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Modeling the regeneration of oak stands in the Missouri Ozark Highlands

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Abstract: This paper describes a method for modeling the regeneration of even-aged oak stands in the Ozark Highlands of southern Missouri. The approach is based on (*i*) a growth model that is applicable to both oak sprouts and advance reproduction and (*ii*) a method for probabilistically estimating future size distributions of trees. The modeling method is illustrated using sprouting frequency, survival, and 5th-year height data for stump sprouts of five oak species. To consider the large residual variation in estimates of future sprout heights, nonlinear regression estimates of heights and their prediction errors are simultaneously used to estimate the probability that a sprout originating from a parent tree of a given species and diameter will grow into a specified 5th-year height class. To account for sprouting and survival failures, those probabilities are multiplied by logistic regression estimates of the probability that a parent tree will produce a sprout that survives to age 5. The resulting joint probabilities facilitate predicting future height distributions of surviving sprouts when the model is applied to a preharvest inventory of overstory trees.

Résumé : Cet article décrit une méthode de modélisation de la régénération de peuplements équiennes de chênes dans les plateaux des Ozarks du sud du Missouri. L'approche est basée sur (*i*) un modèle de croissance applicable à la fois pour les rejets et la régénération préétablie de chêne et (*ii*) une méthode probabiliste permettant d'estimer la distribution future des arbres par dimension. La méthode de modélisation est illustrée en utilisant des données de fréquence des rejets, de survie et de croissance après 5 ans pour des rejets de souche de cinq espèces de chênes. Afin de considérer l'importante variation résiduelle dans les estimés de hauteur prédite des rejets, les estimés de hauteur par régression non linéaire et leurs erreurs de prédiction ont été utilisés simultanément pour estimer la probabilité qu'un rejet produit par un pied mère d'une espèce et d'un diamètre donnés atteigne une classe de hauteur particulière après 5 ans. Afin de tenir compte des échecs de rejets et de survie, ces probabilités ont été multipliées par les estimés de probabilités obtenus par régression logistique qu'un arbre mère produise un rejet qui survive jusqu'à 5 ans. Les probabilités combinées qui en résultent facilitent la prédiction des distributions futures des hauteurs des rejets survivants lorsque le modèle est appliqué à un inventaire des arbres du couvert réalisé avant la récolte.

[Traduit par la Rédaction]

Introduction

The development of predictive regeneration models for even-aged oak and mixed oak–hardwood stands has lagged behind the development of predictive growth and yield models for established stands. Growth and yield models usually are applicable only to stands that are at least 20 years old and thus do not address the regeneration period that follows removal of the overstory. Because oak forests in the United States are often managed as even-aged stands on rotations of 80–120 years, the absence of regeneration models results in an inability to predict the development of stand composition and structure during the first one-sixth to one-fourth of the rotation. One reason for the lack of predictive regeneration models may be the seeming unpredictability of the regeneration process. Regeneration modeling poses special problems related to the nature of oak and associated hardwood reproduction, and to the dynamic characteristics of the regeneration period itself.

Toward resolving those problems, this paper presents a method for predicting the early development of upland oak stands in the Ozark Highlands of southern Missouri. The underlying hypothesis associated with the proposed modeling methodology is that the structural and compositional state of the future stand is encoded in its initial state.

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Oak regeneration dynamics

Regeneration in the Ozark Highlands

The regeneration period is herein defined as approximately the first 20 years after final harvest. This period coincides with Oliver and Larson's (1990) stand initiation and stem exclusion stages of stand development. It is a dynamic period characterized initially by the appearance of new individual trees and species, and in the latter stages, by a rapid decline in stem density associated with self-thinning,

crown differentiation, and rapid shifts in dominance among and within species. In the Ozarks, species such as hickories (*Carya* spp.), sassafras (*Sassafras albidum* (Nutt.) Nees), blackgum (*Nyssa sylvatica* Marsh.), and flowering dogwood (*Cornus florida* L.) influence oak regeneration because of their rapid early growth and high stocking during the regeneration period. These associated hardwoods are usually unimportant as dominant components of older stands. However, they persist from one generation to the next primarily as advance reproduction in the understory of mature oak forests. Hickory, blackgum, sassafras, and flowering dogwood usually are dominant only during the first 2 decades after major overstory disturbances (e.g., timber harvest). These species are characterized by low survival rates (e.g., sassafras and blackgum) and (or) limited size development (e.g., flowering dogwood), which permanently relegate them to the sapling and reproduction substrata (Braun 1972; Dey 1991). Although hickories are capable of attaining dominance, they typically compose a minor proportion of overstory trees in mature stands.

The regeneration of upland oak forests has been long recognized as dependent on the amount and size of reproduction present before final harvest (Sander 1971; Sander and Clark 1971; Carvell 1979; Sander et al. 1984). In the drier (more xeric) oak forests such as those occurring in the Ozark Highlands, oak reproduction often accumulates beneath the canopy of the parent stand for several decades (Liming and Johnston 1944; Merz and Boyce 1956). The oak-dominated forests of the Ozark Highlands have been termed autoaccumulators of oak reproduction (sensu Johnson 1993) because, even in the absence of disturbance, oak seedlings and seedling sprouts gradually accumulate over many years beneath the canopy of the parent stand (Liming and Johnston 1944). The long-term survival of some of the oak reproduction in the understory results in the accumulation of a population of seedling sprouts with large root systems and the potential for rapid shoot growth following release. But until the overstory is removed, the advance reproduction usually remains as a component in the understory with little recruitment into the upper crown classes of the overstory. Oaks in the Ozark Highlands are consequently persistent (sensu Veblen 1992), i.e., they persist over successive generations. In the Ozarks, this persistence is greater than in the more mesic and hydric oak forests of other regions where dominance by oaks may last only one generation because of successional replacement by long-lived, faster growing, and (or) more shade-tolerant species (Loftis 1990*b*; Nowacki et al. 1990).

The overstory also is an important component of an oak stand because a significant proportion of reproduction may originate from the stumps of trees cut during final harvest (Johnson 1975; Wendel 1975; Sander et al. 1984; Lamson 1988). In the Central Hardwood Region, the overstory has been conventionally defined as trees ≥4 cm DBH (Roach and Gingrich 1968). The contribution of this source of reproduction to future stocking depends on the proportion of trees that produce stump sprouts. In general, older and larger trees are less likely to produce stump sprouts than smaller, younger trees (Roth and Sleeth 1939; Johnson 1975, 1977; Ross et al. 1986). Even in older stands, stump sprouts may contribute significantly to future stand stocking because, despite their small numbers, their growth and survival rates usually are high (Johnson and Rogers 1984; Lamson 1988).

In Ozark Highland oak forests, the composition and structure of both the advance reproduction and the overstory are important properties of the initial state of the stand that follows final harvest. Stand replacement, and more generally, succession, are heavily dependent on the composition and structure of the advance reproduction and overstory at the time of overstory removal or destruction. The pattern of stand replacement after final harvest in the Ozark Highlands is consistent with Egler's (1954) concept of the role of initial floristics in plant succession. Namely, succession is driven by initial floristics when the flora present at the time of disturbance controls to a significant extent the future compositional and structural states of the ecosystem. This idea also is represented in the legacy concept of Franklin et al. (1989), wherein the future states of an ecosystem, both structurally and functionally, are inherited from plant propagules, microorganisms, and other biotic characteristics of an ecosystem carried over from a previous state. In the case of oak and many other hardwood forests, the dependence of a stand's future state on its current or initial state has provided a useful basis for the development and application of predictive stand-level regeneration models (e.g., Johnson and Deen 1993; Loftis 1990*a*; Marquis et al. 1992; Sander et al. 1984).

Growth characteristics of oak reproduction

The positive correlation between postharvest height growth and preharvest basal stem diameter of advance reproduction (Sander 1971) and the negative correlation for the same relation in stump sprouts (Johnson 1977) might suggest that the two growth forms are intrinsically different physiologically. However, the distinction between the two forms of reproduction is biologically arbitrary and may largely serve to facilitate a silvicultural definition of a minimum diameter for overstory trees.

We propose that oak advance reproduction and stump sprouts be thought of as a single entity representing a continuum of root sizes from small (e.g., new seedlings) to large (e.g., stump sprouts originating from large overstory trees), which partially determine the growth rate of reproduction. Previous studies have shown that the diameter of the parent stem and the correlated size of the root system affect the growth of oak reproduction. For five species of oaks in the Missouri Ozarks, the correlation between stump diameter and height growth of the dominant stem within a sprout clump was consistently negative for 5-year-old sprouts of all species (Johnson 1977). However, the opposite was reported for oak sprouts in Virginia (Ross et al. 1986). Such discrepancies might be explained by the range of stump diameters observed in any given study, confounding of tree size and age relations, and other factors. However, few studies have examined the growth response across a range of diameters including both advance reproduction and stump sprouts. In one study that did, the height growth of black oak (*Quercus velutina* Lam.) and white oak (*Quercus alba* L.) reproduction originating from parent stems ranging from less than 2.5 cm in basal diameter to over 30 cm was greatest in sprouts originating from

15-cm stems (Johnson 1979). Reproduction originating from stems larger or smaller than 15 cm in diameter grew less. This suggests that the height growth of oak reproduction changes continuously, but not unidirectionally, from small advance reproduction to sprouts originating from the stumps of large-diameter overstory trees (Fig. 1). Basal stem diameter, in turn, is correlated with root size (Canadell and Roda 1991). Up to the threshold diameter of approximately 15 cm that defines maximum growth, increasing root biomass, root absorptive surface area, and carbohydrate reserves may explain the initial increase in height growth.

But what explains the reduction in height growth above the threshold diameter? Assmann (1970) generalized that there are three distinct phases in tree growth: (*i*) juvenile, (*ii*) full vigor, and (*iii*) senescence. The juvenile phase is associated with increasing growth with increasing age, the full-vigor phase is represented by the period of maximum growth, and senescence is characterized by a decline in growth with increasing tree age. Greenwood (1989) suggested that this height growth pattern is related to changes in the maturation state of the tree. But he believed maturation state to be more closely related to tree size than chronological age. Although no causal mechanisms have been established to explain this growth pattern, known as phase change, it nevertheless has long been recognized.

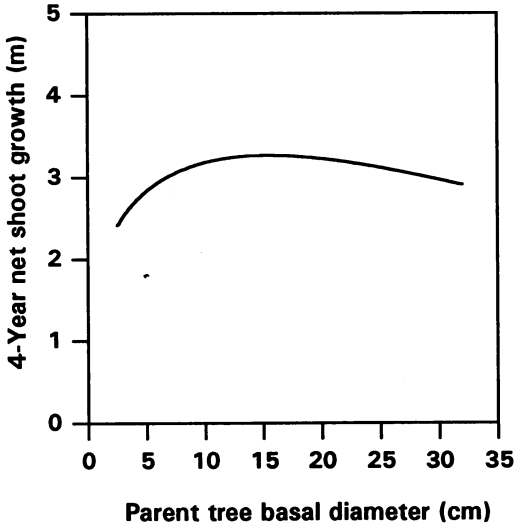
Application of the phase-change hypothesis to the growth of oak reproduction is problematic. Even though the roots of reproduction represent various stages of maturity, the stems they are connected to are always immature initially. An alternative and possibly complementary hypothesis is Borchert's (1975) theory that rate of shoot growth depends on the functional balance between roots and shoots. Accordingly, roots and shoots represent a positive feedback mechanism. Roots, the absorptive subsystem, must maintain functional balance with shoots and leaf area, the complementary assimilative subsystem, to sustain an optimum root–shoot feedback loop and maximum height growth. In the case of oak sprouts, the number and spatial distribution of dormant basal buds that form new shoots after the parent stem is cut may determine, along with total root mass, the functional balance of the complete physiological unit (the genet) (Kharitonovich 1937; Johnson 1979).

Regardless of physiological explanation, apparent root size as reflected in parent stem diameter can provide a common denominator for expressing the growth potential of all forms of oak reproduction, including advance reproduction (seedlings and seedling sprouts) and stump sprouts. This relation also can provide an objective basis for selecting growth functions to model reproduction. However, the basal diameter of advance reproduction and, in the case of stump sprouts, the diameter of the parent stem usually explain less than half the observed variation in height growth of oak reproduction (Sander 1971; Johnson 1977, 1979). This leads to a consideration of other factors that affect oak reproduction.

Factors that affect oak reproduction

Given the largely unknown physiological and physical states of roots and dormant basal buds of oaks, it is perhaps not surprising that large residual variation characterizes

Fig. 1. Estimated net shoot growth of black oak and white oak sprouts during the first 4 years after clearcutting in relation to basal diameter of the parent tree. Basal diameters 4 cm and larger represent stump sprouts originating from harvested overstory trees; smaller trees are advance reproduction. The estimate is given by $\log(H) = -2.140 - 0.02402(\mathrm{BD}) + 2.811(\mathrm{BD}^{0.1})$, where H is 4-year net shoot growth (m) and BD is basal diameter of the parent tree (cm); $R^2 = 0.39$. Differences between species were not significant ($\alpha = 0.05$). (Adapted from Johnson 1979.)



the relation between reproduction growth and parent stem diameter. This may be partly related to an imperfect correlation between root mass and parent stem diameter. Any trend toward a maximum growth rate of reproduction along a continuum of parent stem diameters thus may represent the diameter where the optimum root:shoot ratio occurs most frequently in a genetically and physiologically heterogeneous population of trees in a spatially and temporally variable environment. The model used to express the growth relation in Fig. 1 thus neglects factors known to affect reproduction growth. Among those factors are unspecified variation in spatially and size-dependent competitive relations among and within genets and interactions among those and other factors. During the regeneration period, oak reproduction competes with associated hardwoods, many of which also were present as advance reproduction and which have responded in a burst of growth upon release from the overstory. Because the growth model (Fig. 1) does not account for variation related to competition, such effects accrue to the error term.

Variation in reproduction growth and survival also is related to changing physiological relations within clumps of sprouts. During the early growth of oak stump sprouts, the growth of stems within sprout clumps is influenced by the number and spatial distribution of sprouts (and thus dormant buds) around the stump (Kharitonovich 1937). Early height growth is fastest when sprout density is high and stems are evenly distributed around the stump. This condition apparently best provides the leaf area and vascular connections necessary to support the entire root system

Table 1. Logistic regression models for estimating the probability that a parent tree will produce a stump sprout that survives to age 5.

	Parameter estimates*					
	b_0	b_1	b_2	b_3	b_4	N
White oak	1.7378	−0.2156	−0.0546	0.00131	0.2313	431
Black oak	−0.7523	−0.1059	—	—	0.2017	354
Scarlet oak	5.7710	−0.1383	—	—	—	304
Post oak	2.5338	−0.1176	—	—	—	372
Blackjack oak	2.5856	−0.1128	—	—	—	240

*Models are of the form $Pss = \{1 + \exp[-(b_0 + b_1X_1 + b_2X_2 + b_3X_3 + b_4X_4)]\}^{-1}$, where Pss is the estimated probability that a parent tree will produce a sprout that survives to age 5; X_1 is parent tree basal diameter (cm); X_2 is parent tree age (years) at stump height (15–30 cm); $X_3 = X_1X_2$; and X_4 is oak site index (m) based on Schnur's (1937) curves. All parameter estimates are significantly different from zero at $\alpha = 0.05$.

and thus an effective root–shoot feedback system. But high sprout clump density eventually results in intense intraclump competition, which reduces the growth rate of surviving stems (Johnson and Rogers 1984). As a result, within-clump distribution and density of stems, intraclump competition, and the interaction of those factors with sprout age and site quality also may influence the growth of surviving sprouts. Accounting for the number and spatial distribution of dormant basal buds before the parent stem is cut thus might improve the accuracy of estimates of sprout growth. However, the nondestructive determination of bud numbers and distributions before the parent tree is cut presents difficult if not intractable problems in practical model application. Thus, there are practical limits to accounting for some of the important known factors that define the initial state of the new stand.

The regeneration model

Variation in reproduction development attributable to known but unspecified causal factors may only be a part of the prediction problem in developing regeneration models. Other sources of variation may involve unknown or only probabilistically specifiable factors such as variability in weather, herbivore populations, and seed production of tree and nontree vegetation that may produce essentially stochastic effects. Whatever their source and relative importance, stochastic sources of variation need to be included in models of stand development if those models are to realistically simulate stand dynamics (Stage and Wykoff 1993). Because stochastic variation is likely to predominate during the regeneration period, it should be incorporated into regeneration models. Others have similarly developed regeneration models based on probabilistic approaches that implicitly consider stochastic effects (e.g., Leak 1968; Sander et al. 1984; Ferguson et al. 1986; Lowell et al. 1987; Loftis 1990*a*).

We will illustrate our regeneration modeling strategy using data from oak stump sprouts growing in Ozark Highland clearcuts. The same methodology can be applied to oak advance reproduction and to the advance reproduction and overstory of other hardwoods that are important members of Ozark oak forests (Dey 1991).

The data

Data from a 5-year study of oak stump sprouts in the Missouri Ozarks were used to develop models for estimating sprout heights, sprouting frequency, and sprout survival from site quality and preharvest characteristics of parent tree size and age. Data were obtained from upland oak stands on the Mark Twain National Forest in southern Missouri. Growth and survival of 1546 oak stump sprouts were measured in four stands. Site indices for oaks ranged from 10.7 to 25.9 m based on Schnur's (1937) curves.

All of the white oak and black oak, and two-thirds of the scarlet oak (*Quercus coccinea* Muenchh.), post oak (*Quercus stellata* Wangenh.), and blackjack oak (*Quercus marilandica* Muenchh.) originated from cut stumps. The remaining sprouts arose from the bases of trees whose tops were killed by fire when a portion of the study site burned. Basal diameters (outside bark) of parent trees were determined after the trees were harvested. For white oak and black oak, tree age at stump height, and site index were determined. Approximately 19% of the white and black oaks occurred on poor sites (site index < 15.5 m), 46% on fair sites (site index 15.5–18.2 m), 28% on good sites (site index 18.6–21.3 m), and 6% on excellent sites (site index > 21.3 m). Although the ages of white oaks and black oaks ranged from 30 to 200 years, most trees were between 40 and 140 years. After 5 years, height of the tallest stem in each sprout clump was measured.

The probability of sprouting and surviving to age 5

Unlike advance reproduction, stump sprouts largely originate after the final harvest. The probability that an overstory tree will sprout therefore must be considered along with the probability that at least one sprout stem will survive to some specified future age. Rather than derive two separate probabilities, we directly estimated the single probability of sprouting and surviving to age 5 using the logistic regression function

$$[1] \quad Pss = \{1 + \exp[-(\beta_0 + \beta_1X_1 + \beta_nX_n)]\}^{-1} + \varepsilon$$

where

Pss is the probability that a parent tree will produce a sprout that survives to age 5

Table 2. Nonlinear regression models for estimating 5th-year heights of oak stump sprouts.

	Parameter estimates*						Mean square error
	b_0	b_1	b_2	R_2	N	$P>F$	
White oak	5.8829	0.006 27	3.7629	0.13	128	0.001	0.6304
Post oak	7.1488	0.020 99	5.3082	0.35	64	0.001	0.7331
Scarlet oak	11.6174	0.015 53	12.7096	0.24	181	0.001	1.2075
Blackjack oak	8.9245	0.030 74	7.7683	0.12	103	0.001	0.6011
Black oak	10.7032	0.021 62	9.1835	0.21	86	0.001	1.4264

*Models are of the form $H = b_0\{\exp[-(b_1X_1 + b_2X_2)]\}$, where H is estimated 5th-year height of stump sprout (m); X_1 is stump diameter outside bark (cm); and X_2 is the inverse of X_1.

exp is the base of the natural logarithm

β_0, β_1, and β_n are parameters estimated by regression analysis

$X_1 \ldots X_n$ are independent variables

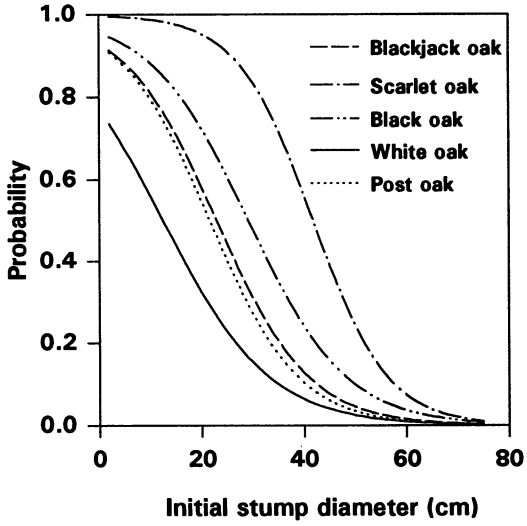
ε is an error term

For each of the five species considered, X_1 is parent tree basal diameter (outside bark). Depending on species, other predictors include parent tree age, the interaction between age and diameter, and site index (Table 1).

The logistic function limits the estimation of probabilities to the interval [0,1]. Because the function is bounded by this closed interval, the function is naturally limited to the possible range of survival probabilities. This is a desirable feature in modeling survival (Hamilton and Edwards 1976; Monserud 1976; Buchman and Shifley 1983; Hamilton 1986).

The resulting probability estimates for sprouting and surviving to age 5 show that, for all species, probabilities decrease with increasing parent tree diameter (Fig. 2). Similar results have been reported for oaks in New York (Spaeth 1928), West Virginia (Wendel 1975), Virginia (Roth and Hepting 1943; Ross et al. 1986), Missouri (Clark and Liming 1953), Wisconsin (Johnson 1975), and Michigan (Lynch and Bassett 1987). For black oak and white oak, site index also is a significant ($p < 0.05$) predictor; probabilities increase with increasing site index. Johnson (1977) found that the frequency of sprouting was greater on good sites than on poor sites for oaks, other factors being equal. However, Lynch and Bassett (1987) reported that the sprouting capacity of Michigan white oak decreased slightly as site index increased from 12.8 to 18.9 m. For white oak, parent tree age and the interaction of age and diameter are significant; probabilities decrease with increasing age (Table 1). Other researchers have noted similar relationships between tree age and sprouting capacity in oaks throughout the eastern United States (Roth and Hepting 1943; Wendel 1975; Johnson 1977; Ross et al. 1986; Lynch and Bassett 1987).

Fig. 2. Estimated probabilities that a parent tree of a given basal diameter will produce a sprout that survives to age 5. For white oak, site index is held constant at 19 m and parent tree age is held constant at 90 years. Black oak was not affected by site or age; for other species, site and age data were not available. Equations are given in Table 1.



5th-year heights of stump sprouts

For each of the five species considered, we developed nonlinear regression models to estimate the 5th-year height of the tallest surviving sprout within each sprout clump. Basal diameter, tree age, and site index were evaluated as independent variables for black and white oak sprouts; age and site index were not available for the other species.

After evaluating numerous nonlinear functions, we selected the following model for estimating 5th-year heights (H) for all five species:

$$[2] \quad H = \beta_0\{\exp[-(\beta_1 D + \beta_2 D^{-1})]\} + \varepsilon$$

where

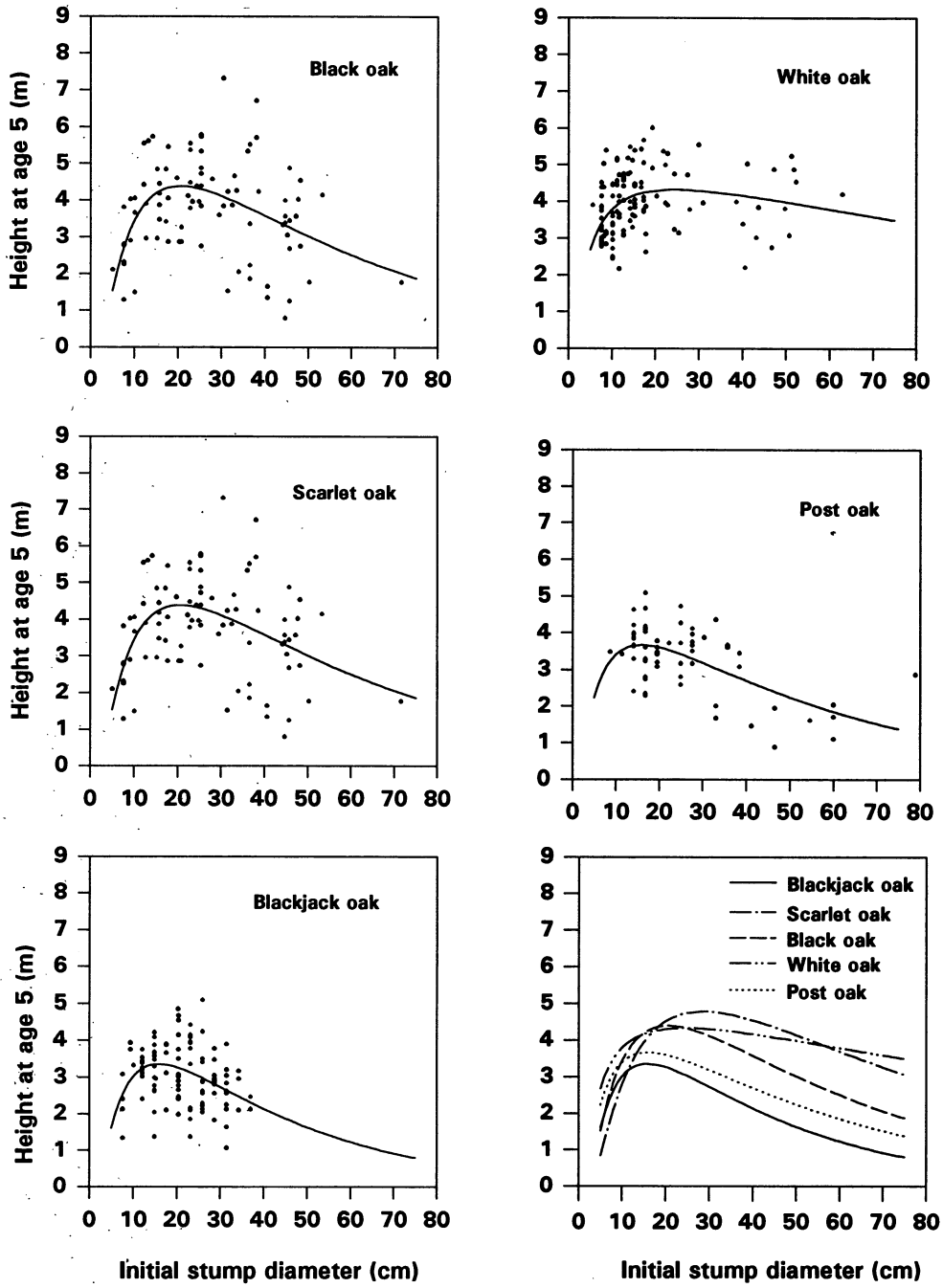
H is 5th-year height (m)

β_0, β_1, and β_2 are parameters estimated by regression analysis

D is parent tree basal diameter (cm, outside bark)

A χ^2 test of predicted versus observed 5th-year height distributions was used to evaluate the performance of each model. Although the independent variables were significant ($p < 0.05$), they explained only 13–35% of the variation in height, depending on species (Table 2).

Fig. 3. Observed and estimated 5th-year heights of oak stump sprouts in relation to parent tree basal diameter. Equations are given in Table 2.



For white oak and black oak, height estimates increase as parent tree basal diameters increase up to about 20 cm; age and site index effects were not significant ($p \geq 0.05$). For scarlet oak, maximum sprout height occurs for basal diameters near 25 cm, and for post and blackjack oaks, it occurs at basal diameters near 15 and 18 cm, respectively. As parent tree diameters increase beyond their respective optima, sprout heights decrease, gradually for white oak and more rapidly for the other species (Fig. 3).

Generating future height distributions

Regression analysis is usually used in tree growth studies to estimate a mean response for a given set of initial conditions. In that setting, the regression equation expresses a single, deterministic outcome, in this case a height at age 5. However, in the present study, we incorporated the residual variation of regression equations into the model to express stochastic effects that determine the future height distributions of sprout populations. This approach is suggested

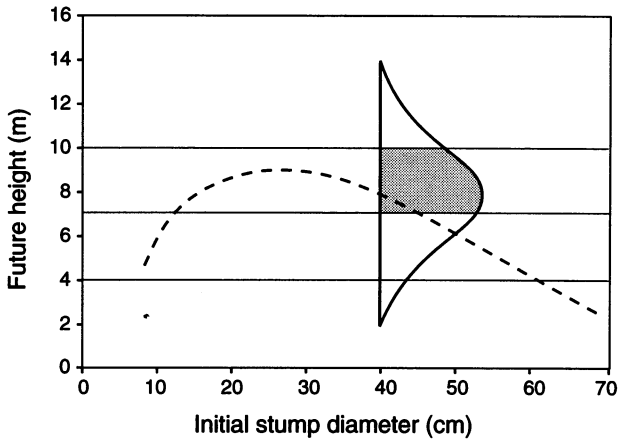
by the consistently small proportion of variance in the height of stump sprouts that can be explained by the independent variable(s) (Table 2, Fig. 3). Although the overall regression models and individual parameter estimates for determining sprout heights are highly significant, the estimates have large standard errors, which results in a lack of precision in the estimates themselves. Moreover, models of stand dynamics that consider the effects of both deterministic and stochastic sources of variation are generally desirable (Miina 1993; Stage and Wykoff 1993).

We incorporated the residual variation into the modeling process as a stochastic factor by assuming that the variation about any given estimate is normally distributed. This error structure is a standard assumption of regression analysis (Neter et al. 1989). Accordingly, the distribution of estimated height for an individual sprout would be normal. By extension, the height distribution of a large population of sprouts for any given value of parent tree diameter would approximate a normal distribution. The distribution of heights in a sample of n trees within a specified parent tree diameter class thus would be normally distributed with mean μ and variance σ^2. In this setting, the assumption of normality pertains to both the probability distribution of an individual sprout and to a population of sprouts originating from parent trees of the same diameter. However, at the population level, the resulting distribution of heights across diameter classes is not constrained to a normal or any other specific distribution.

Estimates of 5th-year heights are used as trajectories along which the normally distributed prediction error is centered (Fig. 4). This approach simultaneously considers the mean trend expressed by the regression model of future heights and the error distribution, which accounts for stochastic variation about the trajectory. In application, a sample population of parent trees from a preharvest inventory can be processed through the appropriate trajectory–dispersion models to generate future height distributions of sprouts, which express the range of variation observed in the field. To generate realistic distributions, the regression estimate (as an estimator of μ) and the regression mean square error (as an estimator of σ^2) are used to probabilistically allocate sprouts to future height classes. The method assumes that the mean square error is homogeneous with respect to the independent variable(s). Inspection of regression residuals showed little evidence of heterogeneity. The normal distribution, centered about the regression-estimated mean sprout height, thus appears to provide a reasonable basis for determining the estimated probability that an individual sprout will grow into a given height class. Probabilities are obtained from tables or computer-generated values of areas under the standard normal curve for standard normal deviates (standardized Z values), which in turn can be used to derive sprout height probabilities from estimates of μ and σ.

The resulting probabilities for individual sprouts can be used to predict the future distribution of sprout heights (number of sprouts by height class) from a preharvest sample of overstory trees. However, the individual-sprout probabilities are conditional, i.e., the probability of a sprout occurring in a given future height class (e.g., H_i) is conditional both on the sprout originating from a parent tree of

Fig. 4. Method of estimating the probability that a sprout originating from a parent tree of a given basal diameter will attain a specified future height. The regression estimate forms the trajectory along which the normal distribution is moved to probabilistically account for the dispersion (residual variation) about the trajectory. The shaded area under the normal curve is proportionate to the probability that a sprout originating from a 40-cm parent tree will occur in the 7- to 10-m height class at a specified future time.



a given diameter (e.g., D_j) and on surviving to the end of the projection period. We could let $P_{Hi|Dj}$ equal the conditional probability that a sprout occurs in future height class H_i given that it originated from parent tree diameter class D_j. If, in a given sample of the overstory there are n trees of diameter D_j, then the frequency of occurrence of sprouts in each H_i is

[3] $F_{Hi|Dj} = n(P_{Hi|Dj})$

However, each observed parent tree has an associated conditional probability of producing a sprout that survives 5 years. Thus each future height class probability ($P_{Hi|Dj}$) must be adjusted (reduced) to account for the probability that a parent tree will fail to produce a sprout that survives to age 5. This adjustment is made by multiplying each future height class probability by the appropriate sprouting or survival probability (Pss) estimated from the appropriate equation in Table 1. The product of those probabilities is an estimate of the joint conditional probability, P', of sprouting and surviving to grow into a given 5th-year height class; e.g.

[4] $P'_{Hi|Dj} = (\mathrm{Pss}_{Dj})(P_{Hi|Dj})$

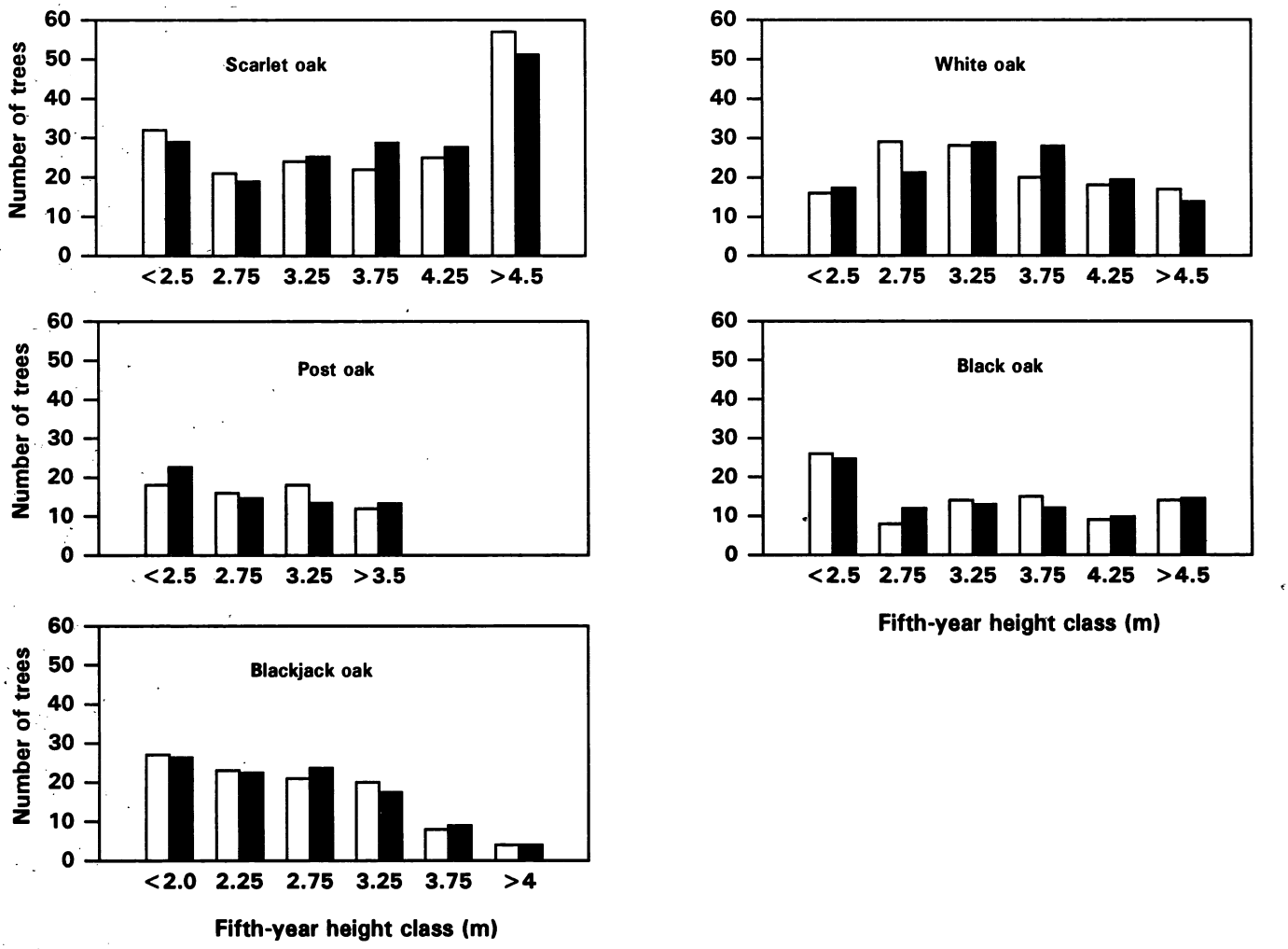
For a sample of n parent trees of diameter D_j, the sum of their $P'_{Hi|Dj}$ produces the frequency of occurrence of surviving sprouters in each future height class, $F'_{Hi|Dj}$, and

[5] $F'_{Hi|Dj} = n(P'_{Hi|Dj})$

The estimated frequency of occurrence of sprouts in height class H_i originating from all the observed diameters in a given sample of parent trees is the sum of the $F'_{Hi|Dj}$ for those diameters. This produces the frequency of occurrence of sprouts

[6] $F'_{Hi} = \Sigma_j (n_j P'_{Hi|Dj})$

Fig. 5. Comparison of observed (open bars) and predicted (closed bars) 5th-year height distributions of stump sprouts for five oak species. Height distributions are based on predictions for the tallest stem per sprout clump.



where j = 1, 2, 3, ..., J and j indexes the set of parent diameters in the sample.

The set of predicted frequencies, $\{F'_{Hi}\}$, comprises the predicted frequency distribution of sprout heights for the sample of parent tree diameters.

Model verification

Because independent data sets were not available to test the regeneration model, the predicted height distributions were tested against the observed distributions. The χ^2 test was used to test the null hypothesis that the predicted height distribution was the same as the observed distribution. The criterion for accepting the null hypothesis was set at $\alpha = 0.10$.

Predicted and observed 5th-year height distributions for all oak species did not differ significantly ($\alpha = 0.10$) based on χ^2 (Fig. 5). Predicted future size distributions of reproduction are unlimited in the form they can assume because they are determined by observed tree diameter distributions and the composition of the overstory.

Discussion and conclusions

The modeling method presented is based on specification of the initial state of the next rotation, which is encoded in the characteristics of the parent stand (as a source of stump sprouts) and advance reproduction at the end of the preceding rotation. However, given that information, the unexplained variation in predicting the growth, sprouting capacity, and survival of reproduction during the regeneration period remains a problem. Exclusively deterministic approaches to regeneration modeling based only on regression estimates or other mathematically derived averages are inadequate because they focus exclusively on a mean response and ignore the stochastic sources of variation implicit in the residual variation.

The approach described here attempts to overcome those problems through (*i*) application of a model that links future growth with the present status of the root system and (*ii*) incorporation of both deterministic and stochastic sources of variation into the modeling process. The former is based on the assumption that the height growth

of oak reproduction, including advance reproduction and stump sprouts, is a function of the size, or maturation state, of the root system and not reproduction origin, per se. Accordingly, all forms of reproduction from new seedlings to stump sprouts lie along a continuum of growth potential determined by root size, which in turn is correlated with basal tree diameter. Rate of height growth at first increases rapidly with increasing basal diameter, reaches a maximum, and then decreases. However, for various physiological and ecological reasons, the relation explains only a small to moderate proportion of the variance in height growth.

To consider the residual variation in the future heights of reproduction and to produce realistic simulations of the size distributions of trees, we simultaneously employed the regression estimates of future tree heights and the normal distribution of prediction errors about the estimate. The approach is similar to that used to assign random error to growth predictions in growth and yield models such as those developed by Stage (1973) and Hilt (1983, 1985). However, in those models, the regression-estimated growth increment for each tree is modified by a randomly derived adjustment based on the residual variation (error) of the regression model. Moreover, the stochastic adjustment is usually constrained to some limits within the error-derived normal distribution (e.g., Stage 1973). In our model, estimation of stochastic effects also is based on the residual variation of the regression model, but the probability of occurrence of each future tree height in each future height class is determined. For each observed tree, those probabilities add a fraction of a tree to each future height class. To derive the population distribution for a given initial state, the fractions are summed within each future height class. The distinction between probabilities for individual trees and proportions of tree populations thus differentiates stochastic from deterministic modes of model implementation (Vanclay 1991). In other words, the model generates and operates on individual-tree probabilities (stochastic mode), but produces a single predicted outcome (deterministic mode) expressed as a proportion of a population of trees. Such models have been defined as producing compatible deterministic and stochastic predictions (Vanclay 1991).

Our model provides a method that accounts for the stochastic nature of tree reproduction and is appropriate in modeling oak and hardwood regeneration. Stochastic effects include recurrent shoot dieback and resprouting, which are normally not necessary to consider in modeling growth and yield.

Statistical comparison of predicted to observed height distributions indicates that the proposed method can accurately simulate future height distributions of reproduction based on preharvest stand and site characteristics. The method is robust in that the distribution of future tree sizes is determined by the observed initial state of the stand and not an assumed state or future size distribution of trees. This approach to modeling has potential application to any forest type or class of ecosystem where the initial state of the arboreal component, i.e., the composition and structure of the overstory and advance reproduction at the time of final harvest, largely determines the character of the next stand. Xeric oak forests that accumulate oak reproduction over several decades, like those in the Ozark Highlands, represent such ecosystems (Johnson 1993).

Not all oak-dominated ecosystems, however, depend exclusively on the accumulation of oak reproduction beneath the parent stand, and thus the initial state, to ensure replacement by oaks. There is evidence that some northern red oak (*Quercus rubra* L.) stands on mesic sites and other oak species on bottomland sites can be regenerated by oak seedlings established after final harvest (Johnson et al. 1989; Golden and Loewenstein 1991; Jacobs and Wray 1992; Loewenstein 1992; Golden 1993; Nix and Lafaye 1993). Also, the relatively rapid but delayed height growth of some bottomland oaks such as cherrybark oak (*Quercus falcata* var. *pagodifolia* Ell.) may enable them to outgrow their nonoak competitors during early to midrotation even when the oaks are initially shorter and relatively crowded (Clatterbuck and Hodges 1988). The development of oak regeneration models therefore should consider time-dependent differences among species' growth and survival rates and ecosystem-specific relations that affect the outcome of interspecific competition. Regeneration models based on ecological characteristics of the Ozark Highlands may not be appropriate in modeling other oak-dominated ecosystems. The applicability of specific height growth, sprouting frequency, and survival models will be known after they are validated using independent data. The overall model presented provides an approach for predicting the development of hardwood reproduction in ecosystems similar to those in the Ozarks.

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