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Modeling and Mapping Oak Advance Reproduction Density Using Soil and Site Variables

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Regenerating oaks (*Quercus* spp.) has remained a widespread and persistent problem throughout their natural range. Research shows that abundant oak advance reproduction is crucial for success. Although it is recognized that oak advance reproduction accumulation is inversely related to site quality, there has been little effort to model oak advance reproduction density as a function of measured levels of light, water, or nutrient supply. The objective of this study was to determine whether oak advance reproduction could be modeled and mapped with site variables. The study was conducted on the Sinkin Experimental Forest in southeastern Missouri in 20 5-ha experimental units. Vegetation and site data were collected in 120 0.5-ha circular plots with nested subplots for the inventory of the midstory (0.01 ha) and reproduction (0.004 ha). Site variables included soil available water capacity, pH, photosynthetically active radiation in the understory, forest stocking, terrain shape, and slope-aspect. Oak advance reproduction abundance was related to soil acidity and available water capacity and to other site information such as slope-aspect. Models for the red oak group species generally exhibited better fit than those for the white oaks. There also was evidence that estimates of soil acidity and available water capacity can be obtained from the SSURGO database and used in these oak advance reproduction models along with other site information to generate maps of estimated oak reproduction densities. These maps could be used for planning silvicultural interventions to increase the abundance and size of oak advance reproduction before forest regeneration.

Keywords: oak advance reproduction, oak regeneration, site factors, modeling, *Quercus* spp.

Oaks (*Quercus* spp. L.) are widely distributed with more than 500 oak species worldwide including at least 20 in Europe and more than 90 species in North America (Mabberley 2008). They are particularly important in eastern North American forests where about 30 oak species occur in 23 different forest types (Little 1979, Johnson et al. 2009). Oaks in eastern North America are highly valued both economically and ecologically (Brose et al. 2012). The durable wood produced from oaks is used for flooring, fine furniture, construction material, and railroad ties (Smith 1993), and acorns are considered the most important wildlife food (McShea and Healy 2002). Even though oaks are abundant and widely distributed, regenerating oaks has remained a widespread and persistent problem in eastern North American forests (Loftis and McGee 1993, Kabrick et al. 2008, Nowacki and Abrams 2008, Arthur et al. 2012) and elsewhere throughout their worldwide range (Watt 1919, Thadami and Ashton 1995, Li and Ma 2003, Götmark et al. 2005, Pulido and Díaz 2005, Zavaleta et al. 2007).

Several decades of research to address the oak regeneration problem has led to the conclusion that the quantity of oaks in the future stand created after harvesting is largely a function of the number and size of the advance reproduction (Carvell and Tryon 1961, Sander et al. 1976, Sander et al. 1984, Loftis 1990, Dey et al. 1996, Belli et al. 1999, Gould et al. 2006). Oak advance reproduction, which includes the seedlings and seedling sprouts that have accumulated in the forest understory before a canopy-removing disturbance, has a greater probability of recruiting into the overstory after a canopy

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disturbance than do new oak seedlings established at the time of canopy removal (Sander 1971, Sander et al. 1984, Johnson et al. 2009).

It has long been recognized that the ability of oak advance reproduction to persist and accumulate in the understory is related to site quality (Carvell and Tryon 1961, Trimble 1973, Sander et al. 1984, Loftis 1990, Lorimer 1993) and other biotic and abiotic factors (Fei and Steiner 2008). Stands having lower site quality generally have less available soil water and/or fewer nutrients and consequently support fewer oak competitors to shade or displace oak seedlings in the understory (Fei and Steiner 2008, Johnson et al. 2009). Oaks are more drought tolerant than many of their competitors and are better able to survive on droughty sites (Johnson et al. 2009). Under these conditions, oak seedlings that establish after an abundant acorn crop are more likely to survive in the understory, particularly in the absence of competitors that otherwise reduce light availability. During the ensuing years, oak shoots may occasionally die back and resprout as the oak root systems continue to grow. Through this process, oaks can develop the large root systems needed for producing rapid shoot growth and remaining competitive with other species after a disturbance to the canopy (Sander 1971, Sander et al. 1984, Johnson et al. 2009).

Despite recognizing a relationship between site variables and oak regeneration potential, there have been few attempts to link measured levels of light or physical measurements of soil water and nutrient supply to the abundance of advance reproduction in undisturbed forest landscapes. In most oak regeneration studies, light, moisture, or nutrient supply gradients have been inferred by using surrogate variables such as site index, slope position, slope-aspect, and canopy cover (Sander et al. 1984, Walters 1990, Dey 1991, Dey et al. 1996, Larsen et al. 1997, Fei and Steiner 2008), physiographic province (Fei and Steiner 2008, Dey et al. 2009), and soil series or land type (Fei and Steiner 2008, Kabrick et al. 2008). These surrogate variables have been used largely because they can be readily determined by observation during routine forest inventories without expensive and time-consuming field and laboratory analyses needed for quantifying resource availability. However, the increasing availability of spatially explicit soil information through the US Soil Survey Geographic (SSURGO) database provides a means for estimating water and nutrient supply. This information can be combined with other stand data such as overstory density or light levels reaching the reproduction layer for mapping estimates of oak advance reproduction density in mature oak forests that have reached the understory reinitiation stage of stand development (*sensu* Oliver and Larson 1996). Maps of oak advance reproduction density can be can used as a planning tool for foresters to identify where in the landscape silvicultural interventions are needed to ensure oak regeneration success.

The objectives of this study were to determine whether models can be developed for estimating oak advance reproduction using metrics of soil water, soil nutrient, and light supply and to determine whether or not these models could be linked to remotely sensed information for predicting oak advance reproduction abundance. Here metrics of soil nutrient and water supply included the soil pH and the available water capacity, terrain shape, and slope-aspect, and metrics of light supply included the measured photosynthetically active radiation in the understory and stand density. This investigation is part of a larger regional study examining oak regeneration dynamics across the southern United States (hereafter referred to as the Regional Oak Study [ROS]). A major objective of the ROS is to further the understanding of oak regeneration and ecology with emphasis on the development of management guidelines that will increase oak regeneration success. In this article, the focus is on the Ozark Highlands where oak advance reproduction generally accumulates and persists in the understory for long periods of time, but where there is still considerable variation that appears to be related to site conditions (Sander et al. 1984, Dey 1991, Kabrick et al. 2008).

Methods

Study Location

The study was conducted in the Sinkin Experimental Forest (SEF) located in southeastern Dent County, Missouri, USA, in stands that had not been harvested or thinned for at least 40 years. Study sites are within the Current River Hills Subsection of the Ozark Highlands (Nigh and Schroeder 2002). Data from a weather station located on the SEF indicated that during the past decade the average annual precipitation was 1,300 mm with about 61% falling between April and September. The average temperature was 14° C annually, 24° C during the summer (June, July, and August), and 2° C during winter (December, January, and February). This region has narrow ridges and steep side slopes with a relief of 60 m. The soils developed in parent materials derived from sandstone and dolomite layers of the Roubidoux and Gasconade formations and are highly weathered, droughty, and strongly acid and contain a high percentage of rock fragments. Information obtained from the Missouri Cooperative Soil Survey[1] indicated that common soil series on ridge tops and upper slopes were derived from the Roubidoux and Gasconade formations and included Coulstone and Clarksville (both Typic Paleudults), Hobson (Oxyaquic Fragiudalfs), Lebanon (Typic Fragiudults), and Nixa (Glossic Fragiudults). Soils on the lower hillsides developed in parent materials derived from the lower portion of the Gasconade formation generally are less weathered. Some of these soils are greatly influenced by the underlying dolomite and consequently contain clayey residuum that has a greater cation exchange capacity, fewer rock fragments, and a greater available water capacity than those in soils in higher landscape positions. The most common soil series on lower hillsides include Clarksville and Doniphan (both Typic Paleudults) and Moko (Lithic Hapludolls). Outcrops of dolomite occur with some of the Moko soils.

Vegetation Data Collection

Vegetation data were collected in 20 rectangular 5-ha experimental units each established along a single hillslope. In these experimental units, four contrasting oak regeneration methods will be compared as part of the ROS. However, the data used in this article were pretreatment and were collected in undisturbed, mature upland oak and oak-pine stands. Within each experimental unit were six circular, 0.05-ha overstory sampling plots positioned evenly within the 20 treatment units, providing a total of 120 sample locations. Trees >25 cm dbh were inventoried within each 0.05-ha (overstory) plot, and trees of 5 to 25 cm dbh were inventoried within a concentrically nested circular 0.01-ha (midstory) plot. Data recorded included species, crown class, and dbh to the nearest 0.1 cm. Trees of <5 cm dbh were inventoried within a 0.004-ha circular (regeneration) plot located 8 m from the center of the 0.05-ha overstory plot at a 45° azimuth. This offset ensured that the advance reproduction was not disturbed during measurement of the overstory and midstory. Trees in regeneration plots were tallied by species in 6 height/diameter classes: (1) ≤30 cm tall; (2) 30–59 cm tall; (3) 60–89 cm tall; (4) 90–120 cm tall; (5) ≥120 cm tall to 3.8 cm

dbh; and (6) ≥3.8–5.0 cm dbh. Heights were determined to the nearest 1.0 cm, and diameters were determined to the nearest 0.1 cm.

Within each overstory plot, a single dominant or codominant tree was selected for site index estimation based on guidelines by Carmean et al. (1989). Preferred site index trees were red oak species (*Quercus* spp. L.; section Lobatae), followed by white oaks (*Quercus* spp. L.; section Quercus) and shortleaf pine (*Pinus echinata* Mill.). The height of each site index tree was measured to the nearest 0.1 m using an Impulse 200 laser. An increment core was removed at breast height of each site index tree, and the rings were counted with the aid of a hand lens. Site index was calculated for individual trees using relationships developed for oaks and shortleaf pine in Missouri (Nash 1963, McQuilkin 1974). All site index values were then converted to a black oak (*Q. velutina* Lam.) site index basis for comparison (McQuilkin 1976).

Inventories indicated that the overstory trees had an average age of 82 years, and oaks were the dominant species, contributing 59% of the basal area. Of the oak species present, white oak (*Quercus alba* L.) comprised 22% of the basal area, black oak 21%, scarlet oak (*Quercus coccinea* Muench.) 12%, and northern red oak (*Quercus rubra* L.) 4%. Shortleaf pine comprised 22% of the basal area. Other species by basal area included hickory species (*Carya* spp.) (7%), slippery elm (*Ulmus rubra* Muhl.) (2%), flowering dogwood (*Cornus florida* L.) (2%), blackgum (*Nyssa sylvatica* Marsh.) (2%), black walnut (*Juglans nigra* L.) (2%), red maple (*Acer rubrum* L.) (1%), and sugar maple (*Acer saccharum* Marsh.) (<1%). Spice bush (*Lindera benzoin* [L.] Blume) and Carolina buckthorn (*Frangula caroliniana* [Walter] A. Gray) were also present in the understory.

Site Variables

In vegetation plots, the slope-aspect, the percent slope, and the shape of the land surface were measured. Slope-aspect was measured from the plot center in the direction of the steepest slope using a handheld compass and clinometer. Aspect was transformed to a linear value ranging from 0 for southwest aspects (azimuth of 225°) to 2 for northeast aspects (azimuth of 45°) following the model developed by Beers et al. (1966), in which the transformed aspect (TASPECT) = cos(45 − aspect) + 1 (Beers et al. 1966). The terrain shape was quantified using the terrain shape index (TSI) as described by McNab (1989) from the center of each plot using a handheld clinometer. Specifically, at each plot center, measurements were made starting in the direction of the aspect and then rotating clockwise in 45° increments for a total of eight slope measurements. The slope from the plot center to the plot perimeter (12.6 m) measured parallel to the land surface was recorded. Slopes were recorded as percentages, with down-slope measurements recorded as negative values and up-slope measurements as positive values. All eight measurements were summed and divided by eight to obtain an average TSI value.

Soils were sampled in a single 1-m-deep excavation within each 0.05-ha overstory plot adjacent to the 0.004-ha reproduction plot. In each pit, soil horizons were identified and described according to standard soil survey procedures (Schoeneberger et al. 2012), the percent volume of coarse fragments of >2 mm in diameter in each horizon was estimated, and samples from each horizon were collected for laboratory analysis. Soil samples were air dried, crushed, sieved to remove coarse fragments, and analyzed for particle size determination by the pipet method, pH, exchangeable base cations including calcium, magnesium, sodium, and potassium, and the exchangeable acidity by titration. All methods were completed according to the US Department of Agriculture (2004). The pH measurements were made using a 1:1 ratio of soil to water (pH_w) and a 1:2 ratio of soil to 0.01 M $CaCl_2$ solution (i.e., salt pH [pH_s]). Percent base saturation (BS) was calculated for each horizon by summing extractable bases (calcium, magnesium, sodium, and potassium) and dividing by the sum of the extractable bases plus exchangeable acidity. Soil pH and BS were converted to a profile basis by weighting values of individual horizons proportionally by their thickness and summing values for each profile. Before this calculation, the pH values were converted to a hydrogen ion concentration basis. An estimate of available water capacity (AWC) was then calculated using the laboratory-determined particle size distribution to identify the texture class for each horizon. Estimates of AWC were assigned to each horizon based on soil texture using numeric values for similar soils in Missouri reported in the Cooperative Soil Survey. Values used were 0.10 cm/cm for sandy loams, 0.14 cm/cm for sandy clay loams, 0.15 cm/cm for clays and silty clays, 0.18 cm/cm for silt loams, and 0.19 cm/cm for clay loams, loams, and silty clay loams. The AWC for each soil horizon was calculated using the formula: AWC (horizon) = [horizon thickness × AWC (for the texture class) × fine-earth fraction]. For horizons with fragipans, the AWC was reduced by 50% if roots were noted within the fragipan. If no roots were present within or below the fragipan, an AWC of 0 was assigned to the fragipan and all underlying horizons. A profile-level AWC was then generated by summing the AWC of each soil horizon to a depth of up to 1 m.

Photosynthetically active radiation (PAR) was measured using Smart Sensors with a HOBO Micro Station (Onset Computer Corporation, Bourne, MA). A PAR sensor was mounted on a camera tripod placed at the regeneration plot center and leveled at a height of 0.9 m, approximately the height at or just above the reproduction canopy. For each plot, PAR was logged every hour for a single 24-hour period and was expressed relative to PAR in full sunlight by dividing the sum of hourly PAR values logged in the vegetation plots by the sum of the hourly PAR values logged over the same 24-hour period nearby in the open. Because of a limited number of sensors, PAR was measured on a subset of plots during a given 24-hour period. All measurements were made during a 4-week time period from September 10 to October 10.

The percent stocking (*sensu* Gingrich 1967) of the overstory and midstory was calculated using the plot inventory data. Stocking values were calculated on a per tree basis and expanded to a per hectare basis at the vegetation plot level. Equations for estimating hardwood stocking were from Gingrich (1967), and equations for estimating shortleaf pine stocking were from Rogers (1983).

Model Development and Comparisons

Multiple linear regression was used to model relationships between the abundance of advance reproduction and metrics indicative of water, nutrient, and light supply including the soil pH_w, AWC, TSI, TASPECT, and PAR. The soil pH_w is a simple indicator of nutrient supply, and the AWC is an estimate of the amount of plant-available water potentially supplied by the soil. The TSI and TASPECT collectively provide information about the land surface shape and orientation, which greatly affect soil water movement and availability. PAR measured 0.9 m above the forest floor provided a measure of the light availability to the advance reproduction in the understory. These variables were selected because collectively they

provide a measure of nutrient, water, and light availability for seedlings and because the soil and terrain metrics are also readily available in other spatial information systems such as in the SSURGO database. Before analysis, the correlation among explanatory variables was examined using the Pearson's correlation coefficients (Proc Corr, SAS version 9.1; SAS Institute, Inc., Cary, NC) to avoid multicollinearity. There was a slight correlation between AWC and TASPECT ($r = 0.24$, $P = 0.01$) and between pH and TASPECT ($r = 0.27$, $P = 0.01$), indicating that soils of southwest-facing slopes have a slightly greater volume of coarse fragments than soils on northeast-facing slopes, which decreases the soil's ability to hold water and supply base cations. However, TASPECT was included in some models along with AWC and pH because it is also a measure of water and nutrient demand by plants rather than of water and nutrient supply.

The model form was $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n$, where Y is the abundance of reproduction per hectare, β_0 is the intercept, and $\beta_1, \beta_2, \ldots \beta_n$ are parameters for the site variables $X_1, X_2, \ldots, X_n$. Initially, the oak reproduction density models were developed by treating each of the 120 sampling locations as independent observations. The general linear mixed models procedure in SAS statistical software (Proc GLIMMIX, SAS version 9.3) was used to estimate model parameters. Because they fit best to the data, the oak reproduction densities were modeled as gamma distributions after adding 0.001 to eliminate 0 values from vegetation plots having no oak seedlings.

However, many of the models for estimating white oak reproduction density and all of the models for estimating the large oak reproduction density failed to converge because of the variability of the data. Consequently, a second modeling approach was taken in which data from the six regularly-spaced sampling points within each of the 20 experimental units were averaged before the analysis and thereby results from each of the experimental units were treated as independent observations (Table 1). Because of its logarithmic scale, soil pH values were averaged as hydrogen ion concentrations and transformed back to pH for model development. Averaging data from the six plots per experimental unit had the effects of normalizing the oak reproduction densities and eliminating the zero values and also reducing the variation in the explanatory variables. This procedure greatly simplified the analytical requirements, and, consequently, the modeling was conducted using the regression procedure in SAS statistical software (Proc Reg, SAS version 9.3) using the same model form as that for the nonaveraged data set.

Because of concern that averaging the data within experimental units may have changed the outcome, models generated using the averaged data were compared with those generated using the nonaveraged data (for models that converged). In most comparisons, the models fit with either data set yielded similar results, suggesting that the data averaging did not substantially change the outcome.

The models examined initially included all five variables (pH_w, AWC, TSI, TASPECT, and PAR), identified as the "full" models in Table 2. However, we recognized that we could have selected different variables or constructed simpler models with fewer explanatory variables. For example, we could have selected the variable pH_s or BS rather than pH_w as a measure of nutrient availability or overstory stocking rather than PAR as a measure of understory light levels. Similarly, we also recognized that simpler models with fewer explanatory variables may be as suitable for estimating oak advance reproduction as the full models with all five variables. To compare alternative models having fewer explanatory variables or with surrogate measures for nutrient supply (e.g., BS or pH_s), an information-theoretic approach was used (Burnham and Anderson 1998). As per this approach, alternative models (hypotheses) were compared using Akaike's information criterion (AIC). The Akaike weights (W_i) were generated as suggested by Burnham and Anderson (1998) and used to judge model fit. To generate W_i, the following formula was used

$$W_i = \frac{\exp\left(-\frac{1}{2}\Delta i\right)}{\sum_{r=1}^{R} \exp\left(-\frac{1}{2}\Delta r\right)}$$

where W_i is the weight of the ith model, Δi is the difference between the lowest AIC score and the AIC score of the ith model, and R is equal to the total number of models compared.

Pearson's correlation coefficients were used to compare oak advance reproduction densities with overstory oak stocking or with the seedling densities of other species.

Table 1. Site and vegetation variables averaged by experimental unit (n = 20).

Variables	Average	SD	Minimum	Maximum
Site variables				
Site index (m)	22	2	19	26
AWC (cm)	8.8	1.3	5.6	10.7
BS	0.27	0.08	0.15	0.41
pH_w	5.1	0.2	4.8	5.4
pH_s	4.3	0.2	3.9	4.6
TASPECT	1.1	0.6	0.1	1.9
TSI	0.99	1.96	−1.88	6.40
PAR (% full sunlight)	10	4	5	25
Vegetation variables				
Percent stocking, all trees	95	12	78	118
Percent stocking, oaks	53	10	30	73
Percent stocking, oaks >25 cm dbh	36	11	16	50
Percent stocking, red oaks	29	12	11	55
Percent stocking, red oaks >25 cm dbh	25	12	7	46
Percent stocking, white oaks	24	10	7	45
Percent stocking, white oaks >25 cm dbh	10	6	3	22
Oak reproduction (stems ha^{-1})	5,133	2,286	2,167	10,917
Large oak (>30 cm tall) advance reproduction (stems ha^{-1})	1,475	990	167	3,958
Red oak advance reproduction (stems ha^{-1})	3,398	1,489	1,125	6,500
White oak advance reproduction (stems ha^{-1})	1,735	1,172	292	4,417

Variables are as follows: SI, site index; AWC, available water capacity; BS, base saturation (decimal form); pH_w, soil pH determined in a 1:1 ratio of soil and water and averaged in hydrogen ion concentration form; pH_s, soil pH determined in a 1:2 ratio with soil and 0.01 M $CaCl_2$ and averaged in hydrogen ion concentration form; TASPECT, Beers-transformed aspect; TSI, terrain shape index; PAR, photosynthetically active radiation; and Stocking, Gingrich (1967) stocking percentage.

Table 2. Oak advance reproduction model alternatives.

Model	Parameter estimates						AIC	W_i	P	R^2	$MSE^{1/2}$
	β_0 (intercept)	β_1 (pH_w)	β_2 (AWC)	β_3 (TASPECT)	β_4 (TSI)	β_5 (PAR)					
All oaks											
1 (full)	49,972[a]	−7,663[a]	−758[a]	−271	77	10,329	284	0.24	0.01	0.78	1,083
2	49,864[a]	−7,245[a]	−849[a]	−449	94		286	0.11	0.01	0.75	1,143
3	50,434[a]	−7,313[a]	−868[a]	−414			285	0.22	0.01	0.75	1,124
4[b]	54,118[a]	−7,992[a]	−946[a]				283	0.42	0.01	0.76	1,111
Red oaks											
5 (full)[b]	25,586[a]	−3,385[a]	−605[a]	−371	−33	7,839[c]	269	0.36	0.01	0.76	732
6	25,504[a]	−3,068[a]	−674[a]	−506	−20		271	0.11	0.01	0.72	789
7	25,380[a]	−3,053[a]	−670[a]	−514			269	0.29	0.01	0.74	765
8	29,944[a]	−3,894[a]	−766[a]				270	0.24	0.01	0.72	787
White oaks											
9 (full)	24,386[a]	−4,279[a]	−153	99	111	2,490	279	0.04	0.04	0.36	941
10	24,360[a]	−4,178[a]	−175	57	115		277	0.09	0.02	0.39	916
11	25,054[a]	−4,261[a]	−199	99			277	0.12	0.01	0.38	920
12	24,174[a]	−4,098[a]	−180				275	0.31	0.01	0.42	893
13[b]	23,826[a]	−4,340[a]					274	0.44	0.01	0.41	897
Large oaks (>30 cm tall and <5 cm dbh)											
14 (full)	7,772	−694	−232	−809[a]	86	754	266	0.13	0.01	0.52	685
15	7,764	−663	−238	−822[a]	87		264	0.37	0.01	0.55	663
16[b]	8,293	−729	−257[c]	−790[a]			264	0.45	0.01	0.54	667
17	15,309[a]	−2,019[c]	−405[a]				268	0.05	0.01	0.40	763

Model form is $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \cdots + \beta_n X_n$, where Y is the oak advance reproduction density (stems/ha), β_0 is the intercept and β_n are parameters for the site variables: X_1 is pH_w, X_2 is AWC, X_3 is TASPECT, X_4 is TSI, and X_5 is PAR (in decimal form). The "full" model includes all five variables and the models listed below each full model are alternative models with fewer variables. AIC is the Akaike information criterion score, W_i is the Akaike weight indicating relative support for the model, P is the overall model P value, R^2 is the coefficient of determination, and $MSE^{1/2}$ is the square root of the model mean square error.

[a] Effect significance, $P < 0.05$.

[b] Models 4, 5, 13, and 16 are the best supported models.

[c] Effect significance $0.05 < P < 0.10$.

Model Validation

To examine the suitability of linking the oak advance reproduction models to SSURGO databases for predicting oak seedling densities in undisturbed stands, modeled data were compared with actual reproduction data (i.e., validation data set) derived from a study conducted elsewhere on the SEF. In the validation data set described by Kabrick et al. (2011), oak advance reproduction <4 cm dbh was tallied in 30-cm height classes in 48 0.02-ha circular plots. For modeling all oak advance reproduction (model 4 in Table 2, which required the soil pH and the AWC), the water pH (weighted by horizon thickness), and the AWC of the validation plot, each for a 100-cm soil depth, were obtained from the Web Soil Survey.[1] For modeling the large oak advance reproduction (model 16 in Table 2, which required the pH, AWC, and slope-aspect) the slope-aspect of each validation plot was derived with a 30-m resolution digital elevation model. When one or more of the 48 validation plots occurred in a location having the same pH and AWC or the same pH, AWC, and slope-aspect class, the modeled oak advance reproduction densities were averaged. This yielded six different data points for validating estimates of the category "all oak" advance reproduction and nine different data points for validating estimates of the large oak advance reproduction. To assess model fit, the root mean square error (RMSE) was calculated

$$\mathrm{RMSE} = \sqrt{\left(\sum_{i=1}^{n} \mathrm{error}^2\right) \Big/ n}$$

where the error is the difference between the actual and the model oak reproduction density for n comparisons. Maps of modeled oak reproduction densities were created for the SEF and surrounding forest area by applying the models to individual soil polygons using the soil pH and AWC values for each soil map unit and the slope-aspect derived from a digital elevation model.

Results

All of the oak advance reproduction abundance models examined (Table 2) produced significant results ($P \leq 0.05$), but some models exhibited better fit than others as indicated by the AIC scores, Akaike weights, and R^2. For example, the best fit model for the category all oaks was model 4, which included pH_w and AWC as the only site variables. However, the best fit model for the red oak group (model 5) also included the site variables TASPECT, TSI, and PAR, suggesting that inclusion of these three variables improved the overall model fit even though they each were not significant effects. For white oaks, the simplest model (model 13), which included pH_w as the only site variable, had the best overall fit. The parameters for these models indicated that, in general, oak advance reproduction increased with decreasing soil water supply and/or increasing soil acidity (Figure 1). The relationship between the advance reproduction and site variables appeared to be more important for red oaks than for white oaks as indicated by the greater R^2.

Because large oak advance reproduction is generally more competitive than small oak advance reproduction after canopy removal (Loftis 1990, Dey et al. 1996, Johnson et al. 2009), models for estimating the density of oaks >30 cm tall were compared (Table 2). This size threshold was selected because research in this region has shown that oak advance reproduction >30 cm tall is from 1 to 10 times more likely to become a canopy dominant after release than smaller oak advance reproduction (Sander et al. 1984). The best fit model (model 16) included the site variables pH_w, AWC, and the variable TASPECT, which was a significant effect in all models for

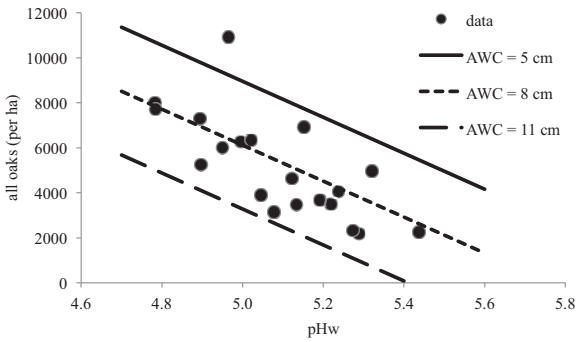

Figure 1. Relationships among oak advance reproduction density, pH_w, and AWC. Lines are modeled values (Table 2, model 4), and filled circles are actual values.

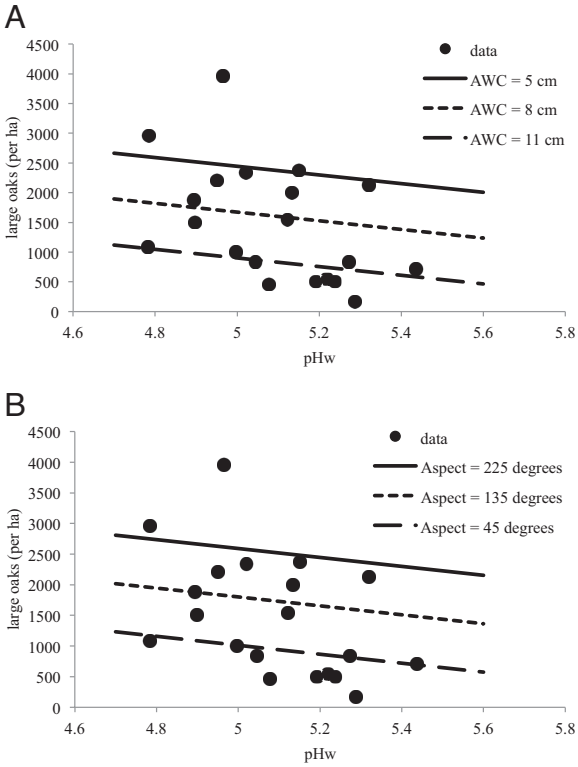

Figure 2. Relationships among large oak advance reproduction density, pH_w, and AWC where slope-aspect = 135° (A) and slope-aspect where AWC = 8 cm (B). Lines are modeled values (Table 2, model 16), and filled circles are actual values.

large oak advance reproduction that were examined. The parameters for these models indicated that large advance reproduction increased as the slope-aspect became more southwesterly (i.e., as TASPECT approached 0) (Figure 2).

Alternative models for estimating the abundance of all oak advance reproduction (model 4) were developed by substituting pH_s (the salt pH), BS, or $BS^{0.5}$ for the pH_w (models 4b through 4d in Table 3) to determine whether these were better predictors of oak advance reproduction density. Although all models were significant, the AIC scores, Akaike model weights, and R^2 each indicated that substituting pH_s or the BS decreased model fit.

Correlations between oak advance reproduction density and oak stocking in the overstory were examined to determine whether the species composition and abundance of the oak advance reproduction was related to the species composition and abundance of the acorn-producing trees in the stand. The only significant correlation occurred with the white oak group species ($r = 0.54$, $P = 0.01$). Consequently the two best white oak models (models 12 and 13 in Table 2) were refit to include the stocking of white oaks of >25 cm dbh, which significantly improved the overall fit of each model (Table 4).

Table 3. Comparison of oak advance reproduction models using different measures of soil nutrient supply.

Model (all oak advance reproduction based on model 4 from Table 2)	AIC	W_i	P	R^2
4.[a] Intercept[b] + AWC[b] + pH_w[b]	283	0.65	0.01	0.76
4b. Intercept[b] + AWC[b] + pH_s[b]	285	0.34	0.01	0.75
4c. Intercept[b] + AWC[b] + BS[b]	294	0.01	0.01	0.59
4d. Intercept[b] + AWC[b] + $BS^{0.5}$[b]	294	0.01	0.01	0.60

Effects are AWC (cm), pH_w, pH_s, and BS. Model form is $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3$. AIC is the Akaike information criterion score, W_i is the Akaike weight indicating relative support for the model, P is the overall model P value, and R^2 is the coefficient of determination.
[a] Model 4 is the best model.
[b] Effect significance $P \leq 0.05$.

Correlations between the oak advance reproduction density and the advance reproduction of other species were also examined (Table 5). In general, oak advance reproduction density was inversely related to the reproduction density of nonoak species. However, there were a few individual species that appeared to be associated, either positively or negatively, with oak advance reproduction. For example, sassafras (*Sassafras albidum* [Nutt.] Nees) advance reproduction density was positively correlated to oak advance reproduction density. In contrast, the combined abundance of spice bush and Carolina buckthorn in the regeneration size class was negatively correlated to the abundance of red oak advance reproduction. These correlations indicated that sassafras reproduction occurs on sites where oak reproduction is abundant, whereas spice bush and Carolina buckthorn are more abundant where oak advance reproduction is either not abundant or simply not present.

To evaluate the utility of linking the oak advance reproduction models with SSURGO data for predicting the oak advance reproduction density, modeled oak advance reproduction densities were compared with actual values made from an independent data set collected in mature stands that had reached the understory reinitiation stage. The soil pH and AWC data required for modeling the advance reproduction density were obtained from the SSURGO database and the slope-aspect was derived from a digital terrain model. Overall, the RMSE ranged from 1,393 stems ha^{-1} for the estimates of the large oak advance reproduction density to 1,490 stems ha^{-1} for the estimates of all oak advance reproduction. There was better agreement between the modeled and actual oak reproduction density for estimating all oaks than for estimating the large oaks (Figure 3). Maps of the modeled oak advance reproduction density were developed using slope-aspect information and the SSURGO soil map unit polygons and their associated estimates of pH and AWC (Figure 4).

Discussion

Models indicated that the abundance of oak advance reproduction increased with decreasing nutrient supply and water holding capacity, and the two most important variables were pH and AWC (Table 2). For the abundance of large (>30 cm tall) oak advance

Table 4. White oak advance reproduction models with and without the stand stocking of white oaks >25 cm dbh (β_1) as a predictor variable.

Models	Parameter estimates				AIC	W_i	P	R^2	$MSE^{1/2}$
	β_0 (intercept)	β_1 (stocking)	β_2 (pH_w)	β_3 (AWC)					
12	24,174[a]		−4,098[a]	−180	275	0.06	0.01	0.42	893
12b[b]	18,281[a]	93[a]	−2,883[a]	−324[a]	268	0.79	0.01	0.60	738
13	23,826[a]		−4,340[a]		274	0.03	0.01	0.41	897
13b	19,151[a]	70[a]	−3,567[a]		271	0.15	0.01	0.51	817

Models 12 and 13 are from Table 2. Model form is $Y = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3$, where Y is the oak advance reproduction density (stems per ha), β_0 is the intercept and β_n are parameters for the variables: X_1 is the stocking of white oaks >25 cm dbh (stocking), X_2 is pH_w, and X_3 is AWC. AIC is the Akaike information criterion score, W_i is the Akaike weights indicating relative support for each model, P is the overall model P value, R^2 is the coefficient of determination, and $MSE^{1/2}$ is the square root of the model mean square error. Missing values indicate where the variable was omitted from the model.
[a] Effect significance, $P < 0.05$
[b] Model 12b is the best model.

Table 5. Pearson's correlations among advance reproduction densities of oaks and other species.

Species	All oaks	Large oaks	Nonoaks	Maples	Flowering dogwood	Sassafras	Blackgum	Spicebush + carolina buckthorn
All oaks	1	0.80 (<0.01)[a]	−0.62 (<0.01)[a]	−0.23 (0.32)	0.14 (0.57)	0.81 (<0.01)[a]	0.14 (0.54)	−0.64 (<0.01)[a]
Large oaks		1	−0.73 (<0.01)[a]	−0.23 (0.32)	−0.14 (0.55)	0.60 (0.01)[a]	−0.09 (0.70)	−0.57 (<0.01)[a]
Nonoaks			1	0.21 (0.38)	0.27 (0.25)	−0.31 (0.18)	−0.06 (0.79)	0.68 (<0.01)
Maples				1	0.12 (0.61)	0.24 (0.32)	0.12 (0.62)	−0.11 (0.63)
Flowering dogwood					1	0.37 (0.11)	0.09 (0.72)	−0.16 (0.50)
Sassafras						1	0.27 (0.25)	−0.5 (0.02)[a]
Blackgum							1	−0.27 (0.26)
Spicebush + Carolina buckthorn								1

Species (groups) are maple = red maple (*Acer rubrum* L.) + sugar maple (*Acer saccharum* Marsh.), flowering dogwood (*Cornus florida* L.), sassafras (*Sassafras albidum* [Nutt.] Nees), blackgum (*Nyssa sylvatica* Marsh.), spice bush (*Lindera benzoin* [L.] Blume) + Carolina buckthorn (*Frangula caroliniana* [Walter] A. Gray). P values are in parentheses.
[a] Significant relationships.

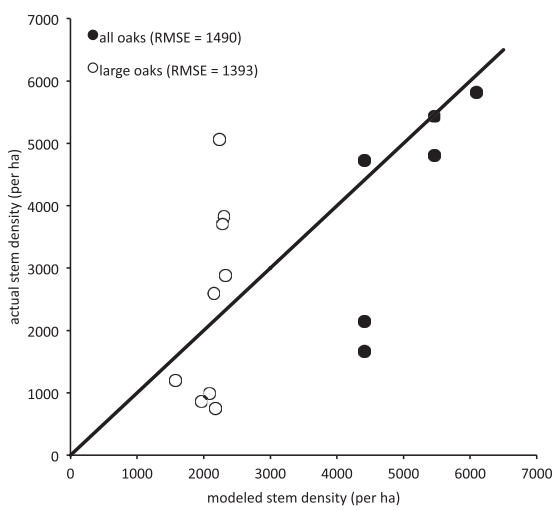

Figure 3. Relationship between the modeled and actual oak advance reproduction density (validation data set). Solid line indicates a 1:1 relationship between modeled and actual oak reproduction density.

reproduction, aspect was also an important and statistically significant determinant, with the relatively drier southwest-facing aspects possessing greater quantities of large oak reproduction than northeast-facing aspects. It has long been recognized that oak advance reproduction is more abundant on southwest-facing slopes (Carvell and Tryon 1961, Hodges and Gardiner 1993, Fei and Steiner 2008, Johnson et al. 2009) because they are drier. Oaks are capable of maintaining greater leaf turgor and photosynthesis rates under drought conditions than associated species in oak-hickory forests (Hinckley et al. 1978, Bahari et al. 1985). The drier site conditions limit the number of oak competitors in the advance reproduction layer by either preventing their establishment or by reducing their survival rate, thereby allowing the relatively drought-tolerant oak advance reproduction to accumulate in the understory (Johnson 1992, Ashton and Larson 1996). Our data confirmed that the abundance of large oak advance reproduction is significantly related to a site's slope-aspect and inversely related to soil AWC, one of the most important metrics of soil water supply. Terrain shape as indicated by the TSI also strongly influences water availability and consequently site quality in the southern Appalachians (McNab 1989), but TSI was not a significant variable in our models.

Although water supply is most commonly identified as an important factor associated with oak advance reproduction abundance, soil pH_w was significant in most of the models that we examined (Table 2), indicating that the abundance of oak advance reproduction increased with increasing soil acidity. Soil pH is also an important indicator of nutrient supply because it is strongly related to base cation concentrations in soil solution (Bigelow and Canham 2002) and inversely related to the concentration of aluminum, which is toxic to many plants (Schaedle et al. 1989, Cronan and Grigal 1995). Although oaks are capable of growing on sites having a wide range in soil pH, many oak species tolerate soil acidity or high soil aluminum concentrations better than do many oak competitors (Cronan et al. 1989, Schaedle et al. 1989). Throughout eastern North America, soil pH or base cation concentrations are reported to be inversely related to oak sapling abundance in oak-northern hardwood stands (Bigelow and Canham 2002), as well as to oak

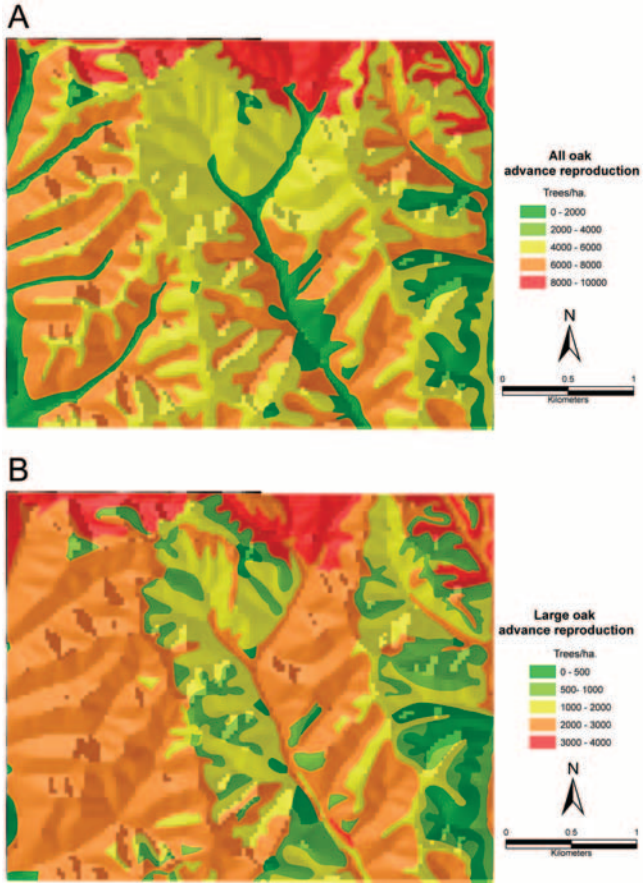

Figure 4. Predicted oak advance reproduction density on the SEF area for all oaks (A) and large (>30 cm tall) oaks (B) by applying models 4 and 16 from Table 2 to SSURGO soil map unit polygons and associated soil pH and AWC values. For large oak advance reproduction, slope-aspect was derived from a digital terrain model and projected onto the soil map unit polygon layer.

overstory abundance in oak-hickory forests (Nigh et al. 1985) and in mixed hardwood forests (Van Breemen et al. 1997). In the Ridge and Valley Province of Pennsylvania, USA, Fei and Steiner (2008) found that oak reproduction was more abundant on well-drained, acid soils and was related to the cover of acid soil indicator plant species such as blueberry or huckleberry. Our study also indicated a strong relationship between oak advance reproduction abundance and measures of soil acidity. Moreover, model comparisons indicated that substituting the pH_s or the BS for the pH_w (models 4b through 4d in Table 3) also yielded highly significant models, although a better fit occurs when the pH_w is used (model 4 in Table 3).

Fit statistics indicated that soil pH and AWC have a greater effect on the quantity of advance reproduction for the red oak group than for the white oak group (Table 2), suggesting that the advance reproduction of principal species in our red oak group (black oak and scarlet oak) is more related to site conditions than is that of the species of the white oak group (primarily white oak). This weaker relationship between white oak advance reproduction and site factors is probably related to the silvics of this species. White oak is moderately shade tolerant, and white oak seedlings are particularly so (Rogers 1990). This shade tolerance may allow advance reproduction of this species to persist better than that of black oak and scarlet oak seedlings where site conditions are favorable for the establishment of oak competitors. Kabrick et al. (2008) examined the abundance of white oak and red oak advance reproduction elsewhere in the Missouri Ozarks and found a greater abundance of red oak advance reproduction on the drier and nutrient-poor ecological land types and a concomitant decrease in the abundance of nonoaks and oak competitors. However, there was no significant relationship between ecological land type and the abundance of white oak advance reproduction.

Low understory light levels are commonly identified as a factor limiting the accumulation of oak advance reproduction (Carvell and Tryon 1961, Walters 1990, Lorimer et al. 1994, Miller et al. 2004, Lhotka and Loewenstein 2009). Accordingly, PAR was expected to be a significant factor related to the abundance of oak advance reproduction. Even though the stands that we examined were about 82 years old and had not been thinned, they exhibited a wide range of PAR (from 5 to 25% full sunlight) (Table 1) because of canopy gaps created by natural mortality and blow down from recent storm events. Despite the wide range in light availability, PAR was only a marginally significant effect ($P = 0.09$) for the red oak group species. The two most abundant species of the red oak group in our study—primarily black oak and scarlet oak—are relatively shade intolerant compared with white oak (Johnson 1990, Sander 1990), which was the dominant species of the white oak group. The overall lack of significance suggests that in undisturbed stands in the Ozark Highlands where PAR averages 10% full sunlight, light availability per se may be less important for accumulating oak advance reproduction than factors related to nutrient and water supply. However, in mesophytic oak ecosystems in which a high density of shrubs and understory species reduces the light reaching the forest floor, light availability may play a more important role. For example, in bottomland oak forests Motsinger et al. (2010) found that survival and retention of natural and planted pin oak (*Quercus palustris* Muench.) seedlings was greater in stands that were thinned from below (PAR = 15% full sunlight) compared with that in undisturbed stands (PAR = 3% full sunlight). Loftis (2004) noted that in mesophytic upland oak ecosystems, oak reproduction "cycles in and out" with seedling establishment after an acorn crop and eventual mortality because of insufficient light.

Correlation analysis also indicated that the abundance of nonoak advance reproduction, with the exception of sassafras, was inversely related to the abundance of oak advance reproduction (Table 5), which was also reported to occur in oak stands elsewhere in the Ozark Highlands (Kabrick et al. 2008) and southern Ohio, USA (Walters 1990). This observation suggests that where soil conditions are more favorable, nonoak advance reproduction has a greater capacity to accumulate in the understory of unharvested stands, occupying the growing space and thereby preventing the establishment or retention of oak seedlings. The correlation analysis also indicated that spice bush and Carolina buckthorn are the two species in the study area that interfere with the establishment or retention of oak seedlings. These two understory shrubs are most abundant where the soils have more base cations and more available water and are conspicuously absent where soils are acidic and droughty.

For white oaks, including a measure of the relative density of large (>25 cm dbh) white oaks in the models improved the overall fit (Table 4). Even with its inclusion, the soil pH and AWC were significant effects, suggesting that in addition to site factors white oak advance reproduction density is also closely linked to the abundance of acorn producers in the parent stand. Johnson (1992) also observed that white oak advance reproduction density was more

strongly related to the basal area of large (>30 cm dbh) white oaks than to that of large (>36 cm dbh) black oaks in xeric oak stands in Michigan. However, we also observed that the abundance of large white oaks capable of producing acorns comprised only 10% (range 3–22%) (Table 1) of the total stocking, which on average was less than half of the stocking of the large (>25 cm dbh) red oaks (mean 25%, range 7–46%) (Table 1). It is conceivable that the abundance of mature, acorn-producing white oaks was below a threshold where small changes in their stocking significantly affected white oak acorn availability and consequently the advance reproduction density.

It is important to recognize that the oak seedlings in a stand at any given time may have accumulated from multiple acorn crops over several years or, in dry oak ecosystems, over several decades (Johnson et al. 2009). Although large numbers of oak seedlings can develop in stands after abundant acorn crops (Johnson et al. 2009), the oak advance reproduction density in undisturbed stands is more of a function of oak seedling persistence (Loftis 2004). Once the large quantity of carbohydrate reserves provided by the germinating acorn are exhausted, oak seedlings need to have sufficient growing space and sunlight to survive and grow. In the absence of disturbances to enhance the retention of oak advance reproduction (e.g., application of prescribed fire, thinning, or herbicides to remove oak competitors), the drier and nutrient-poor site conditions generally favor the long-term accumulation of oak seedlings and seedling sprouts because fewer nonoak seedlings occupy the growing space. Because this process occurs over long time periods (up to decades), oak advance reproduction abundance can be modeled using soil and site properties indicative of the long-term capacity of a given site to supply water and nutrients.

This propensity of an oak ecosystem to accumulate oak advance reproduction was described by Johnson et al. (2009). Ecosystems in which oak seedlings readily accumulate and persist for long periods are referred to as *intrinsic oak accumulators* and those where oak reproduction fails to accumulate as *recalcitrant accumulators*. The authors postulated that sites that are intrinsic accumulators have lower soil moisture and nutrient supplies and consequently support fewer oak competitors to displace the oak advance reproduction. Our findings provided further support for this supposition and also indicated that oak advance reproduction in stands in the understory reinitiation stage of stand development can be modeled with regression equations that incorporate site information such as soil pH, AWC, and slope-aspect. In addition, there is evidence indicating that the soil pH and AWC can be obtained remotely in the SSURGO database and used in the models developed in this study for estimating oak advance reproduction densities. For example, oak advance reproduction density can be modeled at stand or landscape scales (Figure 4) using slope-aspect information and the SSURGO soil map unit polygons and their associated estimates of pH and AWC in the models shown in Table 2.

Management Application

Because of the variability in seedling density in oak stands and the variability of soil properties not captured in the SSURGO database, the modeled and the actual oak advance reproduction density may differ considerably (Figure 3). Seedling density at a single point in time is also affected by the time since natural or silvicultural disturbances that may have substantially altered the overstory canopy or reduced the competitor density in the understory. Therefore, we do not anticipate that our models will replace the need to conduct actual reproduction surveys for forest regeneration planning. Nonetheless, it appears that these models can serve as a tool to identify where in the landscape oak advance reproduction potentially will be limited and consequently where silvicultural interventions are needed for increasing its abundance and size.

Although seedling density and size thresholds for ensuring successful oak regeneration appear to differ by ecoregion (Sander et al. 1984, Spetich et al. 2002, Brose et al. 2008, Steiner et al. 2008, Dey et al. 2009), much has been written about the silvicultural interventions needed for increasing the abundance and size of oak advance reproduction before release (Loftis 1990, Lorimer 1993, Schlesinger et al. 1993, Larsen and Johnson 1998, Brose et al. 2012). The application of the shelterwood method to increase the amount of sunlight reaching the forest floor has been shown to increase the size (Loftis 1990) and/or the abundance (Motsinger et al. 2010) of oak reproduction. Prescribed fire has also become an important silvicultural tool for removing leaf litter to increase acorn germination rates and reducing midstory density to increase light reaching seedlings before a regeneration harvest is conducted and for releasing oaks from mesophytic competitors when applied in conjunction with shelterwood harvests (Brose et al. 1999, 2012, Brose 2010). These disturbances functionally "xerify" the site (*sensu* Johnson et al. 2009, p. 159), meaning that they temporarily cause the forest structure and seedling layer to more closely resemble the composition occurring on drier sites. This includes reductions in the number of seedlings and understory shrubs or small trees that ordinarily are limited by dry site conditions. Silviculture thus can be used to reverse the "mesophication" identified by Nowacki and Abrams (2008) that underlies the oak regeneration problem.

Silvicultural interventions to increase the abundance and size of oak advance reproduction take time to implement or can be costly, often competing for personnel time or other financial resources that can be used for other forest management activities. Models such as those presented here can be used as a planning tool for identifying the location and total land area where oak reproduction is likely to be inadequate and prioritizing where targeted silvicultural interventions are needed to increase the density or size of oak reproduction.

It is important to recognize that specific relationships between abiotic and biotic factors and oak advance reproduction may differ among ecoregions (Dey et al. 2009). In addition, other factors such as seedling browsing by deer may obscure the effects of soil properties, stand density, or light availability on reproduction density (Abrams and Sands 2010).Therefore, the extendibility of these models to other ecoregions would need to be examined before they are applied elsewhere.

Conclusions

For the oak forests examined in this study, data indicated that oak advance reproduction abundance could be modeled using measures of soil pH and AWC and other site information such as slope-aspect. Data suggested that these physical measures of soil acidity and water supply were more important than terrain shape and light availability in undisturbed stands that are in the understory reinitiation stage of stand development. Models for the red oak group species generally exhibited better fit than those for the white oaks, suggesting that the red oak group species are more sensitive to site and stand conditions than are the white oaks. However, white oak advance reproduction models were improved by including as a covariate the stocking of overstory white oaks (i.e., those >25 cm dbh and more likely to provide acorns). There also was evidence that estimates of soil pH and AWC can be obtained from the SSURGO

database and used in these oak advance reproduction models along with other site information to generate maps of estimated oak reproduction densities. These maps identify the location and extent on the landscape where oak advance reproduction density may or may not be sufficient for meeting regeneration goals, and thus be used for planning for silvicultural interventions to increase the abundance and size of oak advance reproduction before forest regeneration.

Endnote

1. For the Web Soil Survey, see websoilsurvey.nrcs.usda.gov/app/.

Literature Cited

ABRAMS, M.D., AND B.A. SANDS. 2010. Oak forest composition on contrasting soil types at the Mohonk Preserve, Eastern New York. *North. J. Appl. For.* 27:105–109.

ARTHUR, M.A., H.D. ALEXANDER, D.C. DEY, C.J. SCHWEITZER, AND D.L. LOFTIS. 2012. Refining the oak-fire hypothesis for management of oak-dominated forests of the eastern United States. *J. For.* 110: 257–266.

ASHTON, M.S., AND B.C. LARSON. 1996. Germination and seedling growth of *Quercus* (section Erythrobalanus) across openings in a mixed-deciduous forest of southern New England, USA. *For. Ecol. Manage.* 80:81–94.

BAHARI, Z.A., S.G. PALLARDY, AND W.C. PARKER. 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in central Missouri. *For. Sci.* 31:557–569.

BEERS, T.W., P.E. DRESS, AND L.C. WENSEL. 1966. Aspect transformation in site productivity research. *J. For.* 64:691–692.

BELLI, K.L., C.P. HART, J.D. HODGES, AND J.A. STANTURF. 1999. Assessment of the regeneration potential of red oaks and ash on minor bottoms in Mississippi. *South. J. Appl. For.* 23:133–138.

BIGELOW, S.W., AND C.D. CANHAM. 2002. Community organization of tree species along soil gradients in a north-eastern USA forest. *J. Ecol.* 90:188–200.

BROSE, P.H. 2010. Long-term effects of single prescribed fires on hardwood regeneration in oak shelterwood stands. *For. Ecol. Manage.* 260: 1516–1524.

BROSE, P.H., D.C. DEY, R.J. PHILLIPS, AND T.A. WALDROP. 2012. A meta-analysis of the fire-oak hypothesis: Does prescribed burning promote oak reproduction in eastern North America? *For. Sci.* 59:322–334.

BROSE, P.H., K.W. GOTTSCHALK, S.B. HORSLEY, P.D. KNOPP, J.N. KOCHENDERFER, B.J. MCGUINNESS, G.W. MILLER, T.E. RISTAU, S.H. STOLESON, AND S.L. STOUT. 2008. *Prescribing regeneration treatments for mixed-oak forests in the Mid-Atlantic region*. USDA For. Serv., Gen. Tech. Rep. NRS-33, Northern Research Station, Newtown Square, PA. 100 p.

BROSE, P.H., D.H. VAN LEAR, AND R. COOPER. 1999. Using shelterwood harvests and prescribed fire to regenerate oak stands on productive upland sites. *For. Ecol. Manage.* 113:125–141.

BURNHAM, K.P., AND D.R. ANDERSON. 1998. *Model selection and inference: A practical information-theoretic approach*. Springer, New York. 353 p.

CARMEAN, W.H., J.T. HAHN, AND R.D. JACOBS. 1989. *Site index curves for forest tree species in the eastern United States*. USDA For. Serv., Gen. Tech. Rep. NC-128, North Central Experimental Station, St. Paul, MN. 142 p.

CARVELL, K.L., AND E.H. TRYON. 1961. The effect of environmental factors on the abundance of oak regeneration beneath mature oak stands. *For. Sci.* 7:98–105.

CRONAN, C.S., R. APRIL, R.J. BARTLETT, P.R. BLOOM, C.T. DRISCOLL, S.A. GHERINI, G.S. HENDERSON, ET AL. 1989. Aluminum toxicity in forests exposed to acidic deposition: The ALBIOS results. *Water Air Soil Pollut.* 48:181–192.

CRONAN, C.S., AND D.F. GRIGAL. 1995. Use of calcium/aluminum ratios as indicators of stress in forest ecosystems. *J. Environ. Q.* 24:209–226.

DEY, D.C. 1991. *A comprehensive Ozark regenerator.* PhD dissertation, University of Missouri-Columbia, Columbia, MO. 283 p.

DEY, D.C., M.A. SPETICH, D.R. WIEGEL, P.S. JOHNSON, D.L. GRANEY, AND J.M. KABRICK. 2009. A suggested approach for design of oak (*Quercus* L.) regeneration research considering regional differences. *New For.* 37:123–135.

DEY, D.C., M. TER-MIKAELIAN, P.S. JOHNSON, AND S.R. SHIFLEY. 1996. *Users' guide to ACORn: A comprehensive Ozark regeneration simulator*. USDA For. Serv., Gen. Tech. Rep. NC-180, Central Forest Experiment Station, St. Paul, MN. 35 p.

FEI, S., AND K.C. STEINER. 2008. Relationships between advance oak regeneration and biotic and abiotic factors. *Tree Physiol.* 28:1111–1119.

GINGRICH, S.F. 1967. Measuring and evaluating stocking and stand density in Upland Hardwood forests in the Central States. *For. Sci.* 13:38–53.

GÖTMARK, F., Å. BERGLUND, AND K. WIKLANDER. 2005. Browsing damage on broadleaved trees in semi-natural temperate forest in Sweden, with a focus on oak regeneration. *Scand. J. For. Res.* 20. 223–234.

GOULD, P.J., K.C. STEINER, M.E. MCDILL, AND J.C. FINLEY. 2006. Modeling seed-origin oak regeneration in the central Appalachians. *Can. J. For. Res.* 36:833–844.

HINCKLEY, T.M., R.G. ASLIN, R.R. AUBUCHON, C.L. METCALF, AND J.E. ROBERTS. 1978. Leaf conductance and photosynthesis in four species of the oak-hickory forest type. *For. Sci.* 24:73–84.

HODGES, J.D., AND E.S. GARDINER. 1993. Ecology and physiology of oak regeneration. P. 54–65 in *Oak regeneration: Serious problems, practical recommendations.* USDA For. Serv., Gen. Tech. Rep. SE-84, Southeastern Forest Experiment Station, Asheville, NC.

JOHNSON, P.S. 1990. Scarlet oak. P. 625–630 in *Silvics of North America. Vol. 2: Hardwoods*. USDA For. Serv., Agri. Handbk. 654, Washington, DC.

JOHNSON, P.S. 1992. Oak overstory/reproduction relations in two xeric ecosystems in Michigan. *For. Ecol. Manage.* 48:233–248.

JOHNSON, P.S., S.R. SHIFLEY, AND R. ROGERS. 2009. *The ecology and silviculture of oaks,* 2nd ed. CABI Publishing, Oxon, UK. 566 p.

KABRICK, J.M., D.C. DEY, S.R. SHIFLEY, AND J.L. VILLWOCK. 2011. Early survival and growth of planted shortleaf pine seedlings as a function of initial size and overstory stocking. P. 277–286 in *Proc. of the 17th Central hardwood forest conference.* USDA For. Serv., Gen. Tech. Rep. NRS-P-78, Northern Research Station, Newtown, PA.

KABRICK, J.M., E.K. ZENNER, D.C. DEY, D. GWAZE, AND R.G. JENSEN. 2008. Using ecological land types to examine landscape-scale oak regeneration dynamics. *For. Ecol. Manage.* 255:3051–3062.

LARSEN, D.R., AND P.S. JOHNSON. 1998. Linking the ecology of natural oak regeneration to silviculture. *For. Ecol. Manage.* 106:1–7.

LARSEN, D.R., M.A. METZGER, AND P.S. JOHNSON. 1997. Oak regeneration and overstory density in the Missouri Ozarks. *Can. J. For. Res.* 27:869–875.

LHOTKA, J.M., AND E.F. LOEWENSTEIN. 2009. Effect of midstory removal on understory light availability and the 2-year response of underplanted cherrybark oak seedlings. *South. J. Appl. For.* 33:171–177.

LI, Q., AND K. MA. 2003. Factors affecting establishment of *Quercus liaotungensis* Koidz. under mature mixed oak forest overstory and in shrubland. *For. Ecol. Manage.* 176. 133–146.

LITTLE, E.L. JR. 1979. *Checklist of the United States trees (native and naturalized).* USDA For. Serv., Agri. Handbk. 541, Washington, DC. 375 p.

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

LOFTIS, D.L. 2004. Upland oak regeneration and management. P. 163–167 in *Upland oak regeneration and management.* USDA For. Serv., Gen. Tech. Rep. SRS-73, Southern Research Station, Asheville, NC.

LOFTIS, D.L., AND C.E. MCGEE (EDS.). 1993. *Oak regeneration: Serious*

problems, practical recommendations (Symposium proceedings). USDA For. Serv., Gen. Tech. Rep. SE-84, Southern Research Station, Asheville, NC. 319 p.

LORIMER, C.G. 1993. Causes of the oak regeneration problem. P. 14–39 in *Oak regeneration: Serious problems, practical recommendations.* USDA For. Serv., Gen. Tech. Rep. SE-84, Southern Research Station, Asheville, NC.

LORIMER, C.G., J.W. CHAPMAN, AND W.D. LAMBERT. 1994. Tall understory vegetation as a factor in the poor development of oak seedlings beneath mature stands. *J. Ecol.* 82:227–237.

MABBERLEY, D.J. 2008. *Mabberley's plant-book: A portable dictionary of plants, their classifications an uses*, 3rd ed. Cambridge University Press, Cambridge, UK, 1021 p.

MCNAB, W.H. 1989. Terrain shape index: Quantifying effect of minor landforms on tree height. *For. Sci.* 35:91–104.

MCQUILKIN, R.A. 1974. *Site index prediction table for black, scarlet, and white oaks in southeastern Missouri*. USDA For. Serv., Res. Pap. NC-108, North Central Forest Experiment Station, St. Paul, MN. 8 p.

MCQUILKIN, R.A. 1976. The necessity of independent testing of soil-site equations. *Soil Sci. Soc. Am. J.* 40:783–785.

MCSHEA, W.J., AND W.M. HEALY (EDS.). 2002. *Oak forest ecosystems: Ecology and management for wildlife*. Johns Hopkins University Press, Baltimore, MD. 432 p.

MILLER, G.W., J.N. KOCHENDERFER, AND K.W. GOTTSCHALK. 2004. Effect of pre-harvest shade control and fencing on northern red oak seedling development in the central Appalachians. P. 182–189 in *Upland oak ecology symposium: History, current conditions, and sustainability.* USDA For. Serv., Gen. Tech Rep. SRS-73, Southern Experimental Station, Asheville, NC.

MOTSINGER, J.R., J.M. KABRICK, D.C. DEY, D.E. HENDERSON, AND E.K. ZENNER. 2010. Effect of midstory and understory removal on the establishment and development of natural and artificial pin oak advance reproduction in bottomland forests. *New For.* 39:195–213.

NASH, A.J. 1963. *A method of classifying shortleaf pine sites in Missouri.* Res. Bull. 824, Missouri Agricultural Experiment Station, Columbia, MO. 53 p.

NIGH, T.A., S.G. PALLARDY, AND H.E. GARRETT. 1985. Sugar maple-environment relationships in the River Hills and Central Ozark Mountains of Missouri. *Am. Mid. Naturalist* 114:235–251.

NIGH, T.A., AND W.A. SCHROEDER. 2002. *Atlas of Missouri Ecoregions*. Missouri Department of Conservation, Jefferson City, MO. 212 p.

NOWACKI, G.J., AND M.D. ABRAMS. 2008. The demise of fire and the "mesophication" of forests in the eastern united states. *Bioscience* 58:123–138.

PULIDO, F.J., AND M. DÍAZ. 2005. Regeneration of a Mediterranean oak: A whole-cycle approach. *Ecoscience* 12. 92–102.

OLIVER, C.D., AND B.C. LARSON. 1996. *Forest stand dynamics*, update ed. John Wiley & Sons, New York. 520 p.

ROGERS, R. 1983. Guides for thinning shortleaf pine. P. 217–225 in *Proc. of the Second biennial southern silvicultural research conference, 1982 Nov. 4–5, Atlanta, GA.* USDA For. Serv., Gen. Tech. Rep. SE-24, Southeastern Research Station, Asheville, NC.

ROGERS, R. 1990. White oak. P. 605–613 in *Silvics of North America. Vol. 2: Hardwoods*. USDA For. Serv., Agri. Handbk. 654, Washington, DC.

SANDER, I.L. 1971. Height growth of new oak sprouts depends on size of advance reproduction. *J. For.* 69:809–811.

SANDER, I.L. 1990. Black oak. P. 744–750 in *Silvics of North America. Vol. 2: Hardwoods*. USDA For. Serv., Agri. Handbk. 654, Washington, DC.

SANDER, I.L., P.S. JOHNSON, AND R.F WATT. 1976. *A guide for evaluating the adequacy of oak advance reproduction.* USDA For. Serv., Gen. Tech. Rep. NC-23, North Central Forest Experiment Station, St. Paul, MN. 16 p.

SANDER, I.L., P.S. JOHNSON, AND R. ROGERS. 1984. *Evaluating oak advance reproduction in the Missouri Ozarks.* USDA For. Serv., Res. Pap. NC-251, North Central Forest Experiment Station, St. Paul, MN. 11 p.

SCHAEDLE, M., F.C. THORNTON, D.J. RAYNAL, AND H.B. TEPPER. 1989. Response of tree seedlings to aluminum. *Tree Physiol.* 5:337–356.

SCHLESINGER, R.C., I.L. SANDER, AND K.R. DAVIDSON. 1993. Oak regeneration potential increased by shelterwood treatments. *North. J. Appl. For.* 10:149–153.

SCHOENEBERGER, P.J., D.A. WYSOCKI, E.C. BENHAM, AND SOIL SURVEY STAFF (EDS.). 2012. *Field book for describing and sampling soils*, version 3.0. USDA National Resources Conservation Service, National Soil Survey Center, Lincoln, NE. 300 p.

SMITH, D.W. 1993. Oak regeneration: The scope of the problem. P. 40–52 in *Oak regeneration: Serious problems, practical recommendations.* USDA For. Serv., Gen. Tech. Rep. SE-84, Southeastern Forest Experiment Station, Asheville, NC.

SPETICH, M.S., D.C. DEY, P.S. JOHNSON, AND D.L. GRANEY. 2002. Competitive capacity of *Quercus rubra* L. planted in Arkansas' Boston Mountains. *For. Sci.* 48:504–517.

STEINER, K.C., J.C. FINLEY, P.J. GOULD, S. FEI, AND M. MCDILL. 2008. Oak regeneration guidelines for the Central Appalachians. *North. J. Appl. For.* 25:5–16.

THADAMI, R., AND P.M.S. ASHTON. 1995. Regeneration of banj oak (*Quercus leucotrichophora* A. Camus) in the central Himalaya. *For. Ecol. Manage.* 78. 217–224.

TRIMBLE, G.R. 1973. *The regeneration of Central Appalachian hardwoods with emphasis on the effects of site quality and harvesting practice*. USDA For. Serv., Res. Pap. NE-282, Northeastern Forest Experiment Station, Upper Darby, PA. 14 p.

US DEPARTMENT OF AGRICULTURE. 2004. *Soil survey laboratory methods manual*. Soil Survey Investigations, Rep. No. 42, Ver. 4.0, Natural Resources Conservation Service, National Soil Survey Center, Lincoln, NE. 735 p.

VAN BREEMAN, N., A.C. FINZI, AND C.D. CANHAM. 1997. Canopy tree-soil interaction within temperature forests: Effects of soil elemental composition and texture on species distributions. *Can. J. For. Res.* 27:1110–1116.

WALTERS, R.S. 1990. *Site quality, fire, and herbicide effects on establishment, growth, and development of regeneration three years after partial cutting of oak stands*. PhD dissertation, State University of New York, Syracuse, NY. 197 p.

WATT, A.S. 1919. On the causes of failure of natural regeneration in British oakwoods. *J. Ecol.* 7. 173–203.

ZAVALETA, E.S., K.B. HULVEY, AND B. FULFROST. 2007. Regional patterns of recruitment success and failure in two endemic California oaks. *Divers Distrib.* 13:735–745.