FUNDAMENTAL RESEARCH

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silviculture

The Impact of Overstory Density on Reproduction Establishment in the Missouri Ozarks: Models for Simulating Regeneration Stochastically

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Predicting the effects of silvicultural choices on regeneration has been difficult with the tools available to foresters. In an effort to improve this, we developed a collection of reproduction establishment models based on stand development hypotheses and parameterized with empirical data for several species in the Missouri Ozarks. These models estimate third-year abundance parameters for established reproduction that originated from either small advance reproduction or new germination. The influence of predisturbance stand conditions was summarized by a simple presence/absence inventory of advance reproduction for each species. The influence of postdisturbance stand conditions was summarized by user-provided estimates of residual overstory density and presence/absence of a residual seed source for each species. The estimated abundance parameters can be used deterministically or with stochastic number generators to simulate regeneration after a variety of harvest-based silvicultural manipulations. This approach has the potential to increase the efficacy of regeneration modeling by reducing the inventory effort typically required and increasing compatibly for species not strongly reliant on advance reproduction.

Keywords: regeneration modeling, stochastic simulation, silviculture, seedlings, recruitment

Forest regeneration is a dynamic process involving the establishment, growth, and mortality of trees. Complex interactions among these three primary components continually shape the regeneration process, but the relative importance of each may vary throughout the development of a stand (Oliver and Larson 1996). At the beginning of the regeneration period (and often before), establishing a new cohort is paramount, and foundational attributes such as the initial density, composition, and size structure of the new cohort will influence developmental dynamics throughout the remainder of the regeneration period (Egler 1954, Gould et al. 2005, Dey 2014).

Management objectives for forest regeneration often include criteria specifying desirable species composition and critical thresholds for abundance. However, given the complexity and variability associated with the regeneration process, objectives beyond simply replacing one group of trees with another are often difficult to achieve (Loftis and McGee 1993, Kabrick et al. 2007). Moreover, the inherent variation present in biological systems often results in years or decades passing before the outcomes of interactions among establishment, growth, and mortality during the regeneration period become apparent (Quero et al. 2011). Given this time frame, the ability to forecast regeneration outcomes via models may expedite silvicultural diagnoses and improve the likelihood of achieving desired regeneration outcomes (Ferguson et al. 1986). However, integrating both deterministic and stochastic elements in a comprehensive framework has been a challenge to modeling regeneration (Weiskittel et al. 2011).

Several approaches have been used to model forest regeneration. The scope can vary from annual seed production (e.g., Rogers and Johnson 1998) to projections of stand composition near the end of the regeneration period (e.g., Loftis 1989, Millington et al. 2013). Weiskittel et al. (2011) differentiate models that incorporate the

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This article uses metric units; the applicable conversion factors are: centimeters (cm): 1 cm = 0.39 in.; square meters (m^2): 1 m^2 = 10.8 ft^2; hectares (ha): 1 ha = 2.47 ac; square meters per hectare (m^2/ha): 1 m^2/ha = 4.356 ft^2/ac.

more stochastic aspects of seed production, dispersal, and germination from those that begin with "established seedlings" and model their subsequent development. Some gap models have incorporated, to varying degrees, estimates of seed production, dispersal, and germination rates (Bugmann 2001, Price et al. 2001). The SORTIE model (Pacala et al. 1993), for example, incorporates models of seed dispersal (Ribbens et al. 1994, Clark et al. 1999b) along with juvenile growth (Pacala et al. 1994, Finzi and Canham 2000, Wright et al. 2000) and mortality (Kobe et al. 1995) for forest types in the northeastern United States and British Columbia, Canada.

The "established seedling" approach described by Weiskittel et al. (2011, p. 157) has proven to be a particularly viable avenue for modeling regeneration within oak (*Quercus*)-dominated forests. This is due, in part, to a logical link between this approach and the regeneration ecology of many species in these forests. There is a voluminous body of research suggesting that regeneration outcomes are largely a product of the density, composition, and structure of reproduction that is present in advance of a releasing disturbance (Egler 1954, Horn 1974, Noble and Slatyer 1980). This is particularly salient for many oaks, as Loftis (2004) summarized with the "First Law of Oak Silviculture": successful oak regeneration originates as advance reproduction and stump sprouts. Accordingly, several models use an inventory of advance reproduction to project regeneration outcomes or evaluate reproduction adequacy. Sander et al. (1976, 1984) were among the first to develop models to evaluate regeneration potential in oak-dominated forests. The probability of reproduction surviving and meeting a predetermined height threshold (which was related to the expected height of a codominant oak) at a specified stand age was derived empirically. This strategy has been labeled the "dominance probability" approach (Johnson et al. 2009), and variants have been applied with success in other settings (e.g., Loftis 1990, Spetich et al. 2002, Weigel and Peng 2002, Dey et al. 2009). Preharvest basal diameter and/or height, tree age, and site productivity are common covariates used to model dominance probabilities. Other approaches use advance reproduction inventories to varying degrees to evaluate reproduction in oak-dominated forests of the United States (e.g., McQuilkin 1975, Belli et al. 1999, McWilliams et al. 1995, Steiner et al. 2008). For example, the SILVAH-OAK program (Marquis et al. 1992, Stout et al. 2007, Brose et al. 2008) uses an advance reproduction inventory to provide management guidelines for oak-dominated forests in the Mid-Atlantic States based on empirical data and expert experience. The fundamental research required to build these models and guidelines has been instrumental to the development and synthesis of regeneration theory for the oak genus.

Perhaps the three most applicable, and readily available, multigenus regeneration simulators for the Central Hardwood region of the eastern United States are the Forest Vegetation Simulator (FVS) (Crookston and Dixon 2005), ACORn (Dey 1991), and REGEN (Loftis 1989). FVS is a powerful growth and yield simulator that can accommodate most major tree species and a range of silvicultural treatments and has been calibrated for forests across the United States using several geographic variants. To date, the "full" regeneration establishment model, which includes stump sprouting and natural regeneration sources, has been calibrated for parts of Montana, Idaho, and Alaska (Dixon 2002). The regeneration model for the southern and central states variants of FVS remains a "partial" establishment model that includes only stump sprouting unless additional regeneration sources are included manually by the user (Dixon 2002). In contrast to the partial establishment model of FVS, both ACORn and REGEN use advance reproduction inventories to account for natural regeneration sources. ACORn simulates regeneration in the Missouri Ozarks after clearcut or classic shelterwood harvests. ACORn projects height and diameter growth as well as survival of inventoried reproduction to create diameter distributions by species, stocking levels, and density measures for a stand at the end of the regeneration period (21 years). Stump sprouting, survival of advance reproduction, and growth of individual stems are projected using empirically derived models. REGEN is an expert system that projects the species composition of dominant and codominant stems at canopy closure in the mixed species forests of the Southern Appalachians after clearcut (or similar) harvesting using combinations of expert experience and empirical data when available. REGEN can accommodate stump sprouting, advance reproduction, and postharvest germination. The REGEN approach has been found to produce reasonable results when adapted for other regions, especially when empirically informed parameterization complements expert opinion (Vickers et al. 2011, Clatterbuck 2015). Keyser and Keyser (2013) successfully incorporated REGEN results into FVS (bypassing the partial establishment model) to examine the impact of various regeneration techniques on species composition in the Southern Appalachians.

Most of the models and evaluations described previously rely on a full inventory of advance reproduction to project regeneration outcomes. Although small plots are typically used for reproduction inventories (e.g., 0.0004 or 0.004 ha), there can be dozens to thousands of stems on a single plot (Brose et al. 2008, Vickers 2009, McWilliams et al. 2015). Consequently, considerable effort may be expended collecting the necessary input data for these models which, in turn, has led to increased interest in simpler alternatives (e.g., Ristau and Stout 2014). Several studies have shown that small reproduction, particularly of heavy seeded species, tend to be a slow growing (Sander 1971), ephemeral population (Loftis 1983) that is unlikely to be competitive after disturbance (Sander et al. 1984, Loftis 1990, Dey 1991, Spetich et al. 2002, Brose et al. 2008, Johnson et al. 2009). Therefore, a pragmatic solution may be to continue projecting the fate of large reproduction using inventoried attributes while estimating the contribution from the population of small reproduction via stochastic modeling. Such an approach would explicitly acknowledge the fate of small reproduction as a large source of the variation in regeneration outcomes (Larsen et al. 1997, Larsen and Johnson 1998, Gould et al. 2006) and would be a hybrid modeling approach in that the fate of large advance reproduction would follow the "established seedling" approach, whereas seed production, dissemination, and germination would implicitly be accounted for in stochastic models (see Weiskittel et al. 2011, p. 157). Moreover, if it can be assumed that the competitive potential of small advance reproduction and seedlings that germinate postdisturbance are more similar than dissimilar, an approach that estimates the combined contribution to future conditions from both populations is plausible. This hybrid approach has the potential to increase the efficacy of regeneration models by eliminating the effort required to enumerate small advance reproduction and increasing compatibly for species with regeneration strategies that do not strongly rely on advance reproduction.

Many existing regeneration models were developed to operate within specific silvicultural systems (often even-aged management using clearcut harvesting), which limits their applicability to other regeneration settings. Foresters have long understood that species differ in their regeneration strategies and their abilities to flourish

after disturbances of varying magnitudes and frequencies (Büsgen and Münch 1929, Assmann 1970, Puettmann et al. 2008). Despite this, relatively little progress has been made toward quantifying and projecting the impact of varied overstory conditions on the development of reproduction, particularly compared to clearcutting in naturally regenerated mixed-species stands. Accordingly, many of the previously described regeneration modeling strategies are not readily adaptable to the more structurally and compositionally diverse forest conditions with continuous canopy cover embodied by current management objectives (Puettmann et al. 2008).

We initiated a research project to model the impact of overstory density on the establishment, growth, and mortality of reproduction in the Missouri Ozarks. The focus of this article is to describe the development and parameterization of reproduction establishment models. Our objective was to estimate third-year abundance parameters for reproduction that originated from either small advance reproduction (height <100 cm) or new germination. In the context of this project, established reproduction was defined as stems present 3 years after disturbance. We expected that this abundance was largely a function of residual overstory density due to its influence on resource availability (Reineke 1933, Yoda et al. 1963, Gingrich 1967, Assmann 1970, Oliver and Larson 1996). We assumed that the abundance could vary by species and parameterized separate models for individual species or species groups (Grubb 1977, Noble and Slatyer 1980, Streng et al. 1989). We recognized that various known and unknown site and micro-site characteristics might affect the ability of some species to become established (Harper et al. 1961, Bigelow and Canham 2002, Fei and Steiner 2008, Kabrick et al. 2008, 2014). To simplify, we hypothesized that presence of advance reproduction might be a useful, integrative species-specific indicator of suitable site conditions for postdisturbance establishment and included it as a possible covariate in our models. In addition, we hypothesized that presence of a residual seed source may increase reproduction abundance for a species (Egler 1954, Ribbens et al. 1994, Clark et al. 1999a, 1999b) and included it as a possible covariate in our models.

Methods

Study Sites

The data used in this project were collected from the Missouri Ozark Forest Ecosystem Project (MOFEP), which encompasses nearly 3,800 ha within the Current River watershed in Carter, Reynolds, and Shannon Counties of southeastern Missouri. The study region is an unglaciated, deeply dissected plateau primarily composed of Ordovician and Cambrian dolomites and sandstones (Kabrick et al. 2000). Average annual precipitation is 115 cm and average annual temperature is 13.5° C (Kabrick et al. 2008). Slope aspect and slope position are important characteristics used for site classification in the region (Nigh et al. 2000). The sites used in this study were on exposed (aspect: 136–315°) or protected (aspect: 316–135°) backslopes with average site indices (*Quercus velutina* Lam., base age 50; McQuilkin 1974) of 21.0 ± 1.3 and 22.0 ± 1.1 m, respectively. Predominant soils on both exposed and protected backslopes were Clarksville and Coulstone (loamy-skeletal, siliceous, semiactive, mesic Typic Paleudults), Scholten (loamy-skeletal, siliceous, active, mesic Typic Fragiudults), Alred (loamy-skeletal over clayey, siliceous, semiactive, mesic Typic Paleudalfs), and Rueter (loamy-skeletal, siliceous, active, mesic Typic Paleudalfs) (Soil Survey Staff 2015). Other less common soils were Gepp (very-fine, mixed, semiactive, mesic Typic Paleudalfs), Poynor (loamy-skeletal over clayey, siliceous, semiactive, mesic Typic Paleudults), and Niangua and Bardley (very-fine, mixed, active, mesic Typic Hapludalfs) (Soil Survey Staff 2015).

Table 1. Mean pre-treatment overstory (dbh ≥11.43 cm) basal area by species group on the 90 0.2-ha plots used in this study.

Species group	Overstory basal area (SD)
	. . . . .(m^2 ha^{-1}) . . . . .
Ashes	0.01 (0.07)
Blackgum	0.36 (0.59)
Black cherry	0.00 (0.03)
Dogwood	0.08 (0.12)
Elms	0.05 (0.15)
Hickories	2.08 (1.96)
Other species	0.06 (0.19)
Red maple	0.05 (0.12)
Red oaks	10.10 (3.83)
Sassafras	0.01 (0.05)
Shortleaf pine	2.12 (3.02)
Sugar maple	0.00 (0.01)
White oaks	5.39 (2.92)
Total	20.31 (2.87)

Values in parentheses are SD.

Overstory species composition on both site classes was heavily dominated (>70% basal area) by oak species (primarily *Quercus velutina*, *Quercus alba* L., *Quercus coccinea* Münchh., and *Quercus stellata* Wangenh.), and compositional differences between the two site classes were subtle (Kabrick et al. 2004). Protected backslopes usually have a slightly higher *Q. alba* component than exposed backslopes, whereas *Q. stellata* and *Pinus echinata* Mill. are more common on exposed backslopes (Kabrick et al. 2004). Shifley and Brookshire (2000) provide detailed documentation of the abundance and diversity of species found across MOFEP. The MOFEP stands used in this study were predominately dense, mature forests before the harvest treatments (Table 1).

Study Design and Data Collection

MOFEP is a long-term, landscape-scale experiment initiated in 1989 by the Missouri Department of Conservation (MDC) to evaluate the effects of forest management on ecosystem composition, structure, and function within the Missouri Ozark Highlands (Brookshire and Shifley 1997). The nearly 3,800-ha experiment was partitioned into 9 multistand compartments that range in size from about 312 to 502 ha. The forest management systems under evaluation at MOFEP include even-aged (≈1,134 ha), uneven-aged (≈1,495 ha), and no-harvest management (≈1,168 ha), each applied to three of the nine multistand compartments. Treatments were applied to individual stands within each compartment on a 15-year harvest cycle. The even-aged treatments included clearcutting with reserves (≤5 m^2 ha^{-1}) for stand regeneration and intermediate thinning as needed on other stands following the guidelines of Roach and Gingrich (1968). The uneven-aged treatment consisted of single-tree selection interspersed with group openings that ranged from one to two tree heights (0.03–0.15 ha) and summed to 5% of the harvested land area, following the guidelines of Law and Lorimer (1989). Areas designated for the no-harvest treatment were maintained as experimental controls. The initial harvest treatments were applied to stands in 1996 and followed MDC (1986) Forest Land Management Guidelines. In the clearcuts and group openings, all live trees >300 cm in total height or >4 cm dbh were felled, with the exception of trees left as reserves (MDC 1986). For additional information on MOFEP, including study rationale, experimental

design, site conditions, inventory methods, and early findings, see Brookshire and Shifley (1997), Shifley and Brookshire (2000), Shifley and Kabrick (2002), and Knapp et al. (2014).

From the original MOFEP study design, woody vegetation was sampled via 648 circular 0.2-ha permanent plot clusters that were randomly located throughout the study area with stratification by site class and stand delineation. Within these 0.2-ha plots, the dbh (137 cm) and species of trees ≥11.43 cm dbh were recorded. The dbh and species of woody midstory vegetation 3.81–11.43 cm dbh were sampled on four 0.02-ha subplots nested within each 0.2-ha plot. The dbh and species of saplings (height ≥100 cm and dbh <3.81 cm) were recorded on 0.004-ha understory plots nested inside each 0.02-ha subplot. Stem counts by species for seedlings (height <100 cm) were recorded from 4 quadrats (1 m^2) nested within each 0.02-ha subplot. A subset of these plot clusters were used for the analyses in this study.

Ninety 0.02-ha subplots were chosen at random in 1995 to receive additional measurement and monitoring. These 90 subplots were equally allocated among exposed and protected backslopes and included 18 that were clearcut, 24 that were thinned, 16 that were harvested with single-tree selection, 8 that were in group openings, and 24 that were in stands that were not harvested. On the 90 0.02-ha subplots, all woody stems with a height ≥100 cm were mapped or tagged in 1995 (1 year pretreatment), 1999 (3 years posttreatment), and again in 2004 (8 years posttreatment). During each inventory all previously untagged stems 100 cm and taller were tagged and measured. The species, dbh, total height, apparent stem origin (obvious sprout or not), and several other attributes were recorded for each stem ≥100 cm in total height. Unfortunately, the pretreatment (1995) mapping and additional measurements were not completed on the 18 clearcut 0.02-ha subplots. For this reason, only reproduction inside the boundaries of the centrally nested 0.004-ha understory plot within the 0.02-ha tagged subplot were used in this study. This was for two reasons: to strengthen the assumption of plot-level homogeneity of environmental establishment conditions and to allow the 0.004-ha understory plot predisturbance inventory (1995) in the ordinary MOFEP data set to substitute for the lack of pretreatment tagging and measurements on the 18 0.02-ha tagged subplots that were clearcut.

Model Approach and Assumptions

Because of the random determination of plot locations within stands, the proportion of a 0.02-ha subplot that was clearcut, thinned, or located within a group opening or single-tree gap varied. This further increased the variability in posttreatment overstory densities of the MOFEP study plots and offered a gradient to estimate the effects of harvesting practices on reproduction establishment. In our modeling approach, the various silvicultural regeneration methods under evaluation at MOFEP are viewed simply as manipulations that result in varying overstory density that is retained long enough to affect regeneration and whose effect can vary spatially throughout the stand.

We sought to estimate the third-year abundance of reproduction that originated from either small advance reproduction (height <100 cm) or new germination. However, the 100-cm (height) sampling threshold that was used probably truncated some proportion of this population from our third-year data. To lessen the impact of this, we assumed any reproduction that was newly tagged during the eighth-year inventory was present during the third-year inventory but shorter than the 100-cm tagging threshold and included them in the third-year abundance estimate used as our response variable. It is possible that some reproduction tagged in the eighth-year inventory germinated after the third-year inventory. It is also possible that some reproduction died without ever reaching the 100-cm height threshold posttreatment, but that ephemeral population was ignored. Because the desired response variable for these models was reproduction that originated from either small advance reproduction or new germination, any reproduction that had an apparent stump-sprout origin were excluded from our response variable. Reproduction that was mapped/tagged as large advance reproduction (≥100 cm) before treatment (1995) or had a third-year dbh >5 cm were also excluded from our response variable. On the 18 clearcut plots that were not tagged before treatment, the pretreatment counts of large advance reproduction from the 0.004-ha understory plots in the ordinary MOFEP data were simply subtracted from the posttreatment count (third- and eighth-year combined as described above) of nonsprout stems in the 0.004-ha tagged understory plot data used for our response variable.

Table 2. Reproduction establishment candidate models.

Candidate	Generalized linear model form	*df*
1	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \beta_4X_1X_2 + \beta_5X_1X_3 + \beta_6X_2X_3 + \beta_7X_1X_2X_3$	8
2	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \beta_4X_1X_2 + \beta_5X_1X_3 + \beta_6X_2X_3$	7
3	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \beta_4X_1X_2 + \beta_5X_1X_3$	6
4	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \beta_4X_1X_2 + \beta_5X_2X_3$	6
5	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \beta_4X_1X_3 + \beta_5X_2X_3$	6
6	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \beta_4X_1X_2$	5
7	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \beta_4X_1X_3$	5
8	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3 + \beta_4X_2X_3$	5
9	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_1X_2$	4
10	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_1X_3$	4
11	$y = \beta_0 + \beta_1X_1 + \beta_2X_2 + \beta_3X_3$	4
12	$y = \beta_0 + \beta_1X_1 + \beta_2X_2$	3
13	$y = \beta_0 + \beta_1X_1 + \beta_2X_3$	3
14	$y = \beta_0 + \beta_1X_1$	2
15	$Y = \beta_0$	1

y = third-year reproduction abundance per 0.004 ha that originated from small advance reproduction (height <100 cm) or new germination, X_1 = residual overstory basal area (m^2 ha^{-1}; dbh ≥11.43 cm), X_2 = presence of advance reproduction (1 if present, 0 if absent; dbh ≤3.81 cm), X_3 = presence of residual seed source (1 if present, 0 if absent; dbh ≥11.43 cm). The *df* for each candidate model only include the covariates listed in this table.

Overstory basal area (m^2 ha^{-1}; dbh ≥11.43 cm) was used to quantify residual overstory density in this study because it is strongly correlated with canopy openness in the Missouri Ozarks (Blizzard et al. 2013) and has proven to be a useful indicator of the resource limitation imposed by overstory trees in other locales (Lorimer 1983, Biging and Dobbertin 1995). We hypothesized that advance reproduction presence (dbh ≤3.81 cm) and residual seed source presence (dbh ≥11.43 cm) may influence the number of seedlings that will become established. Therefore, a suite of candidate models that included combinations of these effects were examined in addition to a model that only included residual overstory density (Table 2).

Estimates of residual basal area (dbh ≥11.43 cm) and presence of residual seed sources were obtained using data collected as part of the ordinary MOFEP inventory protocol on the 0.2-ha overstory plots 2 years posttreatment (1998). Presence data for large advance reproduction (height ≥100 cm; dbh ≤3.81 cm) were obtained from the 0.004-ha understory plots that were nested within the tagged 0.02-ha subplots using the 1995 pretreatment ordinary MOFEP inventory. Presence data for small advance reproduction (height

<100 cm) were obtained from the four quadrats (1 m^2) nested within the tagged 0.02-ha subplots using the 1995 pretreatment ordinary MOFEP inventory. Presence data for both large and small advance reproduction were then combined into a single advance reproduction presence variable for each species.

Given the number of species included in this data set, some were grouped for analyses at the genera or subgenera level. All woody species inventoried were included in one of the following 13 species groups: (1) ashes (*Fraxinus americana* L., *Fraxinus pennsylvanica* Marsh.), (2) blackgum (*Nyssa sylvatica* Marsh.), (3) black cherry (*Prunus serotina* Ehrh.), (4) dogwood (*Cornus florida* L.), (5) elms (*Ulmus alata* Michx., *Ulmus rubra* Muhl., *Ulmus americana* L.), (6) hickories (*Carya tomentosa* Sarg., *Carya glabra* Mill., *Carya ovata* (Mill.) K. Koch., *Carya texana* Buckley, *Carya cordiformis* [Wangenh.] K. Koch.), (7) red maple (*Acer rubrum* L.), 8) red oaks (*Quercus rubra* L., *Quercus velutina, Quercus coccinea, Quercus marilandica* Münchh.), (9) sassafras (*Sassafras albidum* J. Presl.), (10) shortleaf pine (*Pinus echinata*), (11) sugar maple (*Acer saccharum* Marsh.), (12) white oaks (*Quercus alba, Quercus stellata*, *Q muehlenbergii* Engelm.), and (13) other species (see Appendix 1). Because the establishment models were parameterized using these species groups, it was assumed that the within-group composition of the new cohort will be similar to the inventoried within-group composition pretreatment (Vanclay 1992).

A suite of additional candidate models were developed that included the density of large advance reproduction from nontarget species along with various combinations of the previously described covariates to determine whether a metric of interspecific competition within the advance reproduction layer was warranted. Preliminary analyses revealed that including this effect only offered statistical improvement for one species group (dogwood). Based on this, it was determined that this effect did not warrant further inclusion in our analyses or the findings presented herein.

Model Form and Fit

All statistical analyses and random number generation were completed in R statistical software version 3.0.3 (R Development Core Team 2014). The packages and functions used are mentioned in capital letters throughout the remainder of the document.

Because we defined establishment as presence after 3 years, i.e., a count per specified unit of time, it was expected to be well represented by a Poisson distribution (Faraway 2005). The Poisson distribution is a discrete distribution that assumes that the expected value (mean) is equal to the variance, and, therefore, both can be estimated by the single parameter λ. Poisson parameter estimates for regeneration establishment were obtained via the generalized linear models function (GLM) with a log link. Preliminary diagnostics suggested that the assumption of an equal mean and variance was violated for most species groups due to overdispersion; i.e., the variance estimate was considerably greater than the mean. The negative binomial distribution has been recommended as an alternative to the Poisson distribution for overdispersed count data (Hilbe 2011) and has previously been used in forestry research to model ingrowth (Li et al. 2011) The negative binomial distribution is a discrete distribution with two parameters, which are often the mean (μ) and a dispersion parameter (k [or θ in R statistical software]) for ecological data (Bolker 2008). The parameters for all candidate models of seedling establishment were estimated with negative binomial regression with a log link using the negative binomial regression function (GLM.NB) within the MASS package (Venables and Ripley 2002) for those species with sufficient data. The parameters for intercept-only Poisson models were estimated for those species groups (shortleaf pine and sugar maple) with insufficient data for the negative binomial regression function due to rarity. Although zero-inflated models have been successfully used to accommodate excess zeroes in similar applications (Li et al. 2011), preliminary analyses indicated that zero-inflated Poisson models did not provide a statistically superior solution (per the Vuong 1989 test) for rarity in these two species groups.

Before model fitting, the data were inspected for implausible data points that may have resulted from typographical or other data management errors. Implausible data points without obvious remedies were removed. Once parameterized, the candidate models were compared using Akaike's information criterion (AIC) corrected for small sample sizes (AICc) (Burnham and Anderson 1998) as calculated by the AICC function within the AICCMODAVG package (Mazerolle 2015). For a species group, the most parsimonious model within 2 AICc units of the model with the lowest AICc value was selected as the "best" among those considered (Burnham and Anderson 1998) provided that it produced predictions that were visually within the scatter of observed values along the entire observed gradient of residual overstory density (0–30 $m^2\ ha^{-1}$) in all other covariate scenarios. If a candidate model met the AICc criteria to be selected as best but produced estimates outside the range of data, the candidate model with the next lowest AICc that produced reasonable estimates was selected as best. Scattergraphs with fitted model curves for all species groups are provided in Figure 1. Candidate models for a species group that failed to converge after 10,000 iterations of the negative binomial function were considered to be overparameterized or misspecified otherwise and were not included in model comparisons. All data were used during model construction and comparison as data-splitting techniques are rarely effective for model evaluation (Kozak and Kozak 2003). Moreover, minimizing the AIC is asymptotically equivalent to minimizing a cross-validation statistic (Stone 1977).

Obtaining Stochastic Model Output

Stochastic output from parameterized models is often preferred in the context of regeneration simulation (see Dey et al. 1996). In addition to using the expected value (μ) from the parameterized models to estimate third-year abundance from small advance reproduction and new germination deterministically, stochastic output was obtained from the parameterized best models using the RNBINOM and RPOIS random number generation functions in R statistical software (R Development Core Team 2014) for models fit via negative binomial regression and Poisson regression, respectively. Entering the expected value (μ) for stems · 0.004-ha^{-1} in a given covariate scenario and the dispersion parameter (k) provided in Table 3 into the RNBINOM function as the "mu" and "size" arguments, respectively, produced "n" negative binomial distributed random deviates for species modeled via negative binomial regression (Bolker 2008). Multiplying the output values by 250 yields stems · ha^{-1}. Similarly, for species modeled via Poisson regression (shortleaf pine and sugar maple), entering the expected value (μ) for stems · 0.004-ha^{-1} provided in Table 3 into the RPOIS function as the "lambda" argument produced "n" Poisson distributed random deviates. This output can be multiplied by 250 to yield stems · ha^{-1}. Probability mass functions for these distributions were obtained using the DNBINOM and DPOIS functions, respectively.

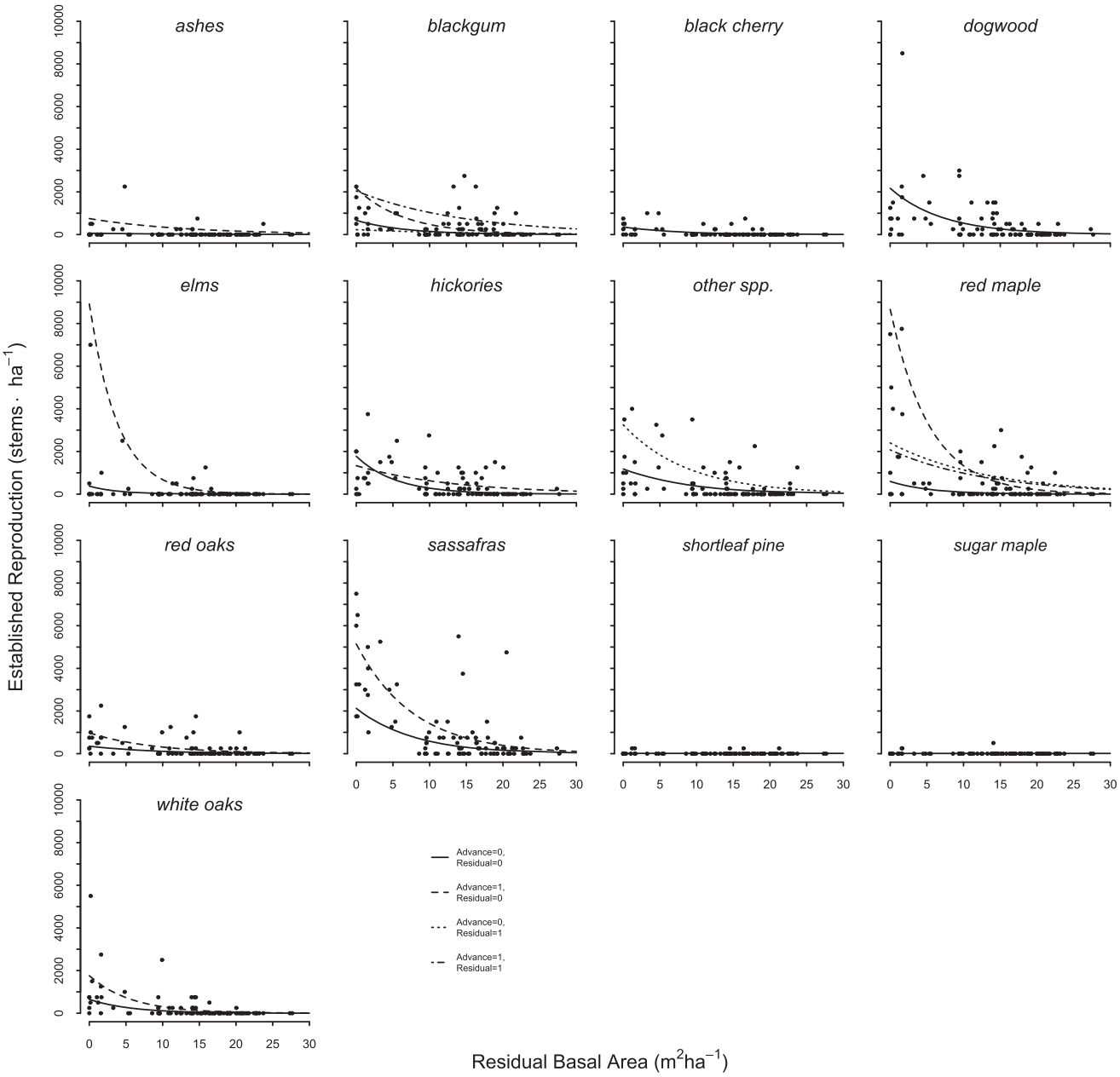

Figure 1. Scattergraph of mean third-year reproduction abundance from small advance reproduction and new germination in the Missouri Ozarks as a function of residual overstory density, presence of advance reproduction, and presence of a residual seed source. Curves are drawn using the models and parameters from Table 3 multiplied by 250 to obtain stems · ha^{-1}. Solid line depicts establishment without advance reproduction ($X_2 = 0$) and without a residual seed source ($X_3 = 0$). Coarse broken line depicts establishment with advance reproduction ($X_2 = 1$) but without a residual seed source ($X_3 = 0$). Fine broken line depicts establishment without advance reproduction ($X_2 = 0$) but with a residual seed source ($X_3 = 1$). Variable broken line depicts establishment with advance reproduction ($X_2 = 1$) and with a residual seed source ($X_3 = 0$).

Results and Application

Parameter estimates for the models of third-year reproduction abundance are provided in Table 3. All models were statistically significant ($\alpha = 0.05$) per the χ^2 goodness-of-fit test (Table 4). The best model for blackgum and red maple was model 5 (Table 3), which, for both species groups, was not the most parsimonious model within 2 AICc units of the lowest AICc (models 11 and 4, respectively). For these two species groups, candidate models with lower AICc than model 5 produced estimates outside the range of observed data and were discarded.

Parameters for shortleaf pine and sugar maple were obtained using only an intercept due to the rarity of these species in the data sets. For all remaining species groups, residual overstory density was included in the best models of third-year reproduction abundance and was statistically significant ($\alpha = 0.05$) for all but ash ($P = 0.0859$). Modeled reproduction abundance declined with increasing residual overstory density for all species that included it as a covariate regardless of other covariate values (Figure 1). For all species groups, modeled reproduction establishment was limited at residual overstory densities greater than $\approx$20 m^2 ha^{-1} (basal area), regardless of the other covariate values.

Table 3. Parameter estimates for "best" models of reproduction establishment.

Species group	"Best" model	Expected value (μ)	Dispersion (k)
Ashes	12	$e^{-1.3965+(-0.0761X_1)+(2.4934X_2)}$	0.3777
Blackgum	05*	$e^{0.9791+(-0.1522X_1)+(1.1785X_2)+(-1.0621X_3)+(0.0840X_1X_3)+(1.0055X_2X_3)}$	1.0708
Black cherry	14	$e^{-0.344+(-0.1377X_1)}$	0.6814
Dogwood	14	$e^{2.1610+(-0.1404X_1)}$	0.5487
Elms	12	$e^{0.4043+(-0.2580X_1)+(3.1708X_2)}$	0.1497
Hickories	09	$e^{1.9595+(-0.1855X_1)+(-0.2857X_2)+(0.1096X_1X_2)}$	0.7365
Other species	13	$e^{1.5508+(-0.1135X_1)+(1.0136X_3)}$	0.4284
Red maple	05*	$e^{0.7704+(-0.1719X_1)+(2.5851X_2)+(1.3941X_3)+(0.1122X_1X_3)+(-2.8237X_2X_3)}$	0.6051
Red oaks	12	$e^{0.3334+(-0.1153X_1)+(1.0313X_2)}$	0.5835
Sassafras	12	$e^{2.1403+(-0.1293X_1)+(0.8838X_2)}$	0.7266
Shortleaf pine†	15	$e^{-2.8904}$	
Sugar maple†	15	$e^{-3.1135}$	
White oaks	12	$e^{0.9538+(-0.1754X_1)+(0.9978X_2)}$	0.7201

X_1 = residual overstory basal area (m^2 ha^{-1}; dbh ≥11.43 cm), X_2 = presence of advance reproduction (1 if present, 0 if absent; dbh ≤3.81 cm), X_3 = presence of residual seed source (1 if present, 0 if absent; dbh ≥11.43 cm). Parameter estimates were obtained via negative binomial regression with a log link. The most parsimonious candidate model within two AICc units of the model with the lowest AICc was selected as "Best," provided that it produced reasonable estimates within the range of the data. Negative binomial regression yields estimates for the two parameters (μ, k) of the negative binomial distribution. These parameter estimates can be used with a negative binomial random number generator to stochastically determine the number of new reproduction to be established after a harvest-based silvicultural manipulation. Expected values are for 0.004-ha plots; therefore, estimates must be multiplied by 250 to obtain stems · ha^{-1}.

* This model was not the most parsimonious candidate within two AICc units of the model with the lowest AICc, but was the model with the lowest AICc that also produced reasonable estimates within the range of the data.

† Intercept-only Poisson regression with a log link was used to estimate the single parameter (λ) of the Poisson distribution for the shortleaf pine and sugar maple species groups due to data limitations (rarity).

Table 4. Model fit details for "best" models of reproduction establishment.

		Covariate P values						
Species group	Model χ^2	Intercept	X_1	X_2	X_3	X_1X_2	X_1X_3	X_2X_3
Ashes	0.9999	0.0251*	0.0858	0.0003*				
Blackgum‡	0.5786	0.0028*	<0.0001*	0.0145*	0.1614	-	0.1264	0.144
Black cherry	0.9913	0.368	<0.0001*					
Dogwood	0.6787	<0.0001*	<0.0001*					
Elms	1	0.5809	0.0002*	0.0004*				
Hickories	0.6345	<0.0001*	<0.0001*	0.6324		0.0216*		
Other species	0.7719	<0.0001*	<0.0001*		0.0433*			
Red maple‡	0.9373	0.0329	<0.0001*	<0.0001*	0.3489		0.1845	0.0036*
Red oaks	0.9298	0.5096	<0.0001*	0.0255*				
Sassafras	0.2756	<0.0001*	<0.0001*	0.0055*				
Shortleaf pine†	1	<0.0001*						
Sugar maple†	1	<0.0001*						
White oaks	0.9746	0.0466*	<0.0001*	0.027*				

X_1 = residual overstory basal area (m^2 ha^{-1}; dbh ≥11.43 cm), X_2 = presence of advance reproduction (1 if present, 0 if absent; dbh ≤3.81 cm), X_3 = presence of residual seed source (1 if present, 0 if absent; dbh ≥11.43 cm). Model χ^2 is the P value resulting from an overall χ^2 goodness-of-fit test where values ≤0.05 would indicate poor model fit.

* Statistical significance ($\alpha = 0.05$). Parameter estimates were obtained via negative binomial regression with a log link. The most parsimonious candidate model within two AICc units of the model with the lowest AICc was selected as "Best," provided that it produced reasonable estimates within the range of the data.

† Intercept-only Poisson regression with a log link was used to estimate the single parameter (λ) of the Poisson distribution for the shortleaf pine and sugar maple species groups due to data limitations (rarity).

‡ This model was not the most parsimonious candidate within two AICc units of the model with the lowest AICc but was the model with the lowest AICc that also produced reasonable estimates within the range of the data.

Presence of advance reproduction was included in the best models of third-year reproduction abundance for 8 of the 13 species groups. The species groups that did not include advance reproduction presence were black cherry, dogwood, other species, shortleaf pine, and sugar maple. The effect of advance reproduction presence on third-year reproduction abundance, when included, was clearly positive for all species groups except hickories. The best model for hickories (model 9) included a statistically significant interaction between residual overstory density and presence of advance reproduction that yielded a slightly positive net effect for advance reproduction presence across much of the gradient of residual overstory density, except below 3 m^2 ha^{-1}, where the effect was slightly negative.

Only blackgum, red maple, and the other species group included presence of a residual seed source in their best model of third-year reproduction abundance. The effect of residual seed source presence on the other species group was statistically significant and positive. The interactions between the effects of advance reproduction presence and residual seed source presence increased the complexity of the models for blackgum and red maple, as well as interactions between residual seed source presence and residual overstory density. Presence of a residual seed source and its interactions with covariates were statistically significant for red maple but not for blackgum.

Estimates provided by the best models indicated that the covariates used in our analyses captured differences in third-year reproduction abundance. When neither advance reproduction nor a residual seed source was present, reproduction abundance across all species groups tended to be lower than when only one or both were present (Figure 2).

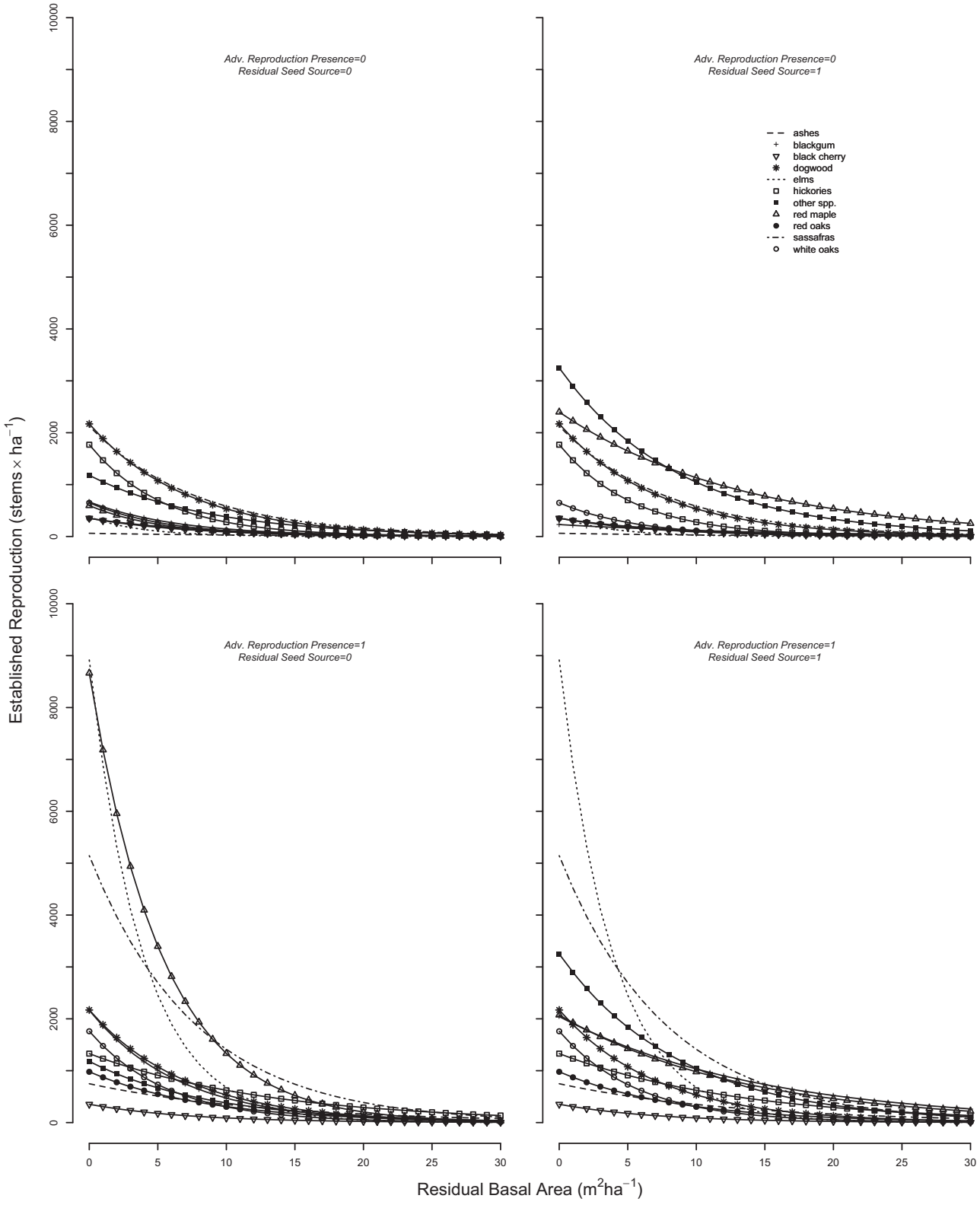

Figure 2. Mean third-year reproduction abundance from small advance reproduction and new germination in the Missouri Ozarks as a function of residual overstory density, presence of advance reproduction, and presence of a residual seed source. Curves are drawn using the establishment models and parameters from Table 3 multiplied by 250 to obtain stems · ha^{-1}. Top row depicts abundance when advance reproduction is absent ($X_2 = 0$); bottom row depicts abundance when advance reproduction is present ($X_2 = 1$). Left column depicts abundance when a residual seed source is absent ($X_3 = 0$), right column depicts abundance when a residual seed source is present ($X_3 = 1$). Estimates for shortleaf pine (13.89 stems · ha^{-1}) and sugar maple (11.11 stems · ha^{-1}) are not displayed as they were produced by intercept-only regression and are invariant to residual overstory density.

The covariates also captured variation in the magnitude and order of interspecific differences in reproduction abundance, but differences were minimal among species groups once residual overstory density exceeded ≈15 m^2 ha^{-1}. In the absence of both advance reproduction and residual seed sources for all species groups (Figure 2, top left), dogwood, sassafras, hickories, and the other species group tended to have the greatest mean reproduction abundance compared with those of the remaining species groups at low residual overstory densities.[1] Mean abundances for the remaining species groups were low across the entire gradient of overstory density in this scenario.

When only a residual seed source was present (Figure 2, top right), mean reproduction abundances for the other species group and red maple exceeded those of dogwood, sassafras, and hickories and tended to be greater than those of all species groups across the entire gradient of residual overstory density. Again, in this scenario, the abundances of the remaining species groups were considerably lower.

In the presence of advance reproduction but no residual seed source (Figure 2, bottom left), elms, red maple, and sassafras tended to be much more abundant, on average, than all remaining species groups when residual overstory density was ≤10 m^2 ha^{-1} (elms) to 15 m^2 ha^{-1} (red maple and sassafras). Although mean abundances for the remaining species groups tended to be considerably lower than those for elms, red maple, and sassafras at low residual overstory densities in this scenario, several species groups had a mean approaching or exceeding 1,000 stems · ha^{-1}.

Total reproduction abundance across species and the interspecific differences among species tended to be greater with both advance reproduction and a residual seed source present (Fig. 2, bottom right). In this scenario, elms tended to have greater abundance at low residual overstory densities (≤5 m^2 ha^{-1}) than all species groups. Apart from elms, sassafras reproduction was more abundant than those for all other species groups when residual overstory density was less than ≈15 m^2 ha^{-1} and exceeded that of elms at residual densities greater than ≈5 m^2 ha^{-1}. The other species group also was considerably more abundant than the remaining species groups at residual overstory densities about 10 m^2 ha^{-1} or less. Most species groups in this scenario had a mean approaching or exceeding 1,000 stems · ha^{-1} at low residual overstory densities.

The parameterized models of third-year reproduction abundance (Table 3) can be used to add new seedling records in regeneration simulators. An example of the stochastic establishment procedure is provided in Figure 3. In this example, red oak establishment was simulated 1,000 times for a plot with a residual overstory density of 5 m^2 ha^{-1}. In this scenario, mean reproduction abundance was 550 stems · ha^{-1} ($\mu = 2.2$ stems · 0.004 ha^{-1}) (Table 3). However, when stochasticity was incorporated via the dispersion parameter from Table 3, the simulation output showed that the distribution of establishment outcomes for red oaks in this scenario was right-skewed rather than symmetrical around the mean. In this example, approximately 40% of the 1,000 random deviates were 0, suggesting that new red oak reproduction often did not establish in this scenario. This is consistent with the probabilities provided by the probability mass function of a negative binomial distribution with the same parameters (38%). In the simulations in which new red oak reproduction did successfully become established in this scenario (≈60%), 1,000 stems · ha^{-1} or less were usually added. According to the probability mass function, the probability that more than 1,000 stems · ha^{-1} would establish is approximately 20%.

An extended example of an application demonstrating the use of the establishment models from data collection to final prediction for

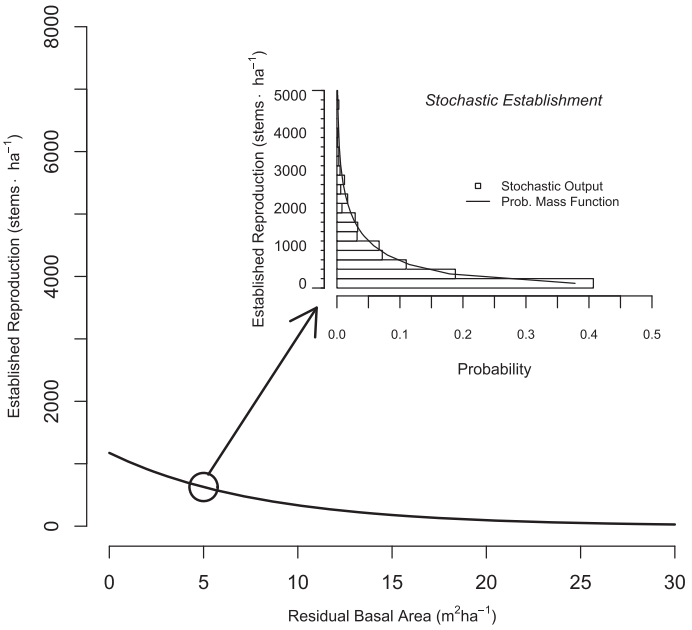

Figure 3. Stochastic reproduction establishment example for red oaks from small advance reproduction and new germination in the Missouri Ozarks. The reproduction establishment curve for red oaks (heavy line) was drawn using the establishment models and parameters from Table 3 $\mu = [e^{0.3334+(-0.1153X_1)+(1.0313X_2)}]$ multiplied by 250 to obtain stems · ha^{-1}. Curve depicts mean reproduction establishment when advance reproduction is present ($X_2 = 1$), but a residual seed source is not present ($X_3 = 0$). When residual overstory basal area is held constant at 5 m^2 ha^{-1} ($X_1 = 5$), $\mu = 550$. This value, along with the dispersion parameter ($k = 0.5835$) from Table 3 are estimates for the two parameters of a negative binomial distribution. These parameter estimates are used in a negative binomial random number generator to stochastically determine the number of new reproduction to be established after a harvest-based silvicultural manipulation. Using these parameters, 1,000 random numbers were generated for this example (inset). Under these conditions, the probability that red oak reproduction was not added to the plot was approximately 40%. In those simulations in which reproduction was added (60%), the number was usually 1,000 stems · ha^{-1} or less.

all species on a single plot is provided in Figure 4. In this example, an overstory inventory produced estimates identical to those in Table 1 (basal area ≈20 m^2 ha^{-1}). On this example plot, a presence/absence inventory of advance reproduction (0.004-ha plot) found that blackgum, dogwood, hickories, other species, red maple, red oaks, sassafras, and white oaks were present. A proposed harvest will leave 5 m^2 ha^{-1} of residual basal area of predominately white oaks but some shortleaf pine as well. The above information was used as input for the establishment models for each species group (Table 3) and produced an average third-year abundance estimate of ≈11,400 stems · ha^{-1} from small advance reproduction and new germination when the estimates for all species groups were combined (Figure 4, top). On average, more than half of the third-year reproduction from these regeneration sources were red maple (30%) and sassafras (24%). Red oaks and white oaks only made up about 11% combined. It is left for the forester to determine whether the abundance and composition estimated by the models are adequate to meet regeneration objectives.

As in the previous single-species example, stochasticity was incorporated in this example for all species groups using the above plot inputs (Figure 4, top) and the dispersion parameters from Table 3.

species	adv. reproduction	overstory basal area	residual basal area	mean estimate
ashes		0.01	0	42
blackgum	present	0.36	0	1010
black cherry		0	0	177
dogwood	present	0.08	0	1075
elms		0.05	0	103
hickories	present	2.08	0	909
other spp.	present	0.06	0	668
red maple	present	0.05	0	3396
red oaks	present	10.1	0	550
sassafras	present	0.01	0	2695
shortleaf pine		2.12	2	14
sugar maple		0	0	11
white oaks	present	5.39	3	732
total	-	20.31	5	11383

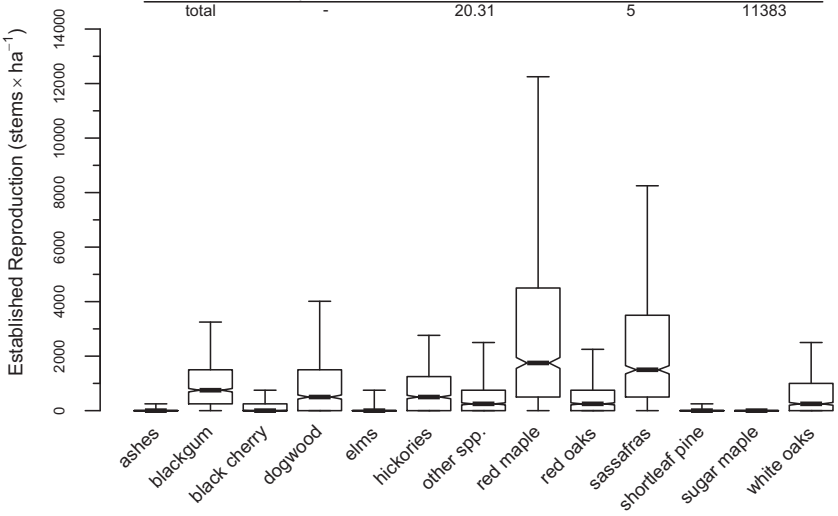

Figure 4. Extended model application example for estimating reproduction establishment from small advance reproduction and new germination in the Missouri Ozarks. In this example, an overstory inventory produced estimates identical to those in Table 1 (basal area ≈20 m^2 ha^{-1}). On this example plot, a presence/absence inventory of advance reproduction (0.004-ha plot) found that blackgum, dogwood, hickories, other species, red maple, red oaks, sassafras, and white oaks were present. A proposed harvest will leave 5 m^2 ha^{-1} of residual basal area of predominately white oaks but some shortleaf pine as well. The above information (top) was used as input for the establishment models for each species group (Table 3), and the output was multiplied by 250 to obtain stems · ha^{-1} for each species. These mean estimates were used with the dispersion parameters from Table 3 to incorporate stochasticity in this example for all species groups using the above plot inputs. We followed the procedure outlined in the Obtaining Stochastic Model Output section of the Methods to produce 1,000 simulations for each species group using statistical software. The box and whisker plots (bottom) summarize those simulations for each species group. The boxes depict the 25th, 50th (median), and 75th percentiles and the whiskers depict the 5th and 95th percentiles of the 1,000 simulations for each species group. The notches on the boxplots depict a 95% confidence interval around the median. Nonoverlapping notches among boxes indicate strong evidence of statistical differences in medians.

We followed the procedure outlined in the Obtaining Stochastic Model Output section of the Methods to produce 1,000 simulations for each species group using statistical software. The boxplots in Figure 4 (bottom) summarize those simulations for each species group and suggest that there is a broad range of possible outcomes for many species in this example scenario. The simulated outcomes for both red maple and sassafras were particularly broad. In most cases, red maple and sassafras were more abundant than all other groups, but they failed to establish in some simulations and established prolifically in others. Conversely, ashes, black cherry, elms, shortleaf pine, and sugar maple rarely established and were scarce when successful. The simulation results suggest that third-year abundance and composition of reproduction originating from small advance reproduction or new germination can vary considerably in a given scenario.

Discussion

Forest regeneration is a defining example of secondary succession (Horn 1974). A fundamental concept of secondary succession is the reliance on regeneration sources disseminated before or immediately after disturbance (Egler 1954). Unsurprisingly, a common input requirement of regeneration models is an advance reproduction inventory. However, the effort required to collect these input data can be considerable, particularly for multispecies inventories that tally and/or measure advance reproduction of all sizes and could be a barrier to using regeneration models for many foresters. Furthermore, several studies have shown that the majority of advance reproduction in Central Hardwood forests tends to be small, unreliable sources of regeneration that exhibit slow growth and high susceptibility to mortality (Sander 1971, Loftis 1983, Dey 1991, Cook et al. 1998, Brose et al. 2008, McWilliams et al. 2015).

To address this apparent inefficiency, we provide models that use a simple species presence/absence advance reproduction inventory to estimate the contribution of small advance reproduction and new germination to the reproduction cohort. Our results suggest that the simple presence/absence inventory of advance reproduction might serve as a parsimonious species-specific indicator of suitable conditions for postharvest establishment. Presence of advance reproduction was included in the best models for 8 of the 11 species groups with sufficient data as a positive (or mostly positive, in the case of interactions) influence (Table 3). The species groups that did not include advance reproduction presence may exhibit more general site requirements for establishment and/or stronger reliance on seed banks or long-distance dispersal mechanisms.

Long-term growth and survival can require a different suite of

environmental conditions from those that promote germination and initial survival (Grubb 1977, Crow 1988, Poorter et al. 2005). It is likely that the utility of various site metrics to explain, or at least capture, differences that impact establishment, growth, or mortality rates of reproduction may be influenced by the stage of cohort development, species' life histories, tree size, resource heterogeneity, the spatial resolution of the metric, and the desired response resolution (i.e., individual tree, plot, or stand), among others. For example, Morrissey et al. (2008) reported prolific establishment of a mesic species (*Liriodendron tulipifera* L.) on xeric sites initially after harvest, but long-term survival was low and primarily attributed to site incompatibility. Thus, the impact of site differences on regeneration dynamics beyond initial establishment may require explicit consideration of various site attributes that were not included in our analyses.

Similarly, preliminary analyses indicated that the impact of interspecific competition within the reproduction layer on third-year reproduction establishment was limited. Whether this is specific to the site conditions and species assemblages found in the Missouri Ozarks or more broadly applicable is unknown. Certainly competition is an important factor in the regeneration process, but this finding suggests it probably has the strongest influence on the growth and survival of stems after establishment. In this context, competition would more strictly refer to the struggle among "neighbors" to acquire limited resources (i.e., light, water, nutrients), with the consequences being differential reductions in growth that culminate in an increased likelihood of mortality for the "inferior" competitor (Kobe et al. 1995, Oliver and Larson 1996, Craine and Dybzinski 2013). Any potential inhibitory effects of dense understories on establishment in our study were probably disrupted by the harvesting operations that released resources and created opportunities for establishment. Such alterations to the understory were even required in the clearcut and group opening harvest operations (MDC 1986).

In many forests within the Central Hardwood region, deer browse substantially limits reproduction establishment. This widespread interruption of the regeneration process has the potential to drastically alter long-term forest dynamics (McWilliams et al. 2015). Recent surveys in the Missouri Ozarks indicated that browse levels were generally low with little evidence of impact on seedling populations (Piva and Treimam 2014). It was, therefore, unnecessary to include browse impact as a possible covariate in our models of reproduction establishment. Similar modeling efforts in more affected locales will probably require greater consideration of both the potential influences of browse on reproduction establishment and the utility of various metrics to capture differences in browse intensity.

The models of third-year reproduction abundance presented herein provide a tool to deterministically estimate or stochastically simulate the contributions from sources of regeneration (small advance reproduction and new germination) that tend to be quite variable and difficult or time-consuming to inventory. However, our models were developed to complement an expedited inventory rather than serve as substitute altogether. For regeneration from more reliable sources, including potential stump sprouts and large advance reproduction (height $\geq$100 cm), we suggest continued use of the "established seedling" modeling approach (Weiskittel et al. 2011, p. 157), which requires direct preharvest tally and/or measurement to project the fate of individual stems. This hybrid approach that we advocate has the potential to increase the efficacy of regeneration modeling by reducing the total inventory effort required, focusing that effort on more reliable regeneration sources and increasing model compatibility for species not strongly reliant on advance reproduction.

Whereas efforts to estimate advance reproduction presence without an inventory could lead to more autonomous regeneration simulators, developing models that provide reliable estimates may be challenging. This is because the density and composition of advance reproduction, particularly large advance reproduction, is often the product of a complex disturbance history. Oak silviculturists, for example, have empirically shown that *intentional* development of large advance reproduction often requires a series of treatments spanning several years (Loftis and McGee 1993). Recognizing the complexity of this dynamic process and the difficulty in capturing multifaceted disturbance histories in a few regression covariates, we recommend that some inventory of advance reproduction and potential stump sprouts remain the starting point for regeneration simulation in oak-dominated forests.

Admittedly, the simple advance reproduction inventory used by our models cannot comprehensively account for the many influences site characteristics may have on reproduction establishment. Because our models do not explicitly account for alterations to seedbed conditions, they may be inadequate when specific site preparation (e.g., scarification, fire) is scheduled and required to promote successful establishment on otherwise suitable sites (e.g., Ferguson et al. 1986). One example of a species with specific seedbed requirements in the Missouri Ozarks may be shortleaf pine, a species that is often difficult to regenerate successfully (Kabrick et al. 2007). Lawson (1990) reported that site preparation treatments such as intentional scarification increase the probability of shortleaf pine germination. Shortleaf pine was a common component of the overstory in our study stands before treatment (Table 1) and was usually reserved during harvest treatments to ensure seed availability (Shifley and Brookshire 2000). Despite these efforts, the rarity of newly established shortleaf pine in our data suggests that conditions for successful shortleaf pine establishment were not created by harvesting alone under any residual overstory density (Figure 1). Consequently, when successful shortleaf pine regeneration is an objective in the Missouri Ozarks, site preparation treatments and/or supplemental underplanting should be considered in stands lacking abundant advance reproduction (Kabrick et al. 2015).

Our results support the expectation that reproduction establishment is driven primarily by residual overstory density because of its impact on resource availability (Reineke 1933, Yoda et al. 1963, Gingrich 1967, Assmann 1970, Oliver and Larson 1996). Larsen et al. (1997) also reported decreasing probability of reproduction occurrence with increasing residual overstory density in the Missouri Ozarks. The strong reliance on disturbance to initiate the regeneration process is consistent with leading hypotheses of forest stand development (Oliver and Larson 1996). Accordingly, the models presented herein are largely "cohort based," i.e., an addition of propagules triggered by a single event. However, the abundance estimates for the highest levels of residual overstory densities in our models essentially represent "ambient" establishment rates (i.e., establishment without discernible disturbance) because those plots were not harvested. Although a rare and unreliable source of canopy recruitment for many species (Shifley et al. 1993), ambient establishment may nonetheless influence regeneration by altering the density and composition of advance reproduction before disturbance. The potential influence of this dynamic from species such as American beech (*Fagus grandifolia* Ehrh.) and maples has been

widely noted in other locales (Abrams 1998, Schuler and Gillespie 2000, Gravel et al. 2011).

A scenario that requires additional research is the role of repeated disturbance, particularly the interaction of disturbance intensity and frequency, on reproduction establishment. The establishment models presented herein were developed for harvest-based silvicultural manipulation and should not be applied to stands with periodic or frequent burning regimes (Knapp et al. 2015). The reliability of our establishment models in repeated harvest scenarios is unknown and may depend on return intervals. The model equations used are somewhat static; i.e., they assume a common starting point: somewhat dense, mature stands in the Missouri Ozarks (Table 1). In the case of unusually frequent disturbance, this assumption may be implausible, and our models may overestimate establishment by failing to account for a preexisting reproduction cohort from a prior disturbance. The solution to this problem is not straightforward. Most metrics of stand density and/or occupancy are not applied at the seedling level (Reineke 1933, Gingrich 1967), and adaptations to these metrics for multicohort stands with complex structure (e.g., Ducey and Knapp 2010) are not widespread. Whereas stand occupancy and self-thinning relationships (e.g., Yoda et al. 1963) theoretically apply at the seedling level, measures at this level are rare and poorly understood. Fei et al. (2006) described aggregate height, a measure of reproduction occupancy, which combined size (height) and abundance into a species-specific metric of site occupancy for even-aged stands. However, the influence of reproduction height-abundance dynamics on subsequent establishment rates in multicohort stands has not been examined. The use of more dynamic equations, i.e., those that track change in initial conditions from successive events, may offer practical improvement (e.g., McGarrigle et al. 2013), but parameterization would probably require considerably more data from tagged individuals than was available from this study, which was one of the largest of its kind in the eastern United States. Additional research into metrics of reproduction occupancy is warranted.

The parameterization of separate models for each species (or species group) provided opportunities to examine the regeneration ecology of each species. There was some evidence of interspecific differentiation in reproduction establishment, particularly at low residual overstory densities (Figure 2). In most scenarios, interspecific differentiation in reproduction establishment was progressively muted with increasing residual overstory density. Vickers et al. (2014) found a similar trend of reduced interspecific differentiation in growth rates of saplings with increasing residual overstory on the same plots used in this study. Species groups such as elms, dogwood, and red maple that tended to be ranked relatively high in reproduction establishment rates tended to be relatively low or intermediate in reported rates of sapling growth across the gradient of residual overstory density examined in this study (Vickers et al. 2014). Conversely, oaks and hickories tended to have relatively low or intermediate rates of establishment but relatively high rates of sapling growth reported in the Missouri Ozarks. This finding suggests that increased density of red maple in the regeneration layer may not necessarily result in a long-term shift in species composition in the Missouri Ozarks, as has been forecast throughout much of the red maple range (Abrams 1998, Fei and Steiner 2007). However, additional quantitative research into the influence of residual overstory density on relative mortality rates among species is warranted to fully understand the implications of interspecific differences in establishment and growth on regeneration dynamics in the Missouri Ozarks.

Although red maple is typically not a major component of the overstory in the Missouri Ozarks (e.g., Table 1), it is often present in the midstory and regeneration layers. On plots without advance reproduction or residual seed sources, red maple establishment was low (Figure 2). However, red maple establishment was among the most prolific of all species examined across the residual overstory gradient when either a residual seed source or advance reproduction was present. Interestingly, presence of both together did not result in substantially different establishment rates than with either alone except when residual overstory density was less than about 10 m^2 ha^{-1}. In this scenario, residual seed source presence along with advance reproduction presence led to lower establishment rates than with advance reproduction presence alone. It is possible that the model estimates in this particular scenario are influenced by a relatively low number of observations as red maple was uncommon in the overstory at low residual overstory densities.

The model estimates for oaks are consistent with the prevailing hypothesis that large advance reproduction is vital for oaks, i.e., the First Law of Oak Silviculture (Loftis 2004, Johnson et al. 2009). Establishment rates from small advance reproduction and new germination tended to be low for oaks, whereas several associated species showed the capacity to establish prolifically, particularly elms, red maple, and sassafras, as well as dogwood, blackgum, and those in the other species group (Figure 2). Furthermore, small oak advance reproduction or new oak seedlings that do establish are unlikely to survive (Sander et al. 1984, Loftis 1990, Dey 1991).

Our models indicate that elms were the most sensitive to treatment intensity and rarely established when residual overstory density exceeded 10 m^2 ha^{-1}. Surprisingly, residual seed source was not included in the best model for elms. Elms can regenerate prolifically after disturbance due, in part, to abundant production of seed that is readily disseminated, primarily by wind (Burns and Honkala 1990). Our models suggest that elm indeed has the potential to establish abundantly and outnumber nearly all other species after extensive disturbance ($\leq$5 m^2 ha^{-1}) but only on plots that had advance reproduction present. This is consistent with Schlesinger et al. (1993), who reported that elm reproduction can be ubiquitous after disturbance on favorable sites but is seldom a concern elsewhere in the Missouri Ozarks.

Establishment rates of sassafras reproduction tended to be high relative to those of most species groups in all scenarios across the gradient of residual overstory density. Vickers et al. (2014) reported that increasing residual overstory density affected the height growth of sassafras the least. This implies that the requirements for successful sassafras regeneration in the Missouri Ozarks are quite general, yet sassafras is seldom a major component beyond the sapling stage (Dey 1991). The decline in sassafras performance beyond the sapling stage may be due to ontogenetic changes in growth and/or mortality rates. Although there has been little quantification of mortality rates for sassafras, Vickers (2015) found the decline in annual height increment with increasing height for sassafras was greater than that for most associated species in the Missouri Ozarks. The establishment rates of sassafras tended to be considerably higher when it was present as advance reproduction. Although this could be a manifestation of favorable site conditions, another possible explanation is the ability of sassafras to regenerate profusely via root sprouting (Griggs 1990). Without an adjacent cut stump, root sprouts were probably not labeled as obvious sprouts during the collection of data used for this study.

As illustrated in Figures 3 and 4, both deterministic and stochastic estimates of reproduction establishment can be obtained from the parameterized models provided in Table 3. The approach used to generate the random deviates for red oaks in Figure 3 can be repeated for all remaining species groups in a variety of covariate scenarios as demonstrated in Figure 4. In the context of regeneration simulation, stochastic output is often preferred (Dey et al. 1996). When this approach is applied to our establishment models, the fate of small reproduction and occurrence of seedling germination are explicitly acknowledged as large sources of variation in regeneration outcomes (Larsen et al. 1997, Larsen and Johnson 1998, Gould et al. 2006). There are both known and unknown sources of variation not included in this approach, some of which are ecological (e.g., Olson et al. 2015) and others statistical (Hobbs and Hooten 2015). Nonetheless, the use of stochastic model output across multiple simulation runs with the same input data encourages consideration of a broader range of outcomes along with the mean outcome. This view is consistent with the ecology of forest regeneration and stand development. Regeneration outcomes are inherently variable and are often strongly influenced by the magnitude and timing of stochastic stimuli (Gleason 1917, Clark and Clark 1994, Oliver and Larson 1996, Brokaw and Busing 2000). In cases where stochastic output is not desired, the estimated distribution parameters can still be used to calculate the probabilities of achieving threshold outcomes for each species via probability mass functions. Depending on the context of application, deterministic estimates of third-year reproduction may provide sufficient information.

Conclusions

Our objective was to estimate third-year abundance parameters for reproduction that originated from either small advance reproduction (height $<$100 cm) or new germination. In the context of this project, established reproduction was defined as stems present 3 years after disturbance. Our model estimates indicate that third-year reproduction abundance from these regeneration sources was largely a function of residual overstory density. Across all species third-year reproduction abundance declined with increasing residual overstory density (basal area) and was limited when densities exceeded $\approx$20 m^2 ha^{-1}. There was evidence of interspecific differences in establishment rates, particularly at low residual overstory densities, but those differences were progressively muted with increasing residual overstory density. The influence of predisturbance stand conditions was summarized by a simple presence/absence inventory of advance reproduction for each species. Our results suggest that the simple presence/absence inventory of advance reproduction might serve as a parsimonious species-specific indicator of suitable conditions for postharvest establishment. Presence of advance reproduction was included in the best models for 8 of the 11 species groups with sufficient data. Only three species groups included presence of a residual seed source in their best model of third-year reproduction abundance. These models can be used to estimate third-year reproduction abundance after a variety of harvest-based silvicultural manipulations both deterministically and stochastically if combined with stochastic number generators.

Our establishment models were developed as one component of a larger effort to model the impact of overstory density on the establishment, growth, and mortality of reproduction in the Missouri Ozarks. Complementary models have been developed to provide estimates of the third-year height and allometric structure of the regenerating cohort based on residual overstory density and other factors (Vickers 2015). Providing early estimates of regeneration outcomes increases the opportunities for foresters to ground-check regeneration projections and intervene if deemed necessary. Thereafter, techniques more common to growth and yield modeling, such as an annualized height growth models that incorporate initial height, residual overstory density, species, and site class can be used to incrementally update the development of the cohort throughout the regeneration period (Vickers et al. 2014). This approach provides opportunities for more detail to be provided at more frequent intervals. For many species in the Missouri Ozarks, establishment from these regeneration sources tends to supplement vegetative reproduction and large advance reproduction (Johnson et al. 2009). These more reliable sources of regeneration can largely be accounted for probabilistically using a collection of sprouting parameters gleaned from the literature (Vickers et al. 2016). Additional research will be required to develop models of sapling mortality in the Missouri Ozarks.

The increased generalization offered by these models greatly increases the breadth of disturbance scenarios that can be examined for their impact on regeneration. The modeling approach and concepts described here are generally adaptable to other species and locales, but the performance or applicability of the parameterized models outside the Missouri Ozarks is unknown.

Supplemental Podcast

This article includes a podcast interview. Visit the online version of this article to listen to the podcast.

Appendix 1

Species included in the "other species" species group for models of reproduction establishment and allometric models are shown in Table A1.

Table A1. Other species group.

Acer negundo L.
Amelanchier arborea Michx.
Asimina triloba (L.) Dunal
Carpinus caroliniana Walt.
Celtis spp.
Cercis canadensis L.
Corylus americana Marshall
Crataegus spp.
Diospyros virginiana L.
Elaeagnus umbellata Thunb.
Gleditsia triacanthos L.
Gymnocladus dioica (L.) K. Koch.
Juglans nigra L.
Juniperus virginiana L.
Lindera benzoin L.
Morus spp.
Ostrya virginiana Mill.
Platanus occidentalis L.
Prunus americana Marshall
Rhamnus caroliniana Walt.
Rhus spp.
Robinia pseudoacacia L.
Sideroxylon lanuginose Michx.
Vaccinium spp.
Viburnum spp.
Unknown

Endnote

1. Please note that comparisons of "best" model estimates among all species in a given covariate scenario may include species groups with models invariant to one or more covariates.

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