifera* L.), following underplanting. These species are common associates in riparian hardwood forests across the southern USA and represent a shade-tolerance range from intermediate to intolerant (Beck and Della-Bianca 1981; Krinard 1990; Vozzo 1990). Seedlings were underplanted within a gradient of structural conditions created by silvicultural manipulation of closed-canopy stands. Structural manipulations were used to emulate the range of canopy and understory environmental conditions that can result from the shelterwood systems commonly prescribed for oak (*Quercus* spp.) dominated stands in the eastern USA (Johnson et al. 2002). Our specific objectives were to (1) describe the species-specific relationship of seedling height growth to canopy structure and seedling characteristics and (2) compare seedling growth models fit using canopy structure variables uniquely measured at the seedling level to those developed with canopy structure variables derived from standard inventory data.

2 Material and methods

2.1 Site description

The study was completed in the riparian forest corridor associated with a 450 ha watershed in Harris County, Georgia, USA (approximately 32° 45′ 17.2″ N, 85° 6′ 16.7″ W). The study area is located within the Southern Appalachian Piedmont ecological section (Cleland et al. 2007), the humid subtropical climatic zone, and the west central climatic division of Georgia. Average annual temperature and precipitation are 16.9 °C and 125.1 cm, respectively. Average annual maximum temperature is 23.3 °C, while average minimum temperature is 10.4 °C (National Climatic Data Center 2014).

Stands within the riparian corridor had a density of 780 trees ha^{-1} (trees >5 cm dbh), basal area of 41 m^2 ha^{-1}, quadratic mean diameter of 27 cm, and an average top height of 32 m. Species in dominant and codominant canopy positions were primarily sweetgum (*Liquidambar styraciflua* L.) (49 % of basal area), yellow-poplar (31 % of basal area), green ash (*Fraxinus pennsylvanica* Marsh.) (5 % of basal area), water oak (3 % of basal area), and boxelder (*Acer negundo* L.) (2 % of basal area). Intermediate and overtopped crown classes were dominated by flowering dogwood (*Cornus florida* L.), two-winged silverbell (*Halesia diptera* Ellis), American hornbeam (*Carpinus caroliniana* Walt.), and eastern hophornbeam (*Ostrya virginiana* (Mill.) K. Koch). Vegetation surveys indicated that the study area lacked desirable tree reproduction, and the principal understory species were Japanese stiltgrass (*Microstegium vimineum* (Trin.) A. Camus), Japanese honeysuckle (*Lonicera japonica* Thunb.), and blackberry (*Rubus* spp.) (Burton et al. 2005; Loewenstein and Loewenstein 2005). Soils were generally fine-loamy, mixed, active, thermic Oxyaquic Udifluvents.

2.2 Study design

This study was designed to evaluate whether canopy openness, vertical canopy structure, and seedling characteristics could be used to predict height growth of underplanted seedlings along a structural gradient created among the study plots. In August 2003, 50 circular plots (0.05 ha) were systematically placed within a 12.6 ha section of the study watershed's riparian forest corridor. Plots were established not less than 12.6 m from adjacent plots or from natural forest gaps (>0.025 ha) and only where the riparian forest corridor was >38-m wide. Our goal was to use silvicultural treatments to create a gradient of 50 to 100 % canopy closure among the plots. To this end, one of four canopy manipulations were randomly assigned among the study plots: (1) no removal; (2) one third of all midstory trees removed; (3) one half of all midstory trees removed; and (4) complete midstory removal. Midstory trees were defined as stems >1.4-m tall that were part of the overtopped, intermediate, and weak codominant crown classes. The no removal and one third removal treatments were each assigned to 10 plots, while the one half removal and full removal treatments were each assigned to 15 plots. The one half and full removal treatments were assigned more replicates because higher variability in post-treatment structure was expected.

Silvicultural manipulations were completed between August and October of 2003. On each plot, we identified trees to be removed based upon the total number of midstory trees in a plot and the removal intensity assigned to that plot. For example, when one half of all midstory trees were to be removed, every other midstory tree within a plot was directionally felled using a chainsaw so that tree removal was distributed across the entire extent of the plot. Models relating post-treatment canopy structure and understory light availability along with relationships among canopy structure measures were presented in Lhotka and Loewenstein (2006).

During November and December of 2003, 12 seedling planting locations were established on a systematic grid in each plot. Because treatments were only applied to the plots, all seedlings were planted within 6 m of plot center to minimize edge effects. In eight of 12 planting locations within each plot, three containerized seedlings, one cherrybark oak, yellow-poplar, and water oak, were planted approximately 35 cm apart in a triangle pattern. Within the remaining four planting locations, one cherrybark oak and yellow-poplar were planted approximately 35 cm apart. Planting stock was purchased from a commercial nursery and consisted of 1-year-old seedlings grown in 40 cm^3 Deepot (Stuewe & Sons, Tangent, OR) containers. The unbalanced nature of the water oak plantings resulted from unforeseen shortages at the nursery. All seedlings were planted using a gas-powered auger and were watered following planting with approximately 5 l of water. Each seedling planting location was protected from browse using a 122-cm tall circular wire enclosure. Wire enclosures were removed following the fifth growing season.

2.3 Data collection and analysis

For each underplanted seedling, post-planting total height (measured to the nearest 0.5 cm) and basal diameter (mm) at the ground line were measured prior to budbreak during the winter of 2004. Mean (± standard deviation) total height of cherrybark oak, water oak, and yellow-poplar planting stock was 45.8 cm (±15.8), 39.7 cm (±13.1), and 21.5 cm (±8.1), respectively. Mean (± standard deviation) basal diameters of cherrybark oak and water oak planting stock were 4.4 mm (±1.4) and 4.2 mm (±1.2), while the basal diameter of yellow-poplar averaged 8.1 mm (±2.0). Total height, basal diameter, and survival status were recorded again following the second (fall 2005) and seventh (fall 2010) growing seasons.

During the first growing season following planting (April to September 2004), basal area (m^2 ha^{-1}), height to the forest canopy (m), and canopy closure (%) were measured at each seedling planting location (n=600). Basal area was determined with a 10 basal area factor (BAF) angle gage, and values were converted to metric units (m^2 ha^{-1}). Height-to-canopy was defined as the vertical distance (m) from a seedling to the nearest overtopping tree crown and was measured above each planting location using a Vertex III digital hypsometer (Haglöf, Sweden). Canopy closure was determined using hemispherical photography and the Hemiview (Delta-T Devices, Cambridge, UK) analysis software. At each planting location, one photograph was taken 1.25 m above the ground using a Nikon Coolpix 5700 (5 megapixel) digital camera and fisheye converter (183° view angle). The following camera settings were used: image quality—1:4 compression JPEG format; saturation—black and white; and image size—full (2560×1920 pixels) (Frazer et al. 2001). All photos were taken during uniformly overcast conditions when the solar disk was completely obscured. Using methods described by Lhotka and Loewenstein (2006), percent canopy closure was calculated at 120°, 90°, 60° photo view angles.

Following silvicultural treatment, all trees >5 cm dbh were inventoried in each 0.05 ha plot. Species, dbh (cm), total height (m), and height (m) to the base of live crown (HBLC) were recorded. Inventory data were used to derive plot-level canopy structure descriptors similar to those variables measured directly at each planting location. Inventory plot data were summarized and basal area (m^2 ha^{-1}), top height (Rennolls 1978), and mean height to the base of live crown were calculated. Because canopy closure is a point-based measure of canopy openness, it cannot be simply derived from area-based inventory data. Plot-level canopy openness was thus represented using canopy cover (Jennings et al. 1999). Canopy cover (%) was calculated by plot using the tree inventory data and the following steps: species-specific allometric crown width equations (Bechtold 2003) were used to estimate each tree's horizontally projected crown; estimated crown areas on a ha^{-1} basis were summed to determine a plot's total projected crown area in m^2 ha^{-1} (CA_{tot}); and percent canopy cover was determined by inputting total projected crown area into the overlap correction function (Eq. 1) presented by Crookston and Stage (1999).

$$\%\,\text{canopy cover} = 100 \times \left(1 - \exp\left(-0.01 \times \left(100 \times \frac{CA_{tot}}{10000}\right)\right)\right) \quad (1)$$

We used a distance-independent, individual-tree approach to predict seedling height growth as a function of canopy openness, vertical canopy structure, seedling size, and seedling competitive position. The dependent variable was the 5-year height increment that followed the second growing season after planting (i.e., Ht_{2010}–Ht_{2005}). This growth increment was selected as it represents the height response of the underplanted seedlings after an initial establishment period. Measurement of second-year seedling size as a basis for subsequent growth is a reasonable scenario given that land management agencies (e.g., USDA Forest Service) require regeneration surveys several years post-planting in order to determine the initial planting efficacy.

Two model types were constructed for each species. The first incorporated canopy structure variables directly measured at the seedling-level including basal area, height-to-canopy, and canopy closure (60°, 90°, 120° photo analysis angles). For the second model type, we utilized plot-level structural variables calculated from inventory data such as basal area, canopy cover, mean height to the base of live crown, and top height. Both models included the same potential predictors related to seedling size and competitive position. Initial seedling characteristics for the growth period were described using total height and basal diameter two growing seasons after planting (2005). Given that the study species were planted together in eight to 12 planting locations per plot, it was important to consider whether competitive position within planting group influenced growth. We used the relative height of a seedling compared to the tallest competitor within a planting location to represent the influence of competitive position.

The multilevel structure of the study design (i.e., planting locations grouped within plots) required a mixed-effects model incorporating plot as a random effect (Fox et al. 2001). The linear mixed model used to analyze seedling growth of each species was defined by Eq. 2.

$$Y_{ij} = \beta_0 + u_j + X_{ij}^T\beta + \varepsilon_{ij} \quad (2)$$

where Y_{ij} is the 5-year height growth of seedling i in plot j, β_0 is the intercept, u_j is the random effect for plot j, ε_{ij} is the error term, and $X_{ij}^T\beta$ is the transposed matrix of the fixed effects describing basal area, canopy openness, vertical canopy structure, seedling size, and seedling competitive position. Models were fit using the nlme package (Pineiro et al. 2014) for the R programming language (R Core Team 2014). For the two model types, variable selection began by evaluating a full model with all fixed effects. Because of multicollinearity among canopy closure values determined using 60°, 90°, and 120° photo angles, the full model for the seedling-level analysis only included canopy closure at a 60° photo angle as it was the closure variable most highly correlated with seedling height growth. Model fit and variable selection followed procedures outlined in Zuur et al. (2009). Starting with the variables whose p values were greater than α= 0.05, we sequentially removed all variables in turn and applied a likelihood ratio test to determine the significance of the variable removed. Models were refit after a given variable was removed, and this iterative selection process was continued until the final model contained only variables whose parameter p value was below α=0.05. We evaluated fit of the final model using the following criteria: absolute bias, root mean square error (RMSE), and the R^2 value. Residual plots were used to assess homogeneity of variance and normality of residuals. Residual analysis indicated that heteroscedasticity was present in the residuals for cherrybark oak. The varFixed option in the nlme package (Pinheiro and Bates 2000; Pineiro et al. 2014) was used to weight the variance of the residuals with the function

$$\mathrm{Var}\left(\varepsilon_{ij}\right) = \sigma^2 \times \mathrm{Diam}_{ij} \quad (3)$$

where Diam is the basal diameter (mm) at the beginning of the growth period for the ith tree on the jth plot and σ^2 is the residual variance. Subsequent residual plots confirmed this variance weighting strategy minimized issues with heteroscedasticity.

3 Results

Silvicultural manipulation of the study plots resulted in a gradient of canopy openness and height to the forest canopy among the 600 seedling planting groups (Table 1). Analysis of hemispherical photos taken at each planting location indicated that canopy closure (60° photo angle) ranged from 53 to 96 % with a mean of 74 %. Height-to-canopy was between 1.1 and 36.5 m and averaged 14.2 m among planting locations. Canopy structure variables based upon inventories of trees >5 cm dbh produced comparable estimates as direct measurement at each planting location (Tables 1 and 2). Plot-level canopy cover ranged from 56 to 93 % with a mean of 77 %. Mean height to base of live crown was 10.5 m, and values among plots ranged from 4.8 to 20.9 m.

We evaluated height growth of cherrybark oak, water oak, and yellow-poplar in the 5-year period following the second growing season (2005) after planting (Table 1). Total height (Ht_{2005}) at the beginning of this 5-year period averaged 73.9, 62.6, and 165.2 cm for cherrybark oak, water oak, and yellow-poplar, respectively. Mean 5-year height growth following the 2005 growing season (i.e., Ht_{2010}–Ht_{2005}) was 58.9, 54.6, and 165.2 cm for cherrybark oak, water oak, and yellow-poplar, respectively. Maximum height increment during the growth period ranged from 556 cm for yellow-poplar to 248 cm for water oak. Minimum values observed were negative indicating that some underplanted seedlings lost height during the growth period due to top dieback. Mean relative height of underplanted seedlings following the 2005 growing season were 0.78 for cherrybark oak, 0.70 for water oak, and 0.96 for yellow-poplar. Survival during the 5-year period was 67, 64, and 36 % for cherrybark oak, water oak, and yellow-poplar, respectively.

In this study, we developed species-specific models to predict seedling height growth as a function of canopy openness, vertical canopy structure, and seedling size and competitive position. The dependent variable for the models was the 5-year height increment following the second growing season after planting (i.e., Ht_{2010}–Ht_{2005}). The fit model incorporating canopy structure variables measured at each seedling planting

Table 2 Mean, standard deviation (SD), minimum (min), and maximum (max) values for plot-level tree inventory-based measures of canopy structure

Tree inventory variables	Label	Mean	SD	Min	Max
Basal area (m^2 ha^{-1})	BA_{plot}	34.85	9.20	12.91	62.84
Canopy cover (%)	Cover	77.24	9.55	56.20	92.72
Top height (m)	TopHt	32.24	3.89	25.94	39.57
Height to base of live crown (m)	HBLC	10.53	3.90	4.76	20.94

Table 1 Mean, standard deviation (SD), minimum (min), and maximum (max) values for variables describing seedling characteristics and canopy structure measured at each planting group

Seedling level variables	Label	Mean	SD	Min	Max
Basal area (m^2 ha^{-1})	BA	28.59	6.52	13.80	52.90
Height to canopy (m)	HtCanopy	14.23	8.21	1.10	36.50
Canopy closure—120° photo angle (%)	$Closure_{120PA}$	82.53	3.47	74.75	93.18
Canopy closure—90° photo angle (%)	$Closure_{90PA}$	77.04	5.41	64.09	92.21
Canopy closure—60° photo angle (%)	$Closure_{60PA}$	74.22	8.44	53.15	95.82
Cherrybark oak (n=279)					
Basal diameter in 2005 (mm)	$Diam_{2005}$	6.04	2.21	2.13	14.48
Total height in 2005 (cm)	Ht_{2005}	73.89	32.78	20.50	204.00
Relative height in 2005	$RelHt_{2005}$	0.78	0.22	0.18	1.00
Height increment (cm)[a]	Ht_{2010}–Ht_{2005}	58.91	52.20	−50.50	351.00
Water oak (n=160)					
Basal diameter in 2005 (mm)	$Diam_{2005}$	5.78	1.64	2.83	11.33
Total height in 2005 (cm)	Ht_{2005}	62.60	22.00	21.00	148.50
Relative height in 2005	$RelHt_{2005}$	0.70	0.25	0.11	1.00
Height increment (cm)	Ht_{2010}–Ht_{2005}	54.57	45.68	−50.50	248.00
Yellow-poplar (n=148)					
Basal diameter in 2005 (mm)	$Diam_{2005}$	14.62	4.78	5.40	27.28
Total height in 2005 (cm)	Ht_{2005}	129.36	48.69	19.50	253.00
Relative height in 2005	$RelHt_{2005}$	0.96	0.11	0.41	1.00
Height increment (cm)	Ht_{2010}–Ht_{2005}	165.21	130.03	−67.00	556.00

[a] Seedling height increment covers the 5-year period following the 2005 growing season

location is presented as Eq. 4.

$$\left(\mathrm{Ht}_{2010}-\mathrm{Ht}_{2005}\right)=b_0+b_1\mathrm{Diam}_{2005ij}+b_2\mathrm{HtCanopy}_{ij}+b_3\mathrm{Closure}_{60PAij}+u_j+\varepsilon_{ij} \quad (4)$$

where Ht_{2005} and Ht_{2010} are total height (cm) at the beginning and end of the 5-year growth period; Diam_{2005} is seedling basal diameter (mm) at the beginning of the growth period; HtCanopy is the height-to-canopy (m) measured above each planting location; $\mathrm{Closure}_{60\mathrm{PA}}$ is percent canopy closure (60° photo angle); b_0, b_1, b_2, and b_3 are fixed effect parameters (Table 3); u_j is the random effect for the jth plot; and ε_{ij} is the model residual for the ith tree on the jth plot. Initial basal diameter (Diam_{2005}) and height-to-canopy (HtCanopy) were significant predictors ($p<0.05$) for all species and were positively related to 5-year height increment. Canopy closure using a 60° photo angle was negatively related ($p=0.008$) to height growth of cherrybark oak, but was not statistically significant ($p<0.05$) in the water oak or yellow-poplar models. When combined with the variables in Eq. 4, initial total height (Ht_{2005}), relative height (RelHt_{2005}), and basal area (BA) were not significant predictors for the three species.

In addition to canopy structure variables measured at the seedling level, we tested metrics of canopy openness and vertical structure determined from plot inventories of all trees >5 cm dbh. The fit model based upon these predictors is presented as Eq. 5.

$$\left(\mathrm{Ht}_{2010}-\mathrm{Ht}_{2005}\right)=b_0+b_1\mathrm{Diam}_{2005ij}+b_2\mathrm{Cover}_j+b_3\mathrm{HBLC}_j+b_4\mathrm{TopHt}_j+u_j+\varepsilon_{ij} \quad (5)$$

Table 3 Fixed-effects parameter estimates for 5-year seedling height growth models by species using seedling-level and tree inventory-based measures of canopy structure

Model and species	Coefficients				
	b_0	b_1	b_2	b_3	b_4
Canopy structure: seedling-level (Eq. 4)[a]					
Cherrybark oak	35.2616	11.7481	1.2989	−0.9227	–
Water oak	−21.8726	9.6888	1.2697	–	–
Yellow-poplar	−114.3425	15.1914	2.5519	–	–
Canopy structure: tree inventory (Eq. 5)[b]					
Cherrybark oak	61.9387	10.7727	−1.1622	1.8152	–
Water oak	−67.4141	12.2316	−1.2621	–	4.5782
Yellow-poplar	−45.0289	13.9584	−2.7350	–	5.9871

[a] Coefficients are as follows: Intercept (b_0), Diam_{2005} (b_1), HtCanopy (b_2), $\mathrm{Closure}_{60\mathrm{PA}}$ (b_3), respectively

[b] Coefficients are as follows: Intercept (b_0), Diam_{2005} (b_1), Cover (b_2), HBLC (b_3), TopHt (b_4), respectively

where Ht_{2005} and Ht_{2010} are total height (cm) at the beginning and end of the 5-year growth period; Diam_{2005} is seedling basal diameter (mm) at the beginning of the growth period; Cover is plot-level percent canopy cover; HBLC is the mean height (m) to base of live crown by plot; TopHt is plot top height (m); b_0, b_1, b_2, b_3, and b_4 are fixed effect parameters (Table 3); u_j is the random effect for the jth plot; and ε_{ij} is the model residual for the ith tree on the jth plot. Similar to Eq. 4, seedling basal diameter (Diam_{2005}) was a significant predictor for all species and was positively related to 5-year height increment. Percent canopy cover was negatively related ($p<0.05$) to height growth of cherrybark oak, water oak, and yellow-poplar. Height to base of live crown was positively related ($p=0.022$) to height growth of cherrybark oak, while top height was positively related ($p<0.05$) to growth of water oak and yellow-poplar. Plot basal area ($\mathrm{BA}_{\mathrm{plot}}$), initial total height (Ht_{2005}), and relative height (RelHt_{2005}) were not significant predictors when combined with the variables in Eq. 5.

Fit statistics by species and model type are presented in Table 4. Model bias was minimal, root mean square errors were between 37.2 and 71.4, and R^2 ranged from 0.24 to 0.70. Model fit was better for yellow-poplar and cherrybark oak when compared to water oak. Within a species, root mean square error and R^2 values were comparable between the model using plot-level canopy variables and the one incorporating canopy variables measured at the seedling level.

Model predictions were also used to explore generalized relationships between initial seedling size and canopy openness. To facilitate species comparisons, a simplified version of Eq. 5 incorporating only seedling basal diameter and plot-level canopy cover was used to predict 5-year height growth across a range of initial diameters and at three levels of cover (60, 75, and 90 %) (Fig. 1). The family of curves shown in Fig. 1 represents the data range observed within the study (Tables 1 and 2). Seedling height growth among all species increased within larger initial diameters and decreased with greater levels of canopy cover. Model coefficients and

Table 4 Fit statistics and model variance components for 5-year seedling height growth models by species using seedling-level and tree inventory-based measures of canopy structure

Model and Species	Fit statistics			Variance components	
	Bias	Rmse	R^2	σ^2 Plot	σ^2 Residual
Canopy structure: seedling-level (Eq. 4)					
Cherrybark oak	−1.33E-14	37.15	0.50	99.40	231.34
Water oak	−4.76E-15	40.16	0.24	93.95	1685.51
Yellow-poplar	7.43E-15	72.27	0.70	1398.89	5840.85
Canopy structure: tree inventory (Eq. 5)					
Cherrybark oak	5.42E-15	37.57	0.49	122.70	234.64
Water oak	−3.35E-15	38.84	0.29	11.66	1519.10
Yellow-poplar	−6.42E-15	71.44	0.70	1332.46	5676.86

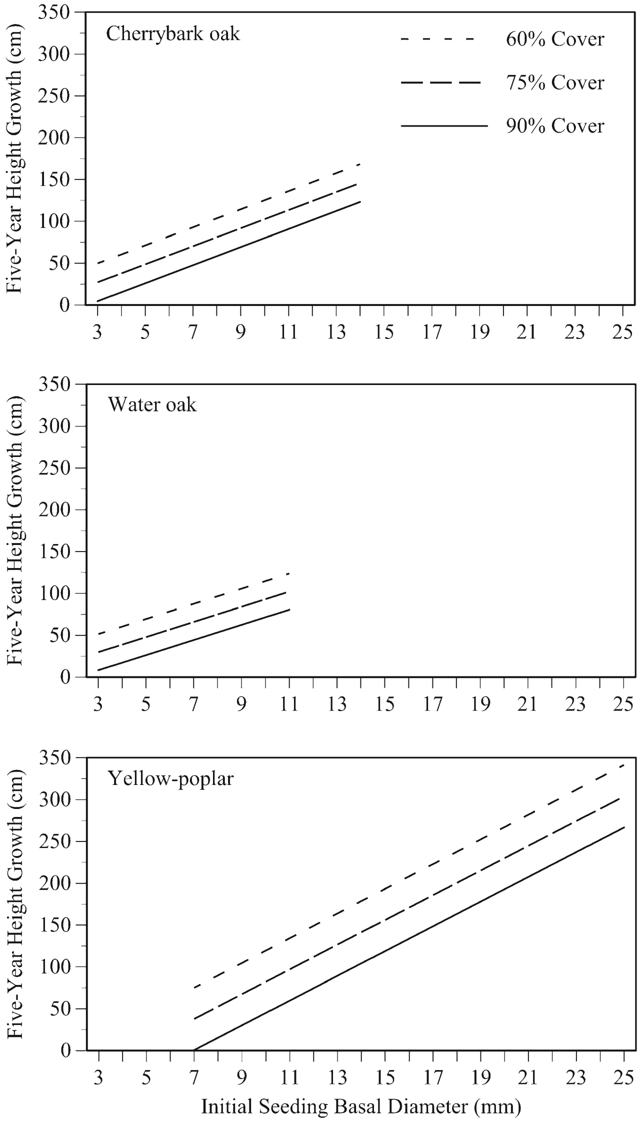

Fig. 1 Generalized relationships between initial seedling basal diameter ($Diam_{2005}$) and 5-year height growth (Ht_{2010}–Ht_{2005}) evaluated at three levels (60, 75, and 90 %) of plot-level canopy cover (Cover) for underplanted cherrybark oak, water oak, and yellow-poplar seedlings. The family of curves were developed using the following models for cherrybark oak (107.83756+10.78096 ($Diam_{2005}$)−1.5077 (Cover), R^2=0.49), water oak (110.71236+9.03465 ($Diam_{2005}$)−1.43991 (Cover), R^2=0.31), and yellow-poplar (120.53562+14.78634 ($Diam_{2005}$)−2.48226 (Cover), R^2=0.70). Initial seedling diameter and canopy cover array used to estimate height growth trends fall within the study's observed data range

predicted trends indicated that the growth of yellow-poplar was more sensitive to increased canopy cover than cherrybark oak or water oak (Fig. 1). Predictions also highlighted that the height growth ranking among species was altered as seedling size and canopy cover increased. For initial diameters ≤11 mm, 5-year height growth was greater for the oak seedlings than yellow-poplar across the canopy cover range. When initial diameters were between 12 and 14 mm, the species with the greatest height growth under 75 and 90 % canopy cover was cherrybark oak, whereas at 60 % canopy cover, yellow-poplar's height growth exceeded the oaks. Cherrybark oak and water oak seedlings with initial basal diameters >15 mm were not sampled (Table 1), and predictions were not extrapolated beyond the observed range (Fig. 1). A wider initial diameter range was observed for yellow-poplar (5.4 to 27.3 mm) (Table 1), and the average initial diameter for yellow-poplar (14.6 mm) was more than twice that of cherrybark oak (6.0 mm) and water oak (5.8 mm). Across the three levels of canopy cover evaluated, predicted height growth of yellow-poplar exceeded 120 cm when initial seedling diameter was >15 mm and 200 cm when diameter was >20 mm (Fig. 1).

4 Discussion

Past research has quantified canopy structure and predicted seedling growth at two general scales. Area-wide measures of canopy structure sampled at the stand or plot have been used to predict seedling growth (Brandeis et al. 2001; Chrimes and Nilson 2005; Lin et al. 2012). Other research has predicted growth using point-based metrics of canopy structure observed at each seedling (Jain et al. 2004; Krueger et al. 2007). Angell et al. (2014) evaluated models at both scales and found that comparable predictions of seedling height growth could be made using individual-tree and stand-level models.

We presented models to predict height growth of individual seedlings using point-based (i.e., seedling level) and area-wide (i.e. tree inventory based) measures of canopy structure. The species evaluated represented a range of shade-tolerance characteristics and displayed varying growth rates across the canopy structure gradient present (Tables 1 and 2). However, seedling level and tree inventory based models for each species included basal diameter of individual seedlings and predictors representing similar aspects of forest structure (Table 3). Models generally supported our hypothesis that growth of tree reproduction developing under forest canopies can be predicted as a function of canopy openness, vertical canopy structure, and seedling size. However, the measure of seedling competitive position used in this study, relative height, was not found to be significant when combined with the variables in Eqs. 4 or 5. This finding indicates that with the study design and analysis employed, we could not confirm a relationship between seedling growth and competitive position.

Parameters indicate that 5-year height growth increased with larger initial seedling basal diameter. Basal diameter measured at the ground line is a metric commonly related to seedling response following silvicultural activities, and related findings support the positive association between seedling size and growth (Loftis 1990; Spetich et al. 2002; Chrimes and Nilson 2005). The importance of seedling diameter as a growth predictor is generally attributed to the high correlation between a seedling's diameter and its root system size (Dey and Parker 1997). Seedlings with a more extensive root system are better able to compete for soil nutrients and available water. Models also show that as the vertical height of the canopy (e.g., HtCanopy, TopHt) and canopy openness (e.g., $\mathrm{Closure}_{60PA}$, Cover) increase, so does seedling height growth. The combined influence of these horizontal and vertical canopy characteristics on the microclimatic conditions that drive understory plant growth is well documented. Research in a variety of forest types shows a strong positive correlation between canopy openness and understory light availability (Jenkins and Chambers 1989; Lieffers et al. 1999; Yirdaw and Luukkanen 2004; Grayson et al. 2012). Related work also indicates that light availability is enhanced with increasing top height (Comeau and Heineman 2003; Lhotka and Loewenstein 2006) and vertical distance from the ground to the forest canopy (Parker et al. 2002; Comeau et al. 2006). Therefore, height growth patterns we observed in response to more open canopies that are higher off the ground is likely attributed to associated increases in understory light availability.

The silvicultural manipulations applied in this study yielded a canopy cover gradient (56 to 93 %) among the plots. Trends shown in Fig. 1 suggest that the ranking of species growth rates across this gradient was influenced by seedling size. For example, at small initial diameters (i.e., <11 mm), cherrybark oak outgrew yellow-poplar and the growth differential between the oaks and yellow-poplar became more pronounced with increasing canopy cover. However, as 12- to 14-mm-diameter seedlings, yellow-poplar would have a height growth advantage at 60 % canopy cover and cherrybark oak would have the advantage under 75 and 90 % canopy cover. This linkage between canopy openness and differences in growth rates among species is congruent with silvical characteristics observed in other research. Yellow-poplar is a shade intolerant, fast growing competitor that can exhibit larger height growth in open conditions than many co-occurring oak species (Beck and Della-Bianca 1981; Beck and Hooper 1986). In contrast, cherrybark oak has been shown to maximize its height growth under intermediate levels of available light such as those provided by the shelterwood method (Gardiner and Hodges 1998). In a management context, predicted growth trends provide evidence of canopy conditions that may favor the development of cherrybark oak or water oak over more shade intolerant competitors like yellow-poplar. Growth trends also underscore the importance of underplanted seedling size as a predictor of height growth as well as a factor that interacts with canopy openness to influence relative growth rates among species.

5 Conclusion

This study evaluated how seedling and canopy structure characteristics interact to affect the height response of tree reproduction planted beneath a forest canopy. We made comparisons between models fit using point-based (i.e., seedling level) and area-wide (i.e., tree inventory based) variables to represent canopy attributes that influence the understory growth environment. Models emphasize the inclusion of independent variables describing seedling size and both the openness and vertical structure of a forest canopy. Using regeneration survey data, plot inventories of trees >5 cm dbh, and published crown width models, we were able to develop height growth models that had fit statistics similar to those requiring the collection of point-based canopy structure data at individual seedlings. While both model types are informative regarding the relationship between canopy structure and seedling development, the constitution of inventory-based models facilitates integration into individual-tree modeling platforms like Forest Vegetation Simulator (FVS). Other benefits of inventory-based models are they incorporate predictors commonly collected by practitioners during stand examinations and do not require inputs based on specialized measurement equipment like hemispherical photography that can increase sampling time and costs. While our findings may be limited to one locale and the response of underplanted seedlings, this study furthers our understanding of the factors related to growth of the study species and presents a framework for developing seedling growth models based upon canopy variables derived from tree inventory data that may be applicable to other species and forest types. Models such as those developed in this study can help practitioners evaluate how silvicultural manipulation of the forest canopy may affect seedling growth patterns and the competitive dynamics among species.

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