An individual-tree diameter growth model for managed uneven-aged oak-shortleaf pine stands in the Ozark Highlands of Missouri, USA

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ABSTRACT

The Pioneer Forest encompasses more than 60,000 ha in the Ozark Highlands of Missouri, USA and has been managed using single-tree selection since the early 1950s. This paper quantifies the influence of tree size and competitive position, stand density, species composition, and site quality on ten-year (1992–2002) diameter increment within oak (*Quercus* spp.) and shortleaf pine (*Pinus echinata* Mill.) stands on the Pioneer Forest. An individual-tree model was developed for each species using mixed-effects regression and 290 inventory plots. Model efficiency (R^2) ranged from 0.26 to 0.57 and fit was generally better for oak species. Basal area in larger trees (BAL) and tree diameter were significant predictors for all species and crown competition factor improved prediction for shortleaf pine and hickory (*Carya* spp.). Effect of species composition and site quality on diameter growth was not consistent across species. Models were evaluated using a subset of data not included in model fitting and the effect of single tree and standwise (1, 3, or 5 sample trees) calibration on model predictions were evaluated. Inclusion of random effects through calibration improved model prediction for all species and fit was best following single tree and 3 tree calibration.

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1. Introduction

Growth and yield models are important tools in forest management planning because they can simulate stand development and production under various management alternatives (Vanclay, 1994). Diameter increment models are a fundamental component of forest growth and yield frameworks. Development of diameter growth models is supported by a large body of research and growth models have been constructed for a wide range of forest regions and management scenarios. Past research has found that individual-tree diameter growth can be expressed as a function of tree size, competitive effects, stand structure and site quality (Lemmon and Schumacher, 1962; Cole and Stage, 1972; Wykoff, 1990; Andreassen and Tomter, 2003). Research also suggests that a distance-independent, individual-tree model structure is flexible enough to predict diameter growth in pure even-aged stands as well as in mixed, multi-aged stands (Monserud and Sterba, 1996; Porté and Bartelink, 2002; Calama et al., 2008).

Diameter growth models are typically developed using continuous forest inventory (CFI) plots and often incorporate multiple repeated observations of individual trees. The hierarchical nature of these data results in spatial and temporal correlation among observations made in the same sampling unit (i.e., plot, tree) (Fox et al., 2001). Because independence of observations is a fundamental assumption of ordinary least squares regression, many recent efforts to develop diameter growth models have incorporated mixed-effects models (Palahi et al., 2003; Calama and Montero, 2005; Budhathoki et al., 2008; Uzoh and Oliver, 2008). Mixed models include fixed-effects that account for the relationships among dependent and independent variables for the population, while random-effects can account for variation associated with a sampling unit. Mixed models account for spatial and temporal correlation by defining the covariance structure of the model's random components and by using this structure during parameter estimation (West et al., 2007). Use of mixed models allows growth models to be calibrated for other locations or growth periods by predicting random components from tree or stand-level covariates and past increment data using best linear unbiased predictors (Lappi, 1991; Calama and Montero, 2005; Adame et al., 2008).

In North America, a large proportion of research involving individual-tree diameter growth has studied commercially important conifer species. A more limited body of work has focused on natural mixed hardwood and pine-hardwood systems (Davis et al., 2001). Because even-aged silviculture dominates hardwood management in the eastern United States, individual-tree

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Table 1
Descriptive statistics for plot level measures of forest structure and species composition.

Plot level variables ($n = 290$)	Mean	Standard deviation	Minimum	Maximum
Basal area (m^2 ha^{-1})	15.50	21.69	0.37	28.62
Stand density (trees ha^{-1})	416.51	621.10	24.71	753.66
Quadratic mean diameter (cm)	21.95	13.86	13.75	37.48
Crown competition factor	108.34	173.37	4.65	200.56
Oak/hickory proportion	0.66	1.23	0.00	1.00
Pine proportion	0.19	1.23	0.00	0.88

diameter growth models for uneven-aged hardwood stands managed using the selection system are uncommon (Peng, 2000; Kiernan et al., 2008). Modeling tree diameter growth in uneven-aged mixed stands also has an added level of complexity due wide variation in tree age and high heterogeneity in vertical and horizontal stand structure (Schütz, 2002; Kiernan et al., 2008).

The Pioneer Forest (MO, USA) is uncharacteristic of the eastern hardwood region because it has been managed using single-tree selection since the early 1950s. Its size (>60,000 ha) and long-term management history provide a unique opportunity to study tree diameter growth in uneven-aged forests of the eastern hardwood region. Our objective is to develop a distance-independent diameter growth model for the Pioneer Forest in order to quantify the empirical relationships between individual tree growth and metrics of tree size, competitive effects, stand structure, and site quality in oak (*Quercus* spp.) dominated stands. Permanent plot data and linear mixed models will be used to develop the diameter growth model. We will present the resulting model structure and trends among the primary species found on the Pioneer Forest. Finally, we will also examine how model calibration effects the prediction of diameter growth from a subset of data not included in the model fitting.

2. Methods

2.1. Study location

The Pioneer Forest covers over 60,000 ha in the Ozark Highlands of southern Missouri. Approximately 36,000 ha were purchased in 1954. Additional land was purchased to bring the size of the forest to 54,000 ha by 1962 and to 61,000 ha by 1972. At the time of original purchase the forest was under stocked, averaging only 32% stocking based on the Gingrich (1967) charts (full site utilization begins at approximately 57% stocking). The forest averaged 195 trees ha^{-1} and 8.3 m^2 ha^{-1} of basal area for all trees $\geq$12.7 cm DBH. By 1992, the forest was fully stocked at 55%. On average, basal area had increased by 68% to 13.9 m^2 ha^{-1} and tree density by 89% to 367 trees ha^{-1} (Loewenstein, 1996). In 2002, basal area averaged 16.5 m^2 ha^{-1} and density 363 trees ha^{-1}. The Pioneer Forest exhibits an uneven-aged structure ($\geq$3 age classes) at a spatial scale of approximately 0.25 ha and has retained a stable negative exponential diameter structure (q-value = 1.7 for 5 cm diameter classes) for over 50 years (Loewenstein, 2008).

Site quality and vegetation vary widely over the forest. However, topography is generally steep with broad flat ridges. The soils are generally rocky and droughty, but range from deep gravel and rock outcrops to soil depths of more than 1.2 m. The soil is derived mainly from dolomitic limestone. Site index (base age 50 years) ranges from 16.8 to 27.4 m for black oak (*Quercus velutina* Lam.) (Larsen, 1980), 17.8 to 28.4 m for scarlet oak (*Quercus coccinea* Muenchh.), and 15.5 to 26.1 m for white oak (McQuilkin, 1974). Although the forest is oak-dominated, shortleaf pine (*Pinus echinata* Mill.) occurs as scattered trees throughout the forest and as pure stands on upper south-facing slopes. Lower north-facing slopes and deep valleys typically support mixed-mesophytic hardwoods. Seven species account for nearly 90% of both tree density and basal

area on the Pioneer Forest (listed in order of frequency): white oak (*Quercus alba* L.), shortleaf pine (*Pinus echinata* Mill.), black oak (*Q. velutina* Lam.), scarlet oak (*Q. coccinea* Muench.), hickory (*Carya* spp.), northern red oak (*Quercus rubra* L.), and post oak (*Quercus stellata* Wang.) (Loewenstein et al., 1995).

2.2. Forest management

The Pioneer Forest is managed with a system that most closely resembles single-tree selection (see Larsen et al., 1999; Loewenstein et al., 2000). The stated silvicultural objective when marking a stand for harvest is to create or maintain a three-tiered forest canopy composed of an overstory, a midstory, and a sapling/reproduction layer. The cutting cycle is approximately 20 years with treatments scheduled when a stand reaches 21.8 to 23.0 m^2 ha^{-1} of basal area. The residual basal area target is approximately 14.9 m^2 ha^{-1}. This target structure is primarily developed by managing the overstory. Only merchantable trees (hardwoods $\geq$25 cm and pine $\geq$22.5 cm DBH) are harvested, although smaller stems are removed where markets exist. Cull trees suppressing potential crop trees are felled. Vigor, potential for increase in value, slope position, aspect and species are use to identify trees for removal. Although some lesser quality trees may be left to ensure optimal spacing and adequate stocking of the site, in general the best trees are left and the worst are cut.

2.3. Data collection and analysis

The study utilized CFI data from the network of permanent plots (0.08 ha) on the Pioneer Forest. The diameter growth model was fit using inventory data from the growth period, 1992 to 2002. Data from permanent plots harvested during this time period were excluded from model development. Model fitting included data from 290 plots. Plot data included species, survival status, and dbh (cm) for all trees >12.7 cm. Descriptive statistics for the plot-level forest structure data are presented in Table 1. Tree-level data are summarized in Table 2.

We used a distance-independent, individual-tree model approach that predicts ten-year diameter growth as a function of tree size, competitive position, stand structure, species composition, and site quality. The following independent variables were evaluated in our analysis:

(1) *Tree Size*: tree diameter, tree diameter squared, and natural logarithm of tree diameter.
(2) *Competitive position*: total basal area of trees larger than subject tree (BAL), the ratio of BAL to tree diameter, and the ratio of BAL to natural logarithm of tree diameter + 1.
(3) *Stand structure*: plot-level basal area, quadratic mean diameter, tree density, and crown competition factor (Krajicek et al., 1961). The natural logarithm of each variable was also tested. Crown competition factor was calculated with the crown width equations utilized by the Forest Vegetation Simulator (FVS)–Southern Variant (Keyser, 2008). It should be noted that crown competition factor calculated with the FVS equations includes the use of open-grown and forest-growth maximum

Table 2
Descriptive statistics for tree level inventory data by species in 1992.

Variable	Mean	Standard deviation	Minimum	Maximum
White oak (n = 2389)				
dbh (cm)	19.94	7.47	12.70	73.91
BAL (m^2 ha^{-1})	9.98	4.79	0.00	27.29
Diameter increment (cm)[a]	2.96	1.42	−1.27	8.89
Shortleaf pine (n = 1023)				
dbh (cm)	23.64	6.86	12.70	49.28
BAL (m^2 ha^{-1})	9.34	5.50	0.00	24.55
Diameter increment (cm)	2.59	1.64	−1.27	7.87
Black oak (n = 887)				
dbh (cm)	22.97	8.21	12.70	58.17
BAL (m^2 ha^{-1})	8.87	5.05	0.00	24.72
Diameter increment (cm)	3.97	1.72	0.25	11.68
Scarlet oak (n = 831)				
dbh (cm)	21.31	7.09	12.70	68.07
BAL (m^2 ha^{-1})	9.53	4.86	0.00	23.46
Diameter increment (cm)	4.46	1.90	0.25	11.43
Hickory (n = 709)				
dbh (cm)	19.88	5.97	12.70	58.17
BAL (m^2 ha^{-1})	10.29	5.02	0.00	28.44
Diameter increment (cm)	1.90	1.21	−0.76	6.60
N. red oak (n = 330)				
dbh (cm)	25.78	9.40	12.70	63.50
BAL (m^2 ha^{-1})	7.62	4.65	0.00	26.33
Diameter increment (cm)	4.49	2.28	0.76	11.43
Post oak (n = 313)				
dbh (cm)	21.45	6.89	12.70	47.75
BAL (m^2 ha^{-1})	9.11	5.14	0.00	21.57
Diameter increment (cm)	1.79	1.00	0.00	5.33

[a] Diameter increment covers the ten-year period between 1992 and 2002.

crown width equations depending on the availability of an open-grown equation for a particular species.

(4) *Species composition*: proportion of basal area composed of oak and hickory species and proportion of basal area composed of shortleaf pine.

(5) *Site quality*: categorical variables describing slope position, aspect, and site productivity class. Site quality variables were categorical because reliable site index estimates were not available for all plots and because aspect and percent slope were not collected as continuous data in the field. Site class 1 includes areas with deep soil (>1.2 m) on north slopes, stream benches, silt loam bottoms, and east slopes. Areas in site class 2 are medium deep soil (0.3–1.2 m) north and east slopes as well as deep soil south slopes and ridgetops. Site class 3 includes hard pan flats, shallow gravelly hollows, shallow south slopes and rocky north slopes.

We focused our analysis on the seven dominant species of the Pioneer Forest: white oak, shortleaf pine, black oak, scarlet oak, hickory, northern red oak, and post oak. Because data have a multilevel structure (trees grouped into inventory plots) (Fox et al., 2001), a linear mixed model incorporating plot as a random effect was used to fit the diameter increment model by species. The linear mixed model used in the analysis was defined by West et al. (2007)

$$Y_i = X_i\beta + Z_j u_j + \varepsilon_{ij} \tag{1}$$

$$u_j \sim N(0, \sigma^2_{plot})$$

$$\varepsilon_{ij} \sim N(0, \sigma^2)$$

where Y_i represents the vector of diameter increments for the ith tree. $X_i\beta$ is the design matrix and coefficients for the fixed effects describing tree size, competitive position, stand structure, species composition, and site quality. $Z_j u_j$ represents the design matrix and coefficients of the random plot effects for the jth plot. The model

covariance structure assumes residuals are uncorrelated and have a constant variance.

Research has indicated that transformation of the dependant variable, diameter increment, is typically needed to meet model assumptions like linearity, normality of residuals, and homogeneity of variance (Wykoff, 1990; Hökkä et al., 1997; Adame et al., 2008). The following dependant variable forms were evaluated: diameter increment ($dbh_{t2} - dbh_{t1}$), squared diameter increment ($dbh^2_{t2} - dbh^2_{t1}$), diameter increment plus a constant value of one ($dbh_{t2} - dbh_{t1} + 1$), and the natural logarithmic transformation of each. Model fitting was completed using the nlme package (Pinheiro et al., 2009) for the R programming language (R Development Core Team, 2010). Variables were selected based upon coefficient significance (α = 0.05) and the Akaike Information Criteria (AIC). We evaluated model fit using the following criteria: absolute bias, root mean square error (RMSE), and model efficiency (i.e., R^2). All fit statistics are based upon on transformed values. Following Uzoh and Oliver (2008), relative importance of individual predictors was assessed by comparing the RMSE of the full model to reduced models that each excluded one of the predictor variables. Residual plots were used to assess homogeneity of variance and normality of residuals.

2.4. Model evaluation and calibration

Model validation methods evaluate the quality of prediction produced by a fit model. Predictive values derived from a mixed-effects model can take two forms: (1) unconditional (population-averaged) predictive values based only on a model's fixed effects or (2) conditional predictive values determined using a model's fixed and random effects (West et al., 2007). When evaluating the predictive ability of a mixed model using validation data (i.e., data not used in model fitting), unconditional predicted values would be assessed unless the random-effects parameters could be estimated using a complementary dataset. In the case of mixed-effects diameter increment models, random parameters and associated conditional predictive values can be estimated using

Table 3
Fixed-effects parameter estimates for the individual-tree diameter increment model (Eq. (3)) by species.

Species	Coefficients[a]							
	b_0	b_1	b_2	b_3	b_4	b_5	b_6	b_7
White oak	2.5753	−0.2342	−0.7614	–	−0.1799	0.2003	–	–
Shortleaf pine	0.3769	0.3930	−0.2020	−0.0040	–	0.4606	–	−0.0717
Black oak	2.8256	−0.2188	−0.5514	–	−0.4019	−0.3005	–	−0.0827
Scarlet oak	2.0777	–	−0.6023	–	−0.1754	–	–	–
Hickory	1.5035	–	−0.3122	−0.0019	−0.2539	–	–	–
N. red oak	2.0133	–	−0.7691	–	–	–	−0.1514	−0.0670
Post oak	1.0868	–	−0.2504	–	–	–	–	–

[a] Coefficients are: intercept (b_0), log(dbh) (b_1), BAL/dbh (b_2), CCF (b_3), oakBA (b_4), pineBA (b_5), SW (b_6), and Site3 (b_7), respectively.

single tree (Calama and Montero, 2005) or standwise calibration (Lappi, 1991; Calama and Montero, 2005; Adame et al., 2008). Single tree calibration uses previous increment data for all trees within a sampling unit to estimate the random effects and determine the conditional predictive values (i.e., future increment based upon fixed and calibrated random effects). Standwise calibration uses previous increment data from a small subset of trees to estimate the random effects within a sampling unit; random parameters are then used to predict future increment for all trees in the sampling unit. In either calibration approach, conditional expectations (best linear unbiased predictors) of the random parameters are determined using the following expression (West et al., 2007)

$$u = DZ'(R + ZDZ')^{-1}e \qquad (2)$$

where u is a vector of estimated random parameters, D is the variance-covariance matrix for the random effects, Z is the design matrix for the random effects, R is the matrix for the residual variance, and e is a vector that represents the unconditional residuals of the model (the difference between observed diameter increments and the model's unconditional predicted values).

Model evaluations typically use an independent dataset or data derived from data splitting or bootstrapping procedures. Huang et al. (2003) provide a thorough review of these data selection methods and state that independently collected data is the best test for a model. The limited usage of single-tree selection systems within the region that surrounds the Pioneer Forest restricts our ability to use an independent evaluation dataset. To assess how several model calibration approaches affect model prediction, we used data from a subset of inventory plots on the Pioneer Forest. The evaluation subset included pre-harvest inventory data from those permanent plots that were excluded from the original model fitting due to harvest disturbance during the growth period 1992–2002. The evaluation dataset included 57 plots with a total of 724 trees and utilized inventory data from two prior (pre-harvest) inventory periods. Model prediction was assessed using data from the 1982 to 1992 growth period, while diameter increments from 1972 to 1982 were used in estimation of random effects with single tree and standwise calibration. While the evaluation subset could have been randomly drawn from unharvested plots in the 1992 to 2002 growth period, the use of previous inventory data on the excluded plots helps to minimize sample size reduction associated with data splitting and allows the model evaluation to include an independent growth period.

Single tree and standwise calibration were used to predict random plot parameters in the evaluation dataset. To determine the random coefficient for each plot by species, a script was written in the R programming language (R Development Core Team, 2010) to solve for u in Eq. (2). Single tree calibration utilized all trees of a given species on a plot to estimate random plot effects. Standwise calibration was completed by randomly selecting 1, 2, and 3 trees per plot. Following Calama and Montero (2005) and Adame et al. (2008), random plot parameters were estimated as the aver-

age from 500 random realizations completed for each standwise selection type (1, 2, or 3 trees per plot). We evaluated the predictive ability of the model among the calibration approaches using the following criteria: absolute bias, RMSE, and model efficiency (Huang et al., 2003).

3. Results

3.1. Model structure

Different forms of the dependant variable were evaluated and the natural logarithm of diameter increment plus a constant value of one ($\log(\text{dbh}_{2002} - \text{dbh}_{1992} + 1)$) was selected. This transformation follows Calama and Montero (2005) and Adame et al. (2008) and resulted in linear relationships with the predictor variables, yielded normally distributed residuals, and limited issues with heteroscedasticity. The fit model incorporated variables describing competitive effects, tree size, species composition, and site quality (Eq. (3)). Not all variables were significant for all species. Model coefficients by species are presented in Table 3.

$$\log(\text{dbh}_{ij2002} - \text{dbh}_{ij1992} + 1) = b_0 + b_1 \log(\text{dbh}_{ij}) + b_2 \frac{\text{BAL}_{ij}}{\text{dbh}_{ij}}$$
$$+ b_3\text{CCF}_j + b_4\text{oakBA}_j + b_5\text{pineBA}_j$$
$$+ b_6\text{SW}_j + b_7\text{Site3}_j + u_j + e_{ij} \qquad (3)$$

where dbh is initial tree diameter (cm), BAL equals total basal area of trees larger than subject tree, CCF is the crown competition factor, oakBA represents the basal area proportion of oak and hickory species, pineBA is the basal area proportion of shortleaf pine, SW is the categorical variable indicating southern or western aspects, and Site3 is the categorical variable identifying site productivity class 3 (lowest productivity), b_0, b_1, b_2, b_3, b_4, b_5, b_6, and b_7 are fixed effect parameters, 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.

In the fit model, BAL/dbh was a significant predictor for all species and was inversely related to ten-year diameter increment. BAL/dbh was also the variable most strongly related to growth for hickory and the oaks. Crown competition factor was negatively related to diameter growth for shortleaf pine and hickory and was the most important predictor of growth for shortleaf pine. Measures of tree size and forest composition were of secondary importance compared to BAL/dbh and crown competition factor. Natural logarithmic transformed tree diameter was inversely related to diameter growth in white oak and black oak, while it was positively correlated with growth for shortleaf pine. Proportion of oak and hickory basal area was a significant predictor for white oak, black oak, scarlet oak, and hickory and was inversely related to growth. Proportion of shortleaf pine basal area was significant and positively related to the growth of shortleaf pine and white oak, while inversely related to the growth of black oak. Categorical vari-
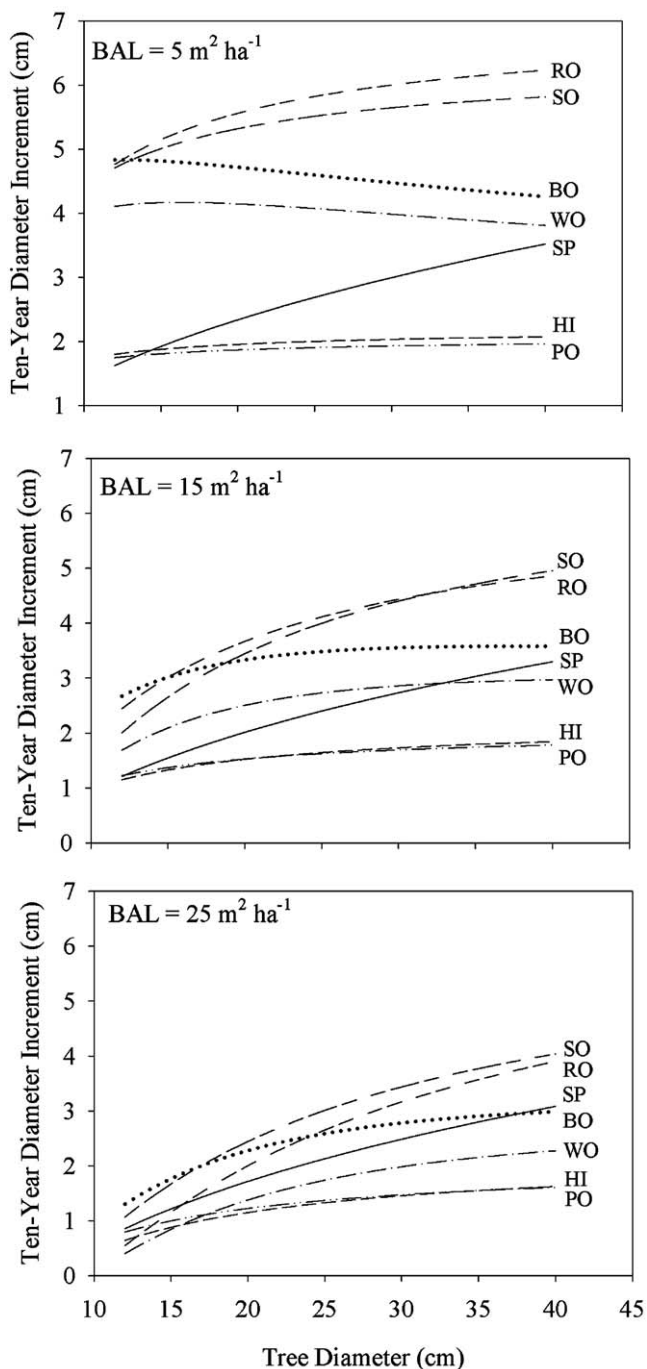
Fig. 1. Relationship between tree diameter (cm) and ten-year diameter increment (cm) by species at three levels of basal area in larger trees (BAL). Species labels include: WO, white oak; SP, shortleaf pine; BO, black oak; SO, scarlet oak; HI, hickory; RO, northern red oak; and PO, post oak.

ables describing aspect and site productivity class were found to be significant predictors of diameter growth. However, the influence of these variables on predicted values was limited and no consistent pattern in significant site variables was seen across species.

Fig. 1 depicts the relationship between diameter increment, BAL, and tree diameter among species. Fig. 1 also highlights diameter growth patterns among species and shows that northern red oak, scarlet oak, and black oak have larger ten-year diameter increments than other species at a given tree diameter or BAL level. Hickory and post oak had the smallest ten-year diameter increment.

3.2. Model evaluation and calibration

Fit statistics by species are presented in Table 4. Model bias is minimal, root mean square errors are between 0.26 and 0.45, and model efficiency (R^2) ranged from 0.26 to 0.57. Model fit was better for oak species than for shortleaf pine or hickory. Fig. 2 highlights the distribution of residuals over 10 cm diameter classes. Mean residuals across diameter classes are centered near zero further indicating that model bias is minimal. The distribution of residuals over tree diameter classes indicates higher variability in prediction with the smallest diameter class. This trend is most pronounced for shortleaf pine and hickory; the two models with the highest residual variance (Table 4).

The fit model (Eq. (3)) was applied to the evaluation data. Single tree and standwise calibration were used to predict the random plot effects by species. Fit statistics for the unconditional predicted values and predictions made following calibration are summarized in Table 5. Absolute bias values show that the model generally under predicts ten-year diameter increment for the evaluation dataset. Inclusion of random effects through calibration improved model prediction for all species. RMSE and model efficiency values indicate that model fit was best following single tree calibration and standwise calibration using three trees. Fit statistics also suggest the quality of prediction following calibration approaches that of the original model fitting data for white oak, black oak, scarlet oak, and hickory.

4. Discussion

4.1. Model structure

Distance independent, individual-tree diameter growth models typically include measures of competitive position and/or stand density to account for the effect of competition (Vanclay, 1994). Basal area of larger trees (BAL) and modifications such as BAL/dbh and BAL/log (dbh + 1) are included in models for a wide variety of tree species and are considered indicators of a tree's competitive position in relation to the other trees in a plot or stand (Wykoff, 1990). We found BAL/dbh to be a significant predictor of diameter growth for all species and most strongly related to growth for white, black, scarlet, and northern red oak. Other research has shown competitive position, measured by BAL or modifications of BAL, to be the strongest individual predictor of diameter growth in both even-aged (Adame et al., 2008; Uzoh and Oliver, 2008) and uneven-aged stands (Pukkala et al., 2009).

Inventory data suggests that the majority of stands on the Pioneer Forest are vertically stratified and have diameter distributions that follow a reverse-J shape (*q*-value 1.29, 2.5 cm diameter classes) (Loewenstein et al., 2000). Crown competition factor data indicate that many stands are near or below the minimum density of full site occupancy (CCF = 100) (Krajicek et al., 1961). These data emphasize that stands in the study area have a distinctly different structure and distribution of available growing space than do non-stratified even-aged stands. Under these conditions, inter-tree competition is more likely influenced by a tree's position in the vertical stratum and the competition for light within the stand's vertical profile than by the lack of horizontal growing space at the stand level. Wimberly and Bare (1996) suggest that BAL is an important predictor of diameter growth because it accounts for one-sided competition for light experienced by a tree. The importance of BAL/dbh in our models is likely due to its ability to identify a tree's social ranking and account for inter-tree competition in the heterogeneous uneven-aged stand structures present within the study area.

Models fit for shortleaf pine and hickory also account for competition using another measure of stand density, crown competition

Table 4
Fit statistics and model variance components for the individual-tree diameter increment model (Eq. (3)) by species.

Species	Fit statistics			Variance components	
	Bias	Rmse	R^2	σ^2 plot	σ^2 residual
White oak	3.811E−18	0.2907	0.4340	0.0172	0.0899
Shortleaf pine	−6.077E−18	0.3600	0.3836	0.0355	0.1398
Black oak	3.054E−17	0.2740	0.4044	0.0207	0.0829
Scarlet oak	−8.697E−17	0.2639	0.4934	0.0272	0.0781
Hickory	−7.195E−17	0.3681	0.2554	0.0135	0.1442
N. red oak	3.499E−17	0.2825	0.5745	0.0357	0.0934
Post oak	−5.498E−17	0.2866	0.4201	0.0456	0.0968

factor. While BAL/dbh is still an important predictor for shortleaf pine, crown competition factor has a greater influence on diameter growth. The secondary importance of competitive position for shortleaf pine is likely attributed to the difference in shade tolerance between it and the hardwood species evaluated. Because

of shortleaf pine's intolerance to shade, it does not survive well when suppressed (Lawson, 1990). As a result, shortleaf pine may not persist when in a subordinate canopy position and its growth may be more influenced by horizontal crown competition than by competition within the stand's vertical profile. This situation might
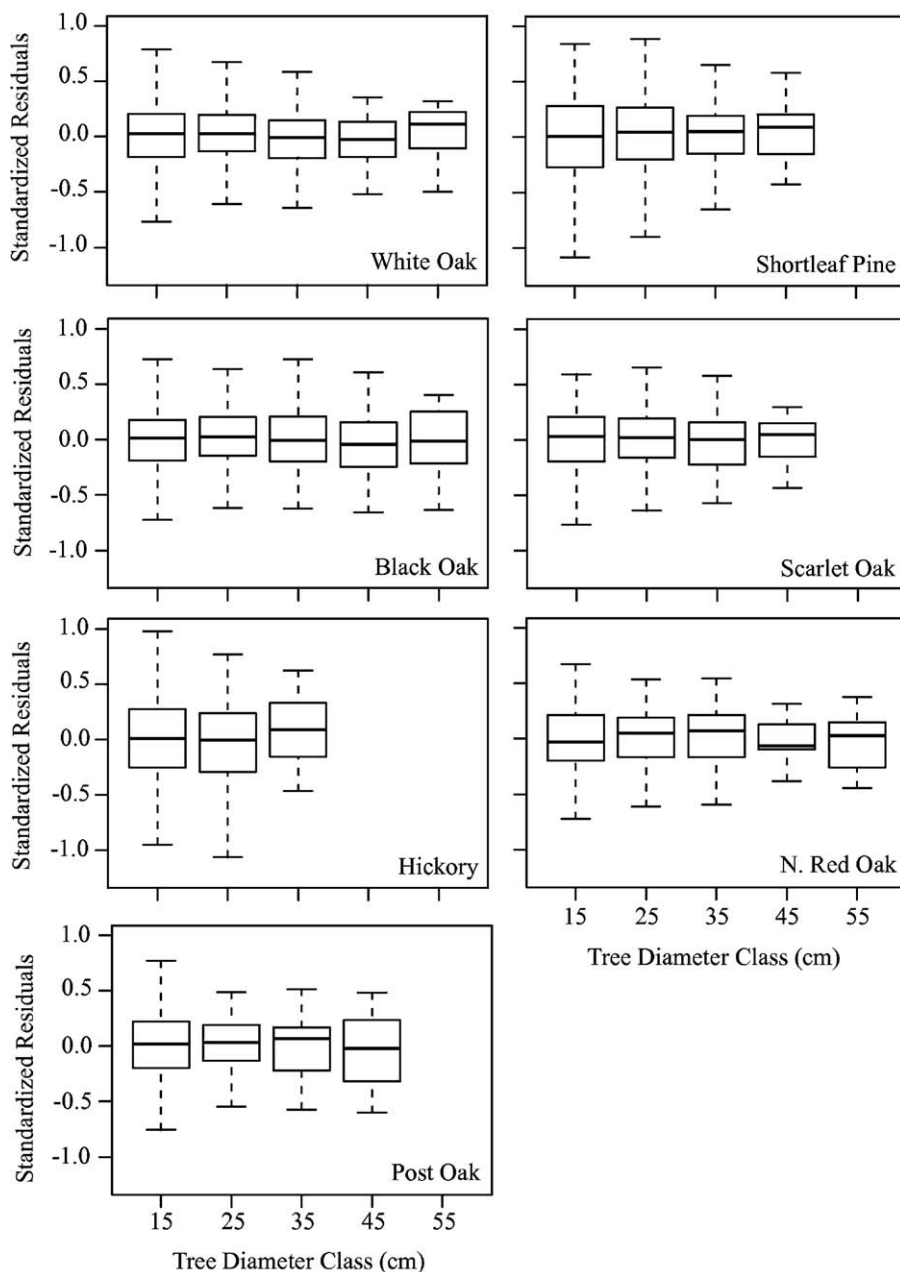

Fig. 2. Standardized residuals by species and diameter class (cm).

Table 5
Fit statistics for fixed effects and calibrated (single tree and standwise calibration) mixed-effects models applied to the evaluation dataset by species.

Species	Fit statistics	Fixed effects	Model calibration			
			Single tree	3 tree	2 tree	1 tree
White oak ($n = 126$)	Bias	−0.0477	−0.0495	−0.0496	−0.0515	−0.0498
	Rmse	0.2960	0.2834	0.2842	0.2864	0.2888
	R^2	0.3475	0.4027	0.3992	0.3908	0.3799
Shortleaf pine ($n = 162$)	Bias	−0.2135	−0.1755	−0.1883	−0.1963	−0.2028
	Rmse	0.4564	0.4222	0.4233	0.4272	0.4376
	R^2	0.1426	0.2187	0.2303	0.2264	0.1970
Black oak ($n = 163$)	Bias	−0.1247	−0.1288	−0.1253	−0.1229	−0.1230
	Rmse	0.2990	0.2714	0.2770	0.2800	0.2856
	R^2	0.2570	0.3933	0.3633	0.3463	0.3199
Scarlet oak ($n = 138$)	Bias	−0.1125	−0.0908	−0.0953	−0.0993	−0.1066
	Rmse	0.2978	0.2486	0.2571	0.2625	0.2750
	R^2	0.2688	0.4712	0.4385	0.4185	0.3697
Hickory ($n = 93$)	Bias	−0.2646	−0.2123	−0.2437	−0.2502	−0.2558
	Rmse	0.4069	0.3657	0.3856	0.3919	0.3980
	R^2	0.0908	0.1492	0.1330	0.1206	0.1078
N. red oak ($n = 25$)	Bias	−0.2184	−0.1572	−0.1689	−0.1803	−0.1953
	Rmse	0.3752	0.3557	0.3590	0.3611	0.3672
	R^2	0.3797	0.3795	0.3797	0.3840	0.3797
Post oak ($n = 17$)	Bias	0.0854	0.0898	0.0907	0.0920	0.0894
	Rmse	0.4813	0.4535	0.4567	0.4646	0.4720
	R^2	0.1521	0.2492	0.2391	0.2131	0.1866

be expected in either an unstratified even-aged stand or where a canopy dominant shade-intolerant cohort is slowly replaced by more tolerant species. Given that much of the shortleaf pine on the Pioneer Forest occurs in pure stands, or as scattered dominant trees, this would seem to be the case and may explain the ranking of variables describing competitive effects for shortleaf pine.

Fig. 1 depicts the predicted ten-year diameter growth of each species in relation to dbh and BAL. The negative coefficient associated with BAL/dbh for each species indicates that diameter growth decreases within increasing BAL and is smallest for trees in highly suppressed competitive positions (i.e., high BAL and small dbh). Models for shortleaf pine and hickory show that growth decreases with increasing stand density. These relationships between competition effects and diameter growth are consistent with established patterns of tree growth and support trends presented by previous research completed within a diversity of forest types (Wykoff, 1990; Vanclay, 1991; Monserud and Sterba, 1996; Uzoh and Oliver, 2008).

Growth patterns highlighted by the models also make sense given the stand structure created by the cutting cycle and marking prescriptions employed on the Pioneer Forest. Following harvest, growing space is available for all trees (recall that the target residual basal area is approximately 15 m² ha⁻¹). However, as the stand recovers from harvest and all trees expand their crowns in response to release, eventually canopy closure occurs and it is the smallest diameter stems that are first affected by competition. Toward the end of the cutting cycle, with increasing BAL (especially in the smallest diameter classes), we observe extremely small diameter increments (Fig. 1). Higher variability observed in the smallest size classes (Fig. 2) may also be a function of temporal variation in growing space availability for these trees. These small, highly variable diameter increments of subordinate trees could be of concern for long term maintenance of diameter structure if suppression results in excessive mortality among the smallest diameter trees. Long-term stability of a reverse-J shaped diameter distribution on the Pioneer Forest suggests that this has not occurred and is likely a function of the fact that harvests are scheduled as stands

approach 22–23 m² ha⁻¹ (Loewenstein, 1996; Loewenstein et al., 2000). Thus, it should be uncommon for many trees to be subjected to a BAL of 25 m² ha⁻¹ or more. As trees are recruited through the vertical strata of an uneven-aged stand, they are less affected by the ebb and flow of growing space present based on time since harvest and diameter growth is more constant and, in most cases, tends to continue to increase with increasing size. Our results for the Pioneer Forest support this uneven-aged growth pattern.

In addition to competition effects, tree size, and species composition, variables describing site productivity also influenced diameter growth. Past research has highlighted the relationship between site quality and diameter growth and has found that both continuous (Monserud and Sterba, 1996; Uzoh and Oliver, 2008) and categorical data (Adame et al., 2008; Pukkala et al., 2009) can be used to quantify site quality. In our models, the categorical variable identifying site productivity class 3 (lowest quality sites) was negatively related to the growth of shortleaf pine, black oak, and northern red oak. Diameter growth of northern red oak was also significantly lower on southern and western aspects than on the more productive north and east slopes. Given the known site sensitivity of northern red oak, the negative impact of poorer quality sites on its diameter growth is consistent with the ecological characteristics of the species. It is unclear why site quality was not found to be a significant predictor for the remaining species. Perhaps the categorical site data available did not appropriately capture the variation in site quality across plots and appropriately represent that variability for those species. Another plausible explanation is that the majority of sites on the Pioneer Forest are low to intermediate quality (12–20 m site index). The influence of this limited productivity range on diameter growth may be difficult to quantify especially given the site data available.

4.2. Model evaluation and calibration

Due to the spatial correlation present among observations made in the same inventory plot (Fox et al., 2001), we used a mixed-

effects model to predict ten-year diameter increment. The inclusion of the random plot effect improved model fit for all species. Other diameter growth studies utilizing mixed-effect models also found that inclusion of random effects for the sampling unit (e.g., tree, plot) improved model fit (Budhathoki et al., 2008; Uzoh and Oliver, 2008; Pukkala et al., 2009). Overall fit of the developed models was generally poorer than previously published research. Model efficiencies can commonly exceed 0.50 for distance-independent individual-tree diameter growth models fit for related forest types (Monserud and Sterba, 1996; Murphy and Graney, 1998; Zhao et al., 2004). The majority of the models we present have model efficiencies below 0.50 (Table 4).

While we evaluated a large suite of predictor variables, it is possible that limited predictive power could have been in part due to data available within the Pioneer Forest CFI database. For example, the lack of accurate tree height and crown geometry data limited our ability to directly assess vertical stand structure and height stratification among trees as well as incorporate important measures of past tree vigor like crown ratio. Relative height (Yang et al., 2009) and crown ratio (Wykoff, 1990; Monserud and Sterba, 1996) have been shown to be significant predictors of diameter growth in mixed-species stands and may be important in uneven-aged stands like those evaluated in this study. There is also the possibility that in some situations it may be difficult to quantify how heterogeneous vertical and horizontal stand structure effects tree growth using the modeling approach presented here. Perhaps, as Peng (2000) suggests, approaches like spatially explicit empirical models or hybrid models integrating physiologic processes need to be evaluated as tools for understanding tree growth in mixed-species, uneven-aged stands. Further research on model structures and statistically techniques used to quantify tree diameter growth in uneven-aged stands is warranted.

The fit models were evaluated using a data subset drawn from plots not included in model fitting; evaluation data also incorporated a different growth period (1982–1992). Inclusion of random effects through calibration improved model performance for all species in the evaluation dataset (Table 5). Our results support Calama and Montero (2005) and Adame et al. (2008) who showed that calibration using a complementary set of previous increment data can greatly improve the predictive ability of a mixed-effects diameter model when applied to an independent dataset. While a slight underprediction bias was seen, RMSE and model efficiency values in our model evaluation suggest the quality of prediction following single tree and standwise calibration using three trees approached that of the original model fitting data for white oak, black oak, scarlet oak, and hickory (Table 5). While calibration did improve model prediction for shortleaf pine, quality of prediction was lower for this species when compared to the other species. The limited number of northern red oak ($n = 25$) and post oak ($n = 17$) observations in the evaluation data limits inferences that can be made about model performance with these species. Our results suggest that calibration can improve prediction of mixed-effects diameter growth models applied outside the dataset used for fitting. From a practical perspective, three tree, standwise calibration may be preferred over single tree calibration as it yielded similar results and required significantly less data.

5. Conclusions

Application of a mixed-effects model was an effective means for estimating tree diameter growth in mixed oak and shortleaf pine stands managed under single-tree selection. The study further supports previous work that predicted individual-tree diameter

growth as function of tree size and competitive position, stand density, species composition, and site quality. Results also highlighted the utility of standwise calibration for improving prediction of diameter growth.

Direct applicability of the presented models is likely restricted to the xeric to dry-mesic oak dominated systems of the Ozark Highlands. Some of the models presented (e.g., hickory) have a marginal predictive ability and readers should exercise caution when using these models for prediction. Nonetheless, the models highlight the need to pay careful attention to the silvics of both crop trees and competitors. They also emphasize the importance of a tree's competitive position as predictor of diameter growth in stands with heterogeneous vertical structure. The concept of social status (vertical structure) affects not only multi-aged forest stands like those evaluated here, but also stratified even-aged stands.

Development of the diameter growth model presented here was by no means a purely theoretical endeavour. Identifying those variables that are significant predictors of growth by species, as well as their relative importance in predicting response, allow us to better understand the relationship between stand structure and growth. Such knowledge is important as it can be utilized to develop or refine silvicultural prescriptions. The model also provides a framework to better understand the biological dynamics that drive tree growth and recruitment under the single-tree selection system practiced on the Pioneer Forest. Such information can help managers create stand-specific prescriptions that enhance growth of desired trees, while maintaining the stand structure required to recruit subordinate trees into the upper strata and to allow for adequate regeneration.

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