Modeling sprout-origin oak regeneration in the central Appalachians

P.J. Gould, S. Fei, and K.C. Steiner

Abstract: We describe the development of individual-tree models to estimate, before overstory removal, the contribution of common central Appalachian oak species (northern red oak (*Quercus rubra* L.), black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus montana* Willd.), and white oak (*Quercus alba* L.)) to stand stocking in the third decade (20–30 years) after harvest. The models incorporate three aspects of sprout-group development: (1) the initial sprouting of overstory oaks (≥5 cm DBH) following cutting, (2) sprout-group survival, and (3) sprout-group size at the end of the regeneration period. Logistic regression was used to model initial sprouting as a function of parent tree species and diameter using measurements on 1173 stumps. Sprout-group survival was extrapolated from 4 year remeasurements on 321 stumps. Sprout-group size, expressed as a percentage of stocking, was estimated from measurements on 429 third-decade sprout groups. Predicted sprout-origin stocking values calculated for mature oak stands compared favorably with stocking values observed in third-decade stands. The models provide forest managers with essential information on stand development following planned regeneration treatments. A similar modeling approach may be useful in other plant communities where sprouting plays an important role in post-disturbance stand development.

Résumé : Nous décrivons la mise au point de modèles à l'échelle de l'arbre visant à estimer, avant la récolte de la canopée, la contribution d'espèces répandues dans le centre des Appalaches (le chêne rouge (*Quercus rubra* L.), le chêne noir (*Quercus velutina* Lam.), le chêne châtaignier (*Quercus montana* Willd.) et le chêne blanc (*Quercus alba* L.)) à la densité relative des peuplements au cours de la troisième décennie (20–30 ans) après la récolte. Les modèles tiennent compte de trois aspects du développement des groupes de rejets : (1) la formation initiale de rejets des chênes du couvert dominant (DHP ≥ 5 cm) après la coupe, (2) la survie des groupes de rejets et (3) la taille des groupes de rejets à la fin de la période de régénération. Une régression logistique a été utilisée pour prédire la formation initiale de rejets en fonction de l'espèce et du diamètre de l'arbre-mère à partir de mesures faites sur 1173 souches. La survie des groupes de rejets a été extrapolée à partir de mesures répétées pendant quatre ans après la coupe sur 321 souches. La taille des groupes de rejets, exprimée en pourcentage de la densité relative, a été estimée à partir de mesures faites sur 429 groupes de rejets au cours de la troisième décennie des peuplements. Les valeurs de densité relative basées sur les rejets calculées pour des peuplements matures de chêne se rapprochent des valeurs observées dans les peuplements au cours de leur troisième décennie. Les modèles fournissent aux aménagistes forestiers une information essentielle sur le développement des peuplements à la suite de coupes planifiées de régénération. Il peut être utile d'appliquer une approche semblable de modélisation à d'autres communautés végétales où les rejets de souche jouent un rôle important dans le développement des peuplements après une perturbation.

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Introduction

Stump sprouting following cutting or other injury is a near-universal trait of woody angiosperms (del Tredici 2001). Sprouting plays a critical role in regenerating disturbed plant communities that experience "top-killing" dis-

P.J. Gould. School of Forest Resources, Pennsylvania State University, 204B Ferguson Building, University Park, PA 16802, USA.
S. Fei. Department of Forestry, University of Kentucky, 204 T.P. Cooper Building, Lexington, KY 40546-0073, USA.
K.C. Steiner.[1] School of Forest Resources, Pennsylvania State University, 104 Ferguson Building, University Park, PA 16802, USA.

[1]Corresponding author (e-mail: kcs@psu.edu).

turbances from agents such as fire and cutting (Bellingham and Sparrow 2000). In temperate broadleaf forest communities and many shrub communities, sprouting is a highly reliable source of post-disturbance regeneration (Kays et al. 1988; Malanson and Trabaud 1988). The contribution of sprouts to a future plant community should be relatively predictable, since a plant's ability to sprout changes relatively slowly with age and size (del Tredici 2001). In contrast, the regeneration potential of existing seedling populations may change significantly interannually and the regeneration potential of buried and invading seeds is difficult to quantify.

Sprouting is important to maintaining oaks in the eastern United States (McIntyre 1936). Oak-dominated stands are difficult to regenerate throughout the region (Lorimer 1993). Poor oak regeneration is often attributable to a lack of oak advance regeneration at the time of harvest (Beck and Hooper 1986; Lorimer 1993). However, sprouts from overstory oaks (≥5 cm DBH) also account for a sizable part of a stand's regeneration potential. Sprouts are a desirable

form of oak regeneration that grow rapidly (McQuilkin 1975) and have the potential to produce high-quality sawtimber (Roth and Hepting 1969; Lamson 1976). Sprouting potential cannot be readily improved by silvicultural treatments, but forest managers can expect some regeneration from stump sprouts in most oak stands managed under even-aged silvicultural systems. Quantitative models that accurately predict the development of sprout-origin regeneration to the end of the regeneration period (at least 20 years after harvest) are needed so that treatments to reach overall regeneration goals can be judiciously prescribed.

For modeling purposes the development of oak stump sprouts can be divided into two phases — the initial emergence of sprouts and the subsequent development of the sprout group (the group of stems originating from a single parent tree) through the regeneration period (Johnson 1975; Cline 1997). Several parent-tree attributes have proved useful for predicting sprouting in Appalachian oaks. The probability of sprouting decreases with increasing parent-tree diameter (Roth and Hepting 1943; Johnson 1975; Weigel and Johnson 1998). A similar trend for sprouting potential to decrease with tree age has also been found (Roth and Hepting 1943; Johnson 1977; Weigel and Johnson 1998). The form of these relationships varies by species. The sprouting potential of white oak (*Quercus alba* L.), in particular, declines sharply with increasing diameter (Weigel and Johnson 1998). Mixed results have been reported regarding the relationship between initial sprouting and environmental factors. Greater sprouting frequencies have been reported for more productive sites, as measured by site index (Johnson 1977; Weigel and Johnson 1998). However, other studies have failed to show statistically significant relationships (Wendel 1975; Dey 1991) or meaningful trends (Lynch and Bassett 1987) between sprouting probabilities and site index.

The development of oak sprout groups follows a characteristic pattern. After the initial flush of sprouts, the number of stems within a sprout group declines rapidly. Mean group densities decline from approximately 10 to 4 or 5 stems during the first decade (McIntyre 1936; Roth and Hepting 1969; Johnson 1975). The rate of within-group thinning then appears to slow considerably. Reported mean group densities range from 4 stems at age 23 (Johnson 1975) to approximately 1.5 stems during the fourth decade after cutting (McIntyre 1936; Roth and Hepting 1969). Sprout-group mortality (i.e., the loss of all stems within a sprout group) appears to be low during the first several decades after cutting. Wendel (1975) reported almost no sprout-group mortality among northern red oak (*Quercus rubra* L.), white oak, and chestnut oak (*Quercus montana* Willd.) sprout groups in West Virginia over a 10 year period. Johnson (1975), examining a chronosequence of stands ranging from 4 to 23 years of age, did not detect any loss of sprout groups over the age range, suggesting that sprout-group mortality was minimal. Roth and Hepting (1969) found that approximately 80% of stumps that sprouted 1 year after cutting retained at least one stem over a 32 year period. Sander et al. (1984), in developing regeneration guidelines for the Missouri Ozarks, suggested that 89% of sprout groups would survive over the first two decades of stand development.

During sprout development, parent-tree characteristics appear to have a decreasing influence on sprout-group charac-teristics. Johnson (1977) and Dey (1991) reported a weak negative relationship between parent-tree diameter and dom-inant sprout height in 5-year-old oak sprouts in the Missouri Ozarks. Johnson (1975) found that larger northern red oak stumps in the Midwest initially produced more sprouts, but differences in sprout numbers were no longer statistically significant after 12 years. In a study in West Virginia, Wendel (1975) found that the height of the tallest sprout in oak sprout groups was uncorrelated with parent-tree diame-ter or vigor 10 years after cutting.
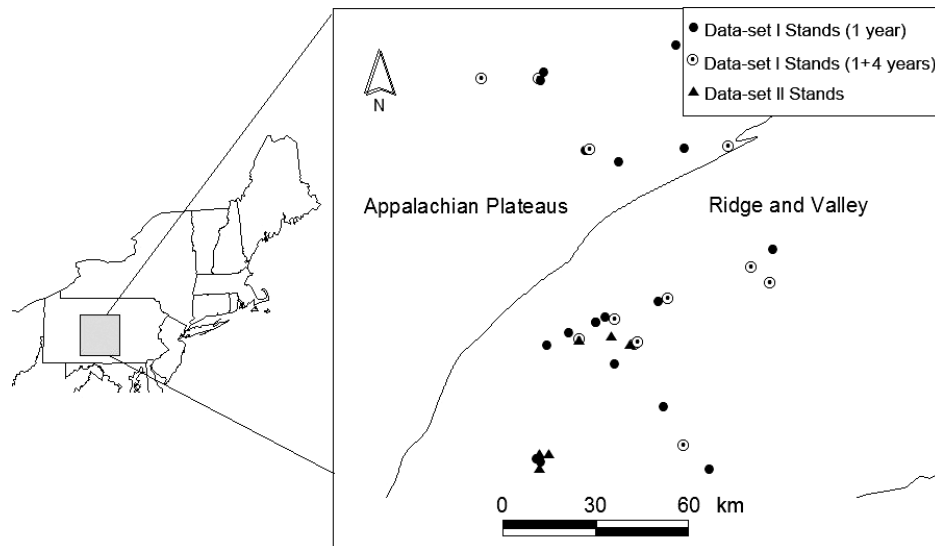
In this paper we describe the development of models of sprout-origin oak regeneration for the central Appalachians based on data from Pennsylvania. Several models have been proposed for predicting oak sprouting in ecologically similar regions (Johnson 1977; Weigel and Johnson 1998; Dey 1991; Weigel and Peng 2002). However, none of these mod-els have attempted to quantify the growing space occupied by sprout groups at the end of the regeneration period. In ad-dition, our models are the first oak sprout model of any kind developed for the central Appalachians. The output unit in our models is expected third-decade sprout-origin oak stock-ing, which is the percentage of stand area occupied by sprout groups in the third decade (20–30 years) after harvest. This stage of stand development is often regarded as mark-ing the end of the regeneration period (Sander et al. 1984; Loftis 1990). The output unit is equivalent to the output from several seed origin oak regeneration models (Sander et al. 1984; Gould et al. 2006) and it efficiently describes the contribution of sprout groups that often contain multiple stems that form a single crown. Stocking is typically mea-sured indirectly and calculated as a function of tree diameter and density (Gingrich 1967). During model development, we addressed the question of whether a widely used stocking equation for mixed-oak stands (Gingrich 1967) accurately estimates the growing space occupied by sprout groups.

Methods

Study area

Models were developed using data from a continuing study of oak regeneration on Pennsylvania State Forest lands (data set I) and supplemental data collected in third-decade stands (24–27 years old) that established following silvicultural clear-cutting on State Forest lands (data set II). Stand locations are shown in Fig. 1. The study region spans two physiographic provinces. The Ridge and Valley province is a folded and faulted region characterized by steep, nearly parallel ridges oriented northeast to southwest. Oak-dominated forests containing scarlet oak (*Quercus coccinea* Muenchh.), white oak, chestnut oak, northern red oak, and black oak (*Quercus velutina* Lam.) are the natural vegetation on the ridges, while valleys are primarily under agricultural production. The Appalachian Plateaus province is an up-lifted region deeply dissected by stream and river valleys. Oak-dominated forests transition into Allegheny hardwoods moving northward on the Appalachian Plateaus, but oaks continue to be locally dominant (Stout 1991). Soils where the stands are located are weathered from sandstone, siltstone, and shale (Cuff et al. 1989). Site index was not ac-curately measured in all the study stands, but forest produc-tivity is typically low to moderate in similar stands (site

Fig. 1. Distribution of study stands in the Ridge and Valley and Appalachian Plateaus physiographic provinces in Pennsylvania, USA.

index = 18–23 m at 50 years of age) (Bowersox and Ward 1972). Most stands in the region regenerated following turn-of-the-century logging, and mature oak stands are typically even-aged and between 80 and 110 years old (Stout 2000). Regional mean annual precipitation ranges from 965 to 1143 mm and frost-free periods range from 140 to 160 days (Cuff et al. 1989).

Data collection

Oak stumps in 30 stands were measured 1 year after harvest to determine initial sprouting frequencies, and stumps were remeasured in 12 stands to determine sprout-group survival (data set I). Permanent plots were established in each of the 30 stands in advance of harvest. Harvests ranged from near-complete overstory removals to first-stage shelterwood treatments. After harvest, plots were revisited and the cut stump closest to each plot center was identified. The species, stump diameter, number of sprouts, and height of the tallest sprout were recorded. Diameters at breast height (DBH) were reconstructed from stump diameters using highly deterministic, species-specific equations developed by Weigel and Johnson (1997). Species were identified on the basis of bark characteristics and ring morphology. About 2% of oak stumps could not be identified to the species level. These stumps were divided among species in proportion to total sample sizes. Data describing the plot-level (percent slope, aspect, post-treatment basal area) and stand-level (slope position) growing environment were also recorded. Distances and directions from plot centers to stumps were recorded to facilitate the relocation of the stumps. In total, 1173 stumps were sampled 1 year after harvest. Oak stumps in 12 stands (N = 321 stumps) were relocated 4 years after harvest and the number of live sprouts and the height of the tallest sprout were recorded. Woven-wire fences were erected around 7 of the 12 remeasured stands within 1 year after cutting to exclude white-tailed deer (*Odocoileus virginianus* (Zimmerman)). Browsing pressure on the remaining stands was judged low enough to permit regeneration without excluding deer. Data set I is summarized in Table 1.

Data to determine the average growing space occupied by

individual sprout groups in the third decade after harvest were collected in six stands (data set II). Stands had been oak-dominated before being regenerated with silvicultural clear-cutting 24–27 years prior to measurement. Sprout groups were sampled along belt transects. All living oaks that fell within the transects were examined to determine their origin (stump sprout or seedling / seedling sprout). Oaks were considered to be of sprout origin only when remnants of a cut stump were found immediately adjacent to the living stems. The species of the sprout group and DBH of upper canopy stems (dominant, codominant, and intermediate crown classes) were recorded. Exposed sprout-group crowns (Webster and Lorimer 2003) were measured along two diameters, first in the longest direction and then perpendicular to the first diameter and passing approximately through the crown center. Approximately equal numbers of northern red oak, black oak, scarlet oak, chestnut oak, and white oak sprout groups were measured. Data set II is summarized in Table 2.

Modeling

We used an individual-tree modeling approach to estimate the contribution of individual parent trees to third-decade oak stocking. Our model reflects three elements of sprout development — initial sprouting, sprout-group survival until the end of the regeneration period, and the area occupied by a sprout group. The model form is

[1] $E(\text{stocking}) = P(\text{sprouting}) \times P(\text{survival})$
$$\times \text{ sprout-group stocking}$$

where

$E(\text{stocking})$ is expected stocking (%) in the third decade after harvest

$P(\text{sprouting})$ is the probability of producing a live sprout group 1 year after harvest

$P(\text{survival})$ is the probability of sprout-group survival from year 1 to the third decade

Sprout-group stocking is the average area occupied (percent stocking) by a sprout group in the third decade.

Table 1. Summary of data set I.

	DBH (cm)							
	Year 1				Year 4			
	N	Mean	Min.	Max.	N	Mean	Min.	Max.
White oak	209	37.6	5.6	99.1	15	24.6	8.6	39.9
Chestnut oak	519	30.2	8.6	68.8	183	27.4	10.7	56.9
Northern red oak	328	41.7	4.8	87.9	88	41.4	12.7	86.6
Black oak	117	39.6	18.5	73.7	35	33.3	18.5	51.1

Table 2. Summary of third-decade sprout-group measurements (data set II).

	N	Stocking (%)*	Mean density (no. of stems / sprout group)	Mean DBH (cm)
White oak	84	0.17d	1.7	15.5
Scarlet oak	77	0.24ab	2.0	19.1
Chestnut oak	87	0.27a	2.3	18.3
Northern red oak	85	0.21bc	2.2	16.3
Black oak	96	0.19cd	1.8	17.3

*Values followed by a different letter differ at the $\alpha = 0.05$ level.

Logistic regression was used to develop models to estimate initialing sprouting probabilities and it was also applied to the year-4 measurements to model subsequent survival. Logistic regression is a statistical method for developing models with a dichotomous response variable (e.g., sprouting success or failure) (Cook and Weisberg 1999). The resulting models estimate the probability of one outcome conditional on a set of independent variables. Independent variables included parent tree species and DBH and a four-level topographic variable (TOPO). Site productivity, usually measured in terms of site index, is potentially important to oak sprouting success (Weigel and Peng 2002). Productivity is also strongly influenced by topography described using variables such as slope position, percentage, and aspect (Bowersox and Ward 1972; McNab 1993). TOPO was used to divide slope positions and slope percentages into four classes: (1) top (ridgetop or upper-slope position and <10% slope), (2) slope (upper, middle, or lower slope position and ≥10% slope), (3) bench (upper, middle, or lower slope position and <10% slope), and (4) bottom (lower or bottom slope position and <10% slope). Both TOPO and species were used as discrete class variables each with four levels representing the four topographic classes and four oak species (*Q. alba*, *Q. velutina*, *Q. montana*, and *Q. rubra*). DBH was used as a continuous variable.

The year-1 sprouting model was fit using the reverse stepwise logistic regression option in the PROC LOGISTIC procedure in the statistical software package SAS® system for Windows, Version 8.02 (SAS Institute Inc. Cary, North Carolina). All model terms (species, DBH, TOPO) and two-way interactions were included in the initial model. Model terms were then removed if they did not significantly contribute to the model as measured, using χ^2-distributed differences in deviation between "full" and "reduced" models fit using the maximum-likelihood method (Collett 2003). Differences in explanatory power between models were examined by comparing rates of concordance (c). Concordance is calculated by identifying all pairs of successful and failed

observations and comparing modeled probabilities of success (p). In this case, pairs consisted of one observation where a stump sprouted and a second observation where the stump failed to sprout. Pairs are in concordance when $p_{successful} > p_{failed}$. The c statistic is the proportion of pairs in concordance, plus one-half the proportion of ties ($p_{successful} \approx p_{failed}$) (SAS® system for Windows, Version 8.02).

The sensitivity, specificity, false-positive rates, and false-negative rates were calculated for the final model for a fixed p value of 0.50. Sensitivity is the percentage of successful observation with predicted success probabilities greater than the fixed p value. Specificity is the percentage of failed observation with predicted success probabilities less than the fixed p value. The false-positive and false-negative rates are the percentages of observations misclassified as successes or failures, respectively, at the fixed p value (SAS® system for Windows, Version 8.02). Lack of fit in the final model was assessed with the Hosmer–Lemeshow statistic. To calculate the Hosmer–Lemeshow statistic, observations are sorted with increasing modeled probabilities of success and divided into approximately 10 groups. The predicted number of successes in each group is calculated using the model, and the observed successes are counted. Predicted and observed success counts are compared against the χ^2 distribution; statistically significant χ^2 values indicate a lack of fit in the model (Collett 2003).

Survival was modeled by assuming that stumps which produced at least one live stem ≥2 m tall by the end of the fourth growing season would continue to be successful until the end of the regeneration period. Sprouts from other stumps were considered failures. This criterion insured that the sprout was beyond the typical browse height of white-tailed deer and in a highly favorably competitive position (Gould et al. 2004). Because our definition of year-4 success was probably conservative (i.e., some "unsuccessful" sprouts likely contribute to third-decade stocking), we assumed 100% survival from year 4 to the third decade of stand development. Species, DBH, TOPO, and post-treatment basal

area were evaluated as potential predictors using the logistic regression procedure described above. However, none of the independent variables was a statistically significant predictor of success. Therefore, a constant value equal to the mean proportion of successful stems was used in the model for all species.

The growing space occupied by third-decade sprout groups was initially calculated using two methods. The first method was to directly calculate stocking using crown diameters. Crown areas were calculated assuming an elliptical crown shape (crown area (m^2) = $\pi(d_1/2)(d_2/2)$) and stocking was then calculated as a percentage of a hectare (crown area / 10 000 m^2 × 100%). The second method was to calculate stocking indirectly using Gingrich's (1967) stocking equation. The equation (SI units) is

[2]   Stocking =

$$0.1\left(-0.021N + 0.027\sum_{i=1}^{N} D_i + 0.002\sum_{i=1}^{N} D_i^2\right)$$

where N is the number of stem in the sprout group, and D_i is the diameter (cm) of stem i.
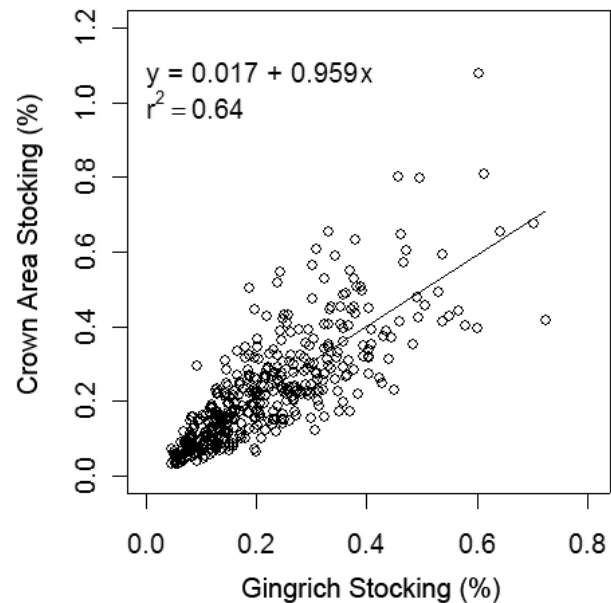
Hypothetically, stocking estimates using eq. 2 should agree with the direct measurements. However, the equivalence of these stocking measures has not been tested for sprout groups and it was unclear whether sprout groups occupy a stand area as predicted using eq. 2. The two measures of stocking were compared using linear regression analysis to determine whether eq. 2 adequately predicts stocking from diameter measurements of sprout groups. Analysis of variance with means separation using Duncan's multiple range test (Neter et al. 1996) was then used to determine whether third-decade stocking varied among species.

The final predictive models (eq. 1) were tested by comparing predicted sprout-origin oak stocking in 34 mature oak-dominated stands with observed sprout-origin oak stocking in a second sample of 31 stands that originated after harvest of oak overstories 20–33 years prior to measurement (for stand descriptions see Gould et al. 2003). Both sets of stands are located on Pennsylvania State Forest land in the Ridge and Valley physiographic province (Cuff et al. 1989). Preharvest overstory compositions in the regenerated third-decade stands were similar to the current overstories in the mature stands, suggesting similar sprouting potentials. However, the two samples are independent and we did not expect predicted and observed oak stocking to match exactly. Instead, we expected general agreement between the means and distributions of sprout-origin oak stocking values.

Results

The year-1 sprouting model that included species, DBH, TOPO, and all two-way interactions had a concordance of 76.0%. Reverse stepwise logistic regression eliminated TOPO and its two-way interactions to yield a final model that included species, DBH, and species × DBH. The concordance of the final model was reduced somewhat compared with the full model to 73.6%. The sensitivity and specificity of the final model at $p = 0.50$ were 89.4% and 42.9%, respectively, indicating that most successful observa-

Fig. 2. Comparison of expected stocking using Gingrich's (1967) stocking equation and directly measured crown area stocking for oak sprout groups.
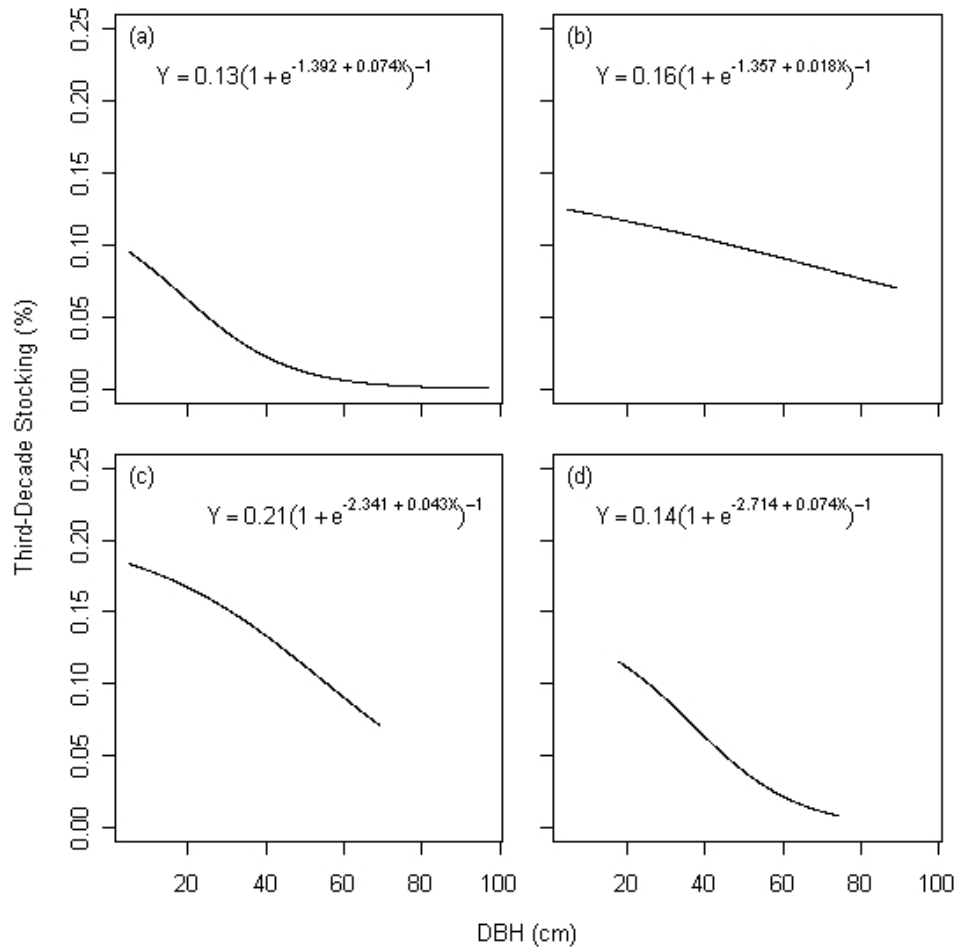

tions, and over one-half of failed observations, had predicted success probabilities >0.50. The false-positive and false-negative rates were 30.2% and 26.9%, respectively. The Hosmer–Lemeshow test did not provide evidence of lack of fit in the final models ($p > 0.28$), indicating that the difference between predicted and observed success did not vary systematically with the independent variables. None of the independent variables were significant predictors of sprout-group survival as measured by year-4 success ($p = 0.11$). Among the stumps that initially sprouted, 76% had at least one stem ≥2 m tall, four growing seasons after cutting. Consequently, P(survival) was not considered to differ by species or DBH, and was set at 76%.

Stocking measured directly from crown area differed little from expected stocking calculated with Gingrich's (1967) stocking equation (Fig. 2). The regression coefficient was 0.959 and its 95% confidence interval included 1.0, indicating that the two measures of stocking are approximately equivalent. Variation between the two measures of stocking appears to increase with stocking, but there is little evidence of a systematic difference. Stocking estimates using Gingrich's (1967) equation were used in the model, since this approach is much more widely used and the estimates of crown area appear accurate for sprout groups.

Mean third-decade stocking by individual sprout groups varied among species ($F_{[4,424]} = 13.9$, $p < 0.001$). Chestnut and scarlet oak sprout groups occupied the most growing space (0.27% and 0.24% stocking, respectively), while white oak occupied the least (0.17% stocking) (Table 2). Sprout groups of all species maintained more than one live stem, on average, into the third decade. Mean sprout-group DBH ranged from 15.5 to 19.1 cm.

Figure 3 illustrates the final models (eq. 1) to predict third-decade stocking based on parent-tree DBH for white oak, chestnut oak, northern red oak, and black oak. The form of each curve is determined by the probability of sprouting.

Fig. 3. Third-decade stocking models for white oak (*a*), northern red oak (*b*), chestnut oak (*c*), and black oak (*d*). Model equations are given in each graph.

The white oak model shows a rapid loss in sprouting ability with increasing diameter. The northern red oak model, in contrast, shows little loss in sprouting ability with increasing diameter. The initial sprouting models were multiplied by the survival constant and estimates of species-specific third-decade stocking. Thus, the *y*-intercepts of the models are strongly influenced by these model terms. For example, chestnut oak occupies more growing space than other species and also has high sprouting potential across the range of diameter classes. Hence, expected third-decade stocking for chestnut oaks is greater than for the other species across the range of diameter classes. White oak, in contrast, has relatively poor sprouting potential and occupies less area in the third decade after harvest. Expected third-decade white oak stocking, therefore, is generally low.
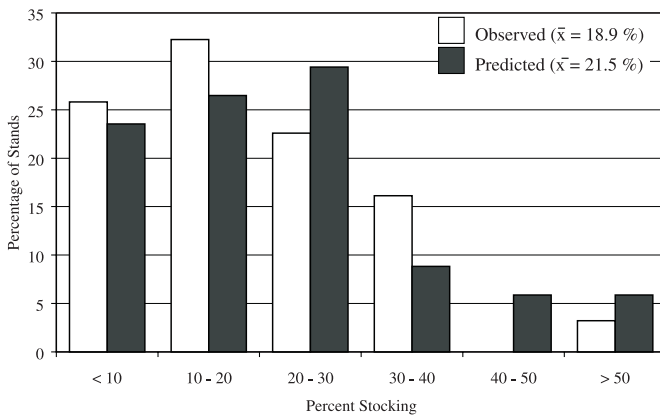
Predicted stocking values calculated for mature oak forests compare favorably with stocking values observed in third-decade stands that regenerated following the harvest of similar overstories (Fig. 4). Observed sprout-origin oak stocking averaged 18.9% among third-decade stands. Predicted stocking calculated in advance of harvest in similar stands averaged 21.5%. The distributions of predicted and observed stocking values are comparable, even though they reflect two independent samples. Less than 10% stocking was observed in, and is predicted in, about one-quarter of

stands. Percentages of stands in most other stocking classes vary by about 6%. Approximately 8% more stands are predicted to reach the higher stocking classes (>40% stocking) than was observed in the actual third-decade stands. While this suggests that the model may overestimate third-decade stocking in some cases, it is also quite possible that the two samples differ in sprouting potential. Notably, the maximum predicted value (59.7% stocking) is close to the maximum observed value (55.2% stocking).

Discussion

Forest-management decisions are strongly influenced by expected outcomes of planned or anticipated disturbances. Tools capable of accurately predicting outcomes in advance of disturbance are critical, as the best management opportunities are often present before disturbance occurs. In even-aged silvicultural systems that rely on natural regeneration, the best opportunities to shape future stands exist prior to final overstory removals. Predictive models can play a critical role in alerting forest managers to potential regeneration problems before stands are harvested and management options become much more limited. Given the widespread oak-regeneration problem, obtaining accurate estimates of sprout-origin regeneration is critical. While previous models

Fig. 4. Distribution of sprout-origin oak stocking for 34 mature stands (predicted; solid bars) and 31 third-decade stands (observed; open bars) in the Ridge and Valley province of Pennsylvania.

provide sprouting probabilities and estimates of sprout-group survival, the present model is the first to more fully quantify the role sprout groups can play in restocking harvested stands.

Most of the model parameters are similar to those of previous models. Parent-tree species and diameter were significant predictors of initial sprouting, but were not useful for predicting development through year 4. The initial sprouting model parameters generally agree with those proposed in other studies of oak sprout group development. Initial sprouting probabilities decline with increasing diameter and vary by species, with white oak exhibiting the lowest sprouting potential for most diameters (Roth and Hepting 1943; Johnson 1975; Weigel and Johnson 1998). The lack of statistically significant relationships between parent-tree characteristics and year-4 success is consistent with other reports of a decreasing influence of parent-tree characteristics over time (Johnson 1975; Wendel 1975; Lowell et al. 1987). Residual basal area, which was not a statistically significant predictor of year-4 success in the present study, may nonetheless influence sprout-group development in some cases. Managers should exercise caution when applying the model to uneven-aged silvicultural systems or lighter shelterwood cuts. TOPO was not a statistically significant predictor of initial sprouting, although other studies have shown oaks to be more likely to sprout on higher quality sites (Johnson 1977; Weigel and Johnson 1998). It is possible that site quality was not adequately reflected in the TOPO variable. However, other researchers have also failed to find a meaningful relationship between sprouting frequencies and site quality (Wendel 1975; Lynch and Bassett 1987; Kays et al. 1988; Dey 1991), suggesting that site quality may not be a consistently important factor influencing sprouting.

Our estimated rate of sprout-group survival between the first year after cutting and the third decade (76%) is similar to, though somewhat lower than, estimates reported elsewhere (Roth and Hepting 1969; Johnson 1975; Wendel 1975). In general, sprout groups are expected to have high survival rates because of their rapid growth and high competitive capacity (McQuilkin 1975). Sprouts that grew following earlier logging operations sometimes toppled following the decomposition of the parent stump (Roth and Hepting 1943, 1969); however, this problem can be remedied by cutting stumps low, which is a common practice today. In the present study, the estimated survival rate reflects the proportion of sprout groups that quickly surpassed the browse height for white-tailed deer. Some stands were fenced after harvest when the forest managers perceived a high level of deer browsing. Therefore, the models do not reflect sprout-group development under a high level of deer browsing, and applying the model under such conditions may produce inaccurate estimates.

The models appear to produce reasonable estimates of the role of sprout groups in third-decade stands. The selection of percent stocking as the output unit in the models is critical to their accuracy. Most comparable models estimate the future contribution of only the single largest stem in each sprout group (Johnson 1977; Sander et al. 1984; Dey 1991; Weigel and Peng 2002; Weigel et al. 2006). Sprout groups often contain multiple stems through the first several decades of development and possibly longer (McIntyre 1936; Roth and Hepting 1969; Johnson 1975). Assuming that sprout groups contain only a single stem understates their importance in developing stands. Percent stocking is also a more relevant measure of the contribution of sprouts to developing stands. A standard regeneration goal is to reach full site occupancy within a reasonable period and, in oak-dominated forests, forest managers often wish to regenerate stands with a high percentage of oak. Expressing regeneration goals in absolute units, such as stems per hectare, has some inherent drawbacks. Tree size and density change rapidly in young stands and are sensitive to site productivity at a given age (Oliver and Larson 1990). Stocking and analogous indices are generally considered more robust measures of site occupancy (Gingrich 1967).

The applicability of Gingrich's (1967) stocking equation to sprout groups had not previously been tested. Our results indicate that it is an accurate approach for indirectly measuring the growing space occupied by sprout groups, assuming that estimates of the number and diameters of surviving stems are available. Several models of seed-origin regeneration (e.g., Sander et al. 1984; Gould et al. 2006) also use percent stocking as the output unit. The present model is an appropriate companion model to estimate sprout-origin oak regeneration in the same units. The modeling approach may also be useful in shrub-dominated plant communities where stem density and basal area are less important measures of site occupancy than the area covered by a given species.

The models can be used with overstory inventory data (e.g., oak densities by diameter class) to estimate, in advance of harvest, the contribution of stump sprouts to third-decade oak stocking. However, they have not yet been thoroughly tested and should be applied cautiously. A model was not developed for scarlet oak, a common species in the central Appalachians, owing to an insufficiency of data on initial sprouting. The northern red oak model may be used as a reasonable substitute. Others researchers (Weigel and Johnson 1998) found similar relationships between parent-tree diameter and initial sprouting for these two species. In the present study, average percent stocking did not differ significantly between the two species (Table 2), which suggests that they have similar patterns of sprout-group development.

Similar individual-tree models may be developed for other plant communities and to meet other modeling objectives. Our generalized approach was to model each parent tree's contribution to a future stand condition based on its predisturbance characteristics. Models may be developed to estimate the contribution of parent trees or shrubs to a range of stand conditions, such as total biomass or fuel load, during a specific period following a disturbance. The species and size of the parent tree are likely to be important predictor variables in many plant communities (del Tredici 2001), although environmental variables related to site productivity may also be important in some cases.

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