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Predicting Forest Regeneration in the Central Appalachians Using the REGEN Expert System

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REGEN is an expert system designed by David Loftis to predict the future species composition of dominant and codominant stems in forest stands at the onset of stem exclusion following a proposed harvest. REGEN predictions are generated using competitive rankings for advance reproduction along with other existing stand conditions. These parameters are contained within modular REGEN knowledge bases (RKBs). To extend REGEN coverage into hardwood stands of the Central Appalachians, RKBs were developed for four site classes (xeric, subxeric, submesic, mesic) based on literature and expert opinion. Data were collected from 48 paired stands in Virginia and West Virginia to calibrate the initial RKBs. Paired stands consisted of one mature uncut hardwood stand adjacent to a regenerating clear-cut stand with similar

site characteristics that was harvested within the previous 20 yr. Data from 17 additional paired stands was collected a year later to validate the performance of REGEN. Predicted values were within 4 percentage points of measured values on average, and model error was typically less than 20 percentage points for species groups. These results confirmed the suitability of REGEN to predict the future species composition of stands regenerated using the clear-cut method in the Central Appalachians of Virginia and West Virginia.

INTRODUCTION

Appalachian Hardwood Regeneration

The mixed hardwood forests of the Appalachians are extremely diverse (Miller & Kochenderfer, 1998). Individual stands can often contain more than 50 different species that vary in shade tolerance, growth rates, and regeneration strategies (Braun, 1950; Burns & Honkala, 1990; Smith, 1994). The long disturbance history of the Appalachians has increased the complexity of these forests (Yarnell, 1998). The regeneration potential of each species in a stand following disturbance is largely determined by shade tolerance, individual growth rates, and the type of disturbance (Smith, Larson, Kelty, & Ashton, 1996). Fast growing shade-intolerant species such as black cherry (*Prunus serotina* Ehrh.) and yellow-poplar (*Liriodendron tulipifera* L.), often regenerate following a heavy disturbance from new seedlings that develop from seed recently dispersed and stored in the forest floor. In contrast, slower growing, more shade-tolerant species such as oaks (*Quercus* spp.) rely on the buildup of large advance reproduction and timely release to compete successfully following a similar disturbance unless site factors offer an ecological advantage to these species (Sander, 1972; Loftis, 1983; Johnson, Shifley, & Rogers, 2002).

Site productivity, primarily determined by moisture availability, is a significant driver of species composition and regeneration potential in the Appalachians (McNab, 1988). Naturally occurring species assemblages are often delineated by moisture availability (Eyre, 1980). Smith (1994) classified forests of the Southern Appalachians into four groups based on productivity (site index) that was largely determined by moisture availability, essentially occurring on sites with xeric, subxeric, submesic, and mesic moisture regimes. Site index for white oak (*Quercus alba* L.) at age 50 averaged less than about 17 m in the xeric communities and more than about 26 m in the mesic communities (Smith, 1994).

Hardwood Regeneration Models

Estimates of future species composition following harvest are important to forest managers and silviculturists to help ensure landowner objectives are met in a predictable and sustainable fashion. Because of the complexity of many Eastern hardwood forests, however, it is often difficult to reliably predict the future species composition that will exist following a proposed harvest using natural regeneration. Several modeling approaches have been used to predict regeneration in oak dominated ecosystems (Rogers & Johnson, 1998). These tools typically follow the model of forest succession based on initial floristics (Egler, 1954), utilize stand stocking guides (e.g., Gingrich, 1967), and incorporate the concept that advance reproduction size impacts regeneration success (Sander, 1972). Probabilistic models and management guidelines have been developed to evaluate regeneration potential in primarily oak dominated Central hardwood forests (Sander, Johnson, & Watt, 1976), the Missouri Ozarks (Sander, Johnson, & Rogers, 1984), the Southern Bottomlands (Belli, Hart, Hodges, & Stanturf, 1999), the Alleghenies (Brose et al., 2008), and the Central Appalachians (Steiner, Finley, Gould, Fei, & McDill, 2008). Other models that produce only quantitative estimates have been published as well (McQuilkin, 1975; Loftis, 1990; Gould, Steiner, Finley, & McDill, 2005). Loftis (1990) and McQuilkin (1975) developed single species models for some oaks. Gould, Steiner, McDill, and Finley (2006) described a methodology for modeling seed origin oak regeneration. In addition, models have been developed solely to quantify contributions to future composition from stump-sprouting (Johnson, 1977; Dey, Johnson, & Garrett, 1996; Gould, Fei, & Steiner, 2007). Most of these tools are limited to oak management. In some cases, multispecies, regional predictive models have been developed (Waldrop, Buckner, Shugart, & McGee, 1986; Dey, 1991), but such models are not available for all areas.

REGEN

Interest in a multispecies, regional predictive model for the Southern Appalachians fostered the development of the REGEN model (Loftis, 1989). The REGEN model is an expert system designed by David Loftis to predict the species composition of upper canopy (dominant and codominant) stems at the onset of stem exclusion following a proposed harvest. REGEN uses numerical rankings of expected species competitiveness in conjunction with existing stand characteristics to generate predictions. Boucugnani (2005) described the development of the computer adaptation of REGEN and documented the underlying framework of the model.

A survey of advance reproduction prior to harvest is required in order to generate predictions in REGEN. Advance reproduction is categorized into five default size classes: germinants (newly germinated seedlings), small seedlings (<6-cm tall), medium seedlings (61- to 122-cm tall), large seedlings

($\geq$122-cm tall), and potential stump-sprouts (trees >122-cm tall and $\geq$5-cm dbh). REGEN allows for probabilistic establishment of stump-sprouts, root-suckers, and new seedlings following harvest using constant or logistic parameters along with multiple simulation runs of the input data. Each plot is stochastically populated with a number of root-suckers and new seedlings established postharvest in addition to the existing advance reproduction pool using those parameters during the prediction process. Advance reproduction of a particular species must be present in the plot before root-suckers of that species are added into the regeneration pool. Those parameters are also used to determine which existing stems are expected to produce a stump-sprout for each simulation run.

REGEN is a competition based model. Each species-size-source combination of reproduction is given a competitive ranking ranging from 1 to 8 decreasing in competiveness; i.e., individuals ranked 1 will outcompete those ranked 2, individuals ranked 2 will outcompete those ranked 3, and so forth. Competition is simulated at the plot level, and future upper canopy species composition is predicted based on the relative competitive rankings of the regeneration pool at each sample plot. REGEN populates each prediction plot by identifying up to six "winning" stems for a 0.01 ac (40.5 m²) plot from the reproduction pool based on competitive rank. Individuals ranked 1 are selected first. If the threshold of six is not met, the selection process moves on to individuals ranked 2, then 3, and so forth until all six "winning" stems have been selected. In the case of ties for the selection of the final "winning" stem, each equally ranked individual is selected proportionally (e.g., if there are five individuals of equal rank, each one is selected as 0.2 of an individual). This fragmentation is resolved when "winning" stems per plot are scaled to stems per acre (0.40 ha) in the summary output. On plots where stump-sprouts are chosen, fewer "winning" stems are added to compensate for the greater space requirements of stump-sprouts. If one stump-sprout is selected, only three additional individuals will be selected. If two stump-sprouts are selected, only one additional individual is selected. If three or more stump-sprouts are selected, the top two are chosen and the remaining "winning" stem is selected proportionally using the tiebreaker logic described earlier. The stochastic element and numerous simulation runs of input data allow summary statistics to be provided with model output.

A REGEN Knowledge Base (RKB) contains all competitive rankings and parameters used to process input data. RKBs are modular, which allows REGEN to be adapted to different regions by creating custom RKBs. Efforts are currently underway to expand REGEN applicability throughout the Appalachians. This article documents work to adapt REGEN to hardwood forests in the Central Appalachians of Virginia and West Virginia.

METHODS

Model Building

To adapt REGEN to the Appalachians of Virginia and West Virginia, four pre-liminary RKBs were created in an attempt to address species variability that resulted from site productivity differences associated with moisture availabil-ity. The four RKBs were designed to predict regeneration on xeric, subxeric, submesic, and mesic sites. These four site classes roughly approximate the four forest types described by Smith (1994) and were delineated using the methodology proposed by McNab, Loftis, and Shefield (2003). In this methodology, certain species serve as indicators of moisture availability and provide insight into relative site quality (McNab et al., 2003). The initial rankings and parameters for these four RKB's were based on relevant liter-ature, including: silvical characteristics (Burns & Honkala, 1990), reported species composition following clear-cutting (e.g., Beck & Hooper, 1986; Ross, Sharik, & Smith, 1986; Loftis, 1989), and site productivity interactions (e.g., Doolittle, 1958).

Stump-sprouting, root-suckering, and new seedling establishment prob-abilities were initially taken from the literature when possible. The Silvics Manual in particular served as a source of information for several species (Burns & Honkala, 1990). However, because data found in existing litera-ture was often from different forest types and climates, the information from these sources was modified or supplemented as necessary, based on the experience of the authors to create the four custom RKBs. In these RKBs, stump-sprouts were considered the most competitive source of regeneration for a species when applicable, and rankings subsequently decreased for smaller size classes. Although competition within a species (large vs. small seedling) was fairly straightforward, the rankings also had to maintain com-petitive relationships amongst species across all size classes. Therefore, the difference in competitive rank between a large stem of advanced reproduc-tion compared to a medium stem, for example, may not be uniform across all species.

Because these rankings were designed to predict upper canopy species composition at the onset of stem exclusion, species that may be numer-ous in the lower canopy and possibly ascend into the upper canopy in later stages of development were not necessarily given a high rank. Conversely, early successional species, which were expected to be numer-ous, but ultimately short lived in the upper canopy, were ranked highly. Generally, more mesic species such as basswood (*Tilia* spp.) decreased in rank as moisture availability decreased, while xeric species such as Virginia pine (*Pinus virginiana* Mill.) increased in rank. Sweet birch (*Betula lenta* L.) and yellow-poplar were expected to be strong initial competitors and were given a superior rank in all site classes except for xeric. Black locust (*Robinia pseudoacacia* L.) and eastern white pine (*P. strobus* L.)

were also among the most competitive species across all site classes. Red maple (*Acer rubrum* L.) sprouts were considered very competitive across all four site classes. Oaks were among the most competitive species in the xeric and subxeric RKBs and decreased as moisture availability increased. Chestnut (*Quercus prinus* L.) and scarlet (*Q. coccinea* Muenchh.) oaks were more competitive in the xeric and subxeric classes and decreased as moisture availability increased, while northern red oak (*Q. rubra* L.) became increasingly competitive up to the submesic RKB.

Following the development of the preliminary knowledge bases, field data were collected to evaluate the performance of the initial parameters and to serve as a database to improve those parameters with subsequent iterative trials. This model calibration data set was collected using a paired stand sampling approach. This approach utilized sample sites which consisted of a mature hardwood stand free from obvious recent disturbance adjacent to a regenerating clear-cut stand of similar site characteristics. According to available landowner records, the mature stands were no less than 70 yr old, while the regenerating clear-cut stands ranged in age from 5 to 20 yr old. This approach assumed that the two stands were once contiguous and of similar composition and productivity. It was further assumed that any mature stand would regenerate in a similar fashion to its paired regenerating clear-cut stand when harvested similarly. Slope, aspect, and landscape position were used to indirectly estimate site index using the Forest Site Quality Index (Meiners, Smith, Sharik, & Beck, 1984) to ensure similar site productivity between paired mature and regenerating clear-cut stands. This methodology provides estimates of site index in areas of similar rainfall based on moisture retention potential (Meiners et al., 1984). Paired stands were also classified into site classes using indicator species as proposed by McNab et al. (2003) in their ecological classification system. The species moisture weights from their methodology was applied to a list of sampled tree species that were ≥5-cm dbh in each mature stand to classify each paired stand into one of four moisture regimes: xeric, subxeric, submesic, and mesic.

Sampling Sites and Procedures

A total of 48 paired stands were located in Virginia and West Virginia to serve as a source of data to calibrate our RKBs (Figure 1). Forty-five of the 48 paired stands were located within the Appalachian Plateau Physiographic Province, while the remaining 3 were located in the Ridge and Valley Province (Fenneman, 1938). The difference in estimated oak site index between all paired mature and regenerating clear-cut stands was about 0.9 m on average. A maximum difference of about 4 m was estimated for one pair. All paired stands in this study fell on subxeric or submesic sites, with 38 paired stands on submesic sites and 10 paired stands on subxeric sites.
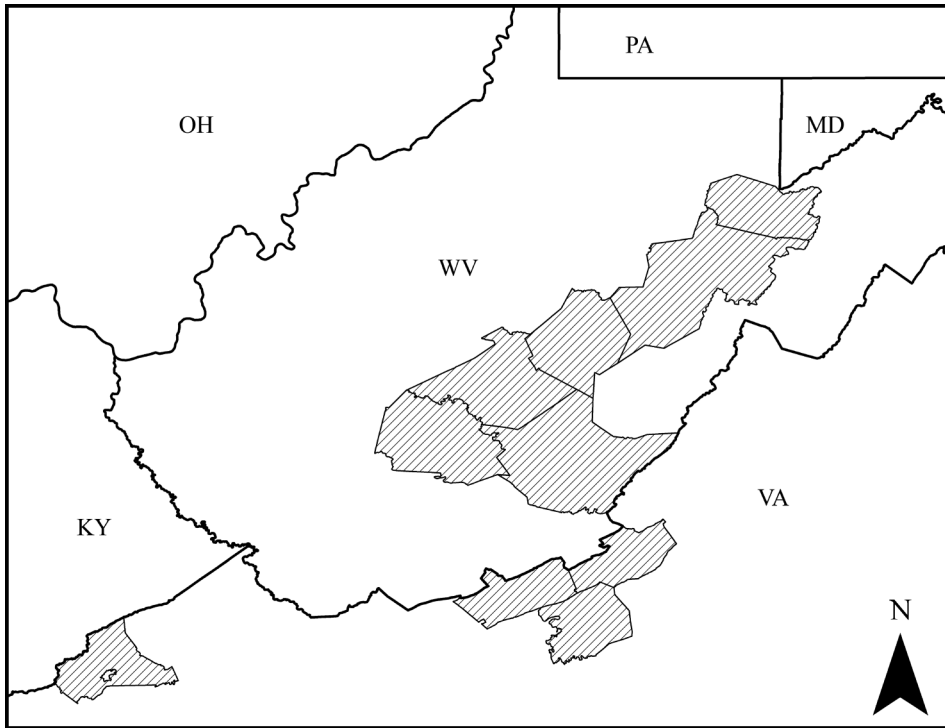
FIGURE 1 Location of sample sites in the Central Appalachians. Shaded areas represent counties in which paired stands were located.

For this reason, only the subxeric and submesic RKBs were tested with field data. Trends observed in these site classes were extended into the xeric and mesic RKBs according to the authors expectations, but those RKBs have not been field tested.

The paired stands for model calibration were sampled between May and September, 2008. In the mature stands, about 2 fixed-radius plots per hectare were established with a maximum of 20 plots per stand. Plots were established using a systematic grid with a plot spacing of 50.3 m and a row spacing of 80.5 m. The distance from the stand boundary to the first plot was randomly determined but no less than 40.2 m. Advance reproduction was measured in a 16.2 m^2 fixed-radius circular plot by species and REGEN size class (Large: $\geq$122 cm, Medium: $\geq$61cm, Small: <61 cm, Germinant: newly germinated seedlings), and dbh of all stems $\geq$5-cm dbh within the plot was also measured. At each fixed-radius plot center, a basal area sampling point was also established on which the basal area of all stems $\geq$5-cm dbh was measured using a 2.3 BAF prism. Advance reproduction from the mature stand inventories was later scaled up to represent 40.5 m^2 (0.01 ac) to meet the input requirements of the REGEN computer

program. Regenerating clear-cut stands were sampled at a density of about 2 fixed-radius circular plots per hectare, using 4 m^2 plots unless stands had developed such that plots of this size were frequently unpopulated. In this case, sample plots were reestablished as 16.2 m^2 plots throughout the stand. In the regenerating stands, regeneration was tallied by species, stem origin (seed or sprout), and crown class (dominant, codominant, intermediate, suppressed).

An additional 17 paired stands were sampled in September and early October of 2009 to serve as a model validation data set. Twelve paired stands were located within the Appalachian Plateau Physiographic Province, while the remaining 5 were located in the Ridge and Valley Province (Fenneman, 1938). Sampling procedures were identical to those described above for the model calibration data set, with the exception of fixed-radius plot sizes. In the validation paired stands, advance reproduction was tallied on all mature stands using 40.5 m^2 circular plots. On the regenerating clear-cut stands, regeneration was tallied on 16.2 m^2 plots exclusively. The difference in estimated oak site index between these additional paired mature and regenerating clear-cut stands was about 0.3 m on average, with a maximum of about 0.3 m. In the validation data set, 14 of the stands were classified submesic, with the remaining 3 as subxeric.

Because of the complex assemblages of species that occur in this area, eight species groups were created for the purposes of data analysis and presentation following data collection: (a) black cherry, (b) conifers, (c) maples, (d) midstory, (e) oaks, (f) other overstory, (g) pioneer, and (h) yellow-poplar (Table 1). Species groups were composed of either a single species that was numerous throughout the area or multiple species that are expected to occupy similar stand structural positions.

The composition of the paired stands examined in this study was typical of Central Appalachian hardwoods. Mean basal area of the 48 mature stands in the model calibration dataset was 27.1 m^2 per hectare dominated by oaks and maples. These stands had 914 stems per hectare ≥5-cm dbh, with maples making up the greatest proportion (Table 2). In the 48 regenerating clear-cut stands in the model calibration data set, maples and pioneer species were the most numerous in the upper canopy (dominant and codominant), while maples and midstory species were the most numerous in the lower canopy positions (intermediate and suppressed; Table 3). The composition of the paired stands in the validation data set was similar to those in the model calibration data set. Oaks and maples dominate the 28 m^2 per hectare of basal area in the 17 mature stands in the validation data set (Table 2). In the 17 regenerating clear-cut stands in the validation data set, maples and pioneer species were the most numerous groups in the upper canopy, and maples and midstory were the most numerous groups in the lower canopy (Table 3).

TABLE 1 Species Groupings Used in This Study for the Central Appalachians

Group	Species
Black cherry	Black cherry (*Prunus serotina* Ehrh.)
Conifers	E. white pine (*Pinus strobus* L.), hemlock (*Tsuga* spp.), pitch pine (*Pinus rigida* Mill.), red spruce (*Picea rubens* Sarg.), shortleaf pine (*Pinus echinata* Mill.), Table Mountain pine (*Pinus pungens* Lamb.), Virginia pine (*Pinus virginiana* Mill.)
Maples	Red maple (*Acer rubrum* L.), sugar maple (*Acer saccharum* Marsh.)
Midstory	Am. chestnut (*Castanea dentata* [Marsh.] Borkh.), Am. holly (*Ilex opaca* Ait.), beech (*Fagus grandifolia* Ehrh.), blackgum (*Nyssa sylvatica* Marsh.), dogwood (*Cornus* spp.), ironwood (*Ostrya virginiana* [Mill.] K. Koch.), sassafras (*Sassafras albidum* [Nutt.] Ness.), serviceberry (*Amelanchier* spp.), sourwood (*Oxydendrum arboreum* [L.] DC.), striped maple (*Acer pensylvanicum* L.)
Oaks	Black oak (*Quercus velutina* Lam.), chestnut oak (*Quercus prinus* L.), n. red oak (*Quercus rubra* L.), scarlet oak (*Quercus coccinea* Muenchh.), white oak (*Quercus alba* L.)
Other overstory	Ash (*Fraxinus* spp.), basswood (*Tilia* spp.), buckeye (*Aesculus flava* Ait.), cucumbertree (*Magnolia acuminata* L.), Fraser magnolia (*Magnolia fraseri* Walt.), hickory (*Carya* spp.), yellow birch (*Betula alleghaniensis* Britton)
Pioneer	Ailanthus (*Ailanthus altissima* [Mill.] Swingle), American sycamore (*Platanus occidentalis* L.), bigtooth aspen (*Populus grandidentata* Michx.), black locust (*Robinia pseudoacacia* L.), fire cherry (*Prunus pensylvanica* L.f.), royal paulownia (*Paulownia tomentosa* [Thunb.] Sieb. & Zucc. Ex Steud.), sweet birch (*Betula lenta* L.)
Yellow-poplar	Yellow-poplar (*Liriodendron tulipifera* L.)

Model Calibration

Preliminary model results from the advance reproduction survey in the mature stands using the initial rankings (predicted) were compared to the upper canopy species composition of the regenerating clear-cut stands (measured) in the model calibration data set. The primary model output evaluated was the predicted species composition expressed as a proportion of total stand composition. That allowed predictions from REGEN to be uniformly compared to the measured species composition of regenerating clear-cut stands which varied somewhat in age, density, and development. Based on these intermediate results, competitive rankings for each species in each RKB were adjusted in an iterative process to achieve the best fit. Sprouting probabilities and other parameters were also amended according to the results of preliminary model runs. The final rankings developed for the four site classes are presented in Tables 4 and 5.

Statistical Analysis

On both the model calibration and validation data sets, tests for normality indicated a nonnormal distribution. Further analyses were conducted using

TABLE 2 Mean Composition of the Mature Sample Stands in the Central Appalachians

| | Model calibration data set | | | | | | Model validation data set | | | | | |
| | Overall (n = 48) | | Subxeric (n = 10) | | Submesic (n = 38) | | Overall (n = 17) | | Subxeric (n = 3) | | Submesic (n = 14) | |
Species group	BA (SE ±) (m²/ha)	TPH (SE ±) (stems/ha)	BA (SE ±) (m²/ha)	TPH (SE ±) (stems/ha)	BA (SE ±) (m²/ha)	TPH (SE ±) (stems/ha)	BA (SE ±) (m²/ha)	TPH (SE ±) (stems/ha)	BA (SE ±) (m²/ha)	TPH (SE ±) (stems/ha)	BA (SE ±) (m²/ha)	TPH (SE ±) (stems/ha)
Black cherry	1.8 (0.7)	30 (10)	0 (0.0)	0 (0)	2.3 (0.7)	37 (12)	0.5 (0.2)	17 (5)	0.0 (0.0)	0 (0)	0.7 (0.2)	20 (5)
Conifers	0.9 (0.2)	40 (15)	0.7 (0.5)	25 (22)	1.1 (0.5)	42 (17)	1.1 (0.7)	2 (2)	0.9 (0.5)	20 (20)	1.1 (0.7)	0 (0)
Maples	6.0 (0.7)	321 (25)	3.0 (0.7)	368 (72)	6.9 (0.7)	309 (25)	6.4 (0.9)	254 (22)	3.7 (1.1)	329 (47)	7.1 (0.9)	237 (25)
Midstory	2.3 (0.2)	175 (20)	1.4 (0.5)	210 (57)	2.5 (0.5)	165 (20)	2.1 (0.5)	163 (32)	1.8 (0.7)	309 (131)	2.3 (0.7)	131 (25)
Oaks	10.8 (1.1)	165 (22)	16.8 (1.4)	316 (40)	9.4 (1.4)	126 (20)	10.6 (1.6)	173 (40)	20.0 (1.1)	455 (79)	8.5 (1.6)	114 (25)
Other overstory	2.3 (0.2)	106 (17)	0.7 (0.2)	59 (32)	2.8 (0.5)	119 (20)	3.9 (0.9)	74 (15)	0.7 (0.5)	17 (10)	4.4 (1.1)	86 (17)
Pioneer	0.7 (0.2)	30 (7)	0.2 (0.2)	10 (7)	0.9 (0.2)	35 (10)	0.9 (0.2)	30 (10)	0.0 (0.0)	0 (0)	1.1 (0.2)	35 (12)
Yellow-poplar	2.3 (0.5)	52 (12)	0.0 (0.0)	2 (2)	2.8 (0.5)	64 (15)	2.5 (0.9)	32 (12)	1.1 (0.9)	20 (20)	2.8 (1.1)	37 (15)
Totals	27.1	919	22.8	990	28.7	897	28.0	745	28.2	1149	28.0	660

Note. BA = basal area; TPH = tress per hectare.

TABLE 3 Mean Composition of the Regenerating Clear-cut Sample Stands in the Central Appalachians

| | Model calibration data set | | | | | | Model validation dataset | | | | | |
| | Overall (n = 48) | | Subxeric (n = 10) | | Submesic (n = 38) | | Overall (n = 17) | | Subxeric (n = 3) | | Submesic (n = 14) | |
Species group	Lower canopy	Upper canopy	Lower canopy	Upper canopy	Lower canopy	Upper canopy	Lower canopy	Upper canopy	Lower canopy	Upper canopy	Lower canopy	Upper canopy
					(stems/ha)							
Black cherry	944(511)	618(237)	86(64)	99(84)	1,169(642)	753(294)	37(15)	96(27)	0(0)	0(0)	44(17)	119(32)
Conifers	15(7)	12(7)	57(30)	5(5)	2(2)	15(10)	47(27)	57(52)	104(104)	289(289)	35(27)	7(5)
Maples	2,492(348)	1,079(222)	1,371(272)	1,126(366)	2,789(422)	1067(264)	1,840(225)	543(97)	803(198)	474(195)	2,065(230)	558(104)
Midstory	2,193(368)	818(274)	1,351(415)	422(210)	2,416(447)	921(343)	1,210(240)	274(64)	1,203(603)	207(175)	1,10(269)	289(72)
Oaks	1,647(558)	622(151)	2,169(1240)	1,275(509)	1,509(630)	452(128)	598(153)	440(106)	1,050(573)	783(361)	501(143)	366(101)
Other Overstory	761(188)	457(84)	237(89)	326(99)	899(230)	492(104)	472(128)	205(54)	351(161)	165(82)	496(153)	212(64)
Pioneer	986(168)	1,030(257)	348(309)	652(568)	1,153(188)	1129(289)	509(141)	543(121)	0(0)	0(0)	618(156)	659(126)
Yellow-poplar	995(163)	580(91)	469(198)	474(190)	1,131(195)	608(104)	578(291)	361(148)	1,647(1647)	741(741)	351(119)	279(106)
Total	10,033	5,216	6,088	4,379	11,068	5436	5,291	2,519	5,158	2659	5,320	2,489

Note. Lower canopy = suppressed and intermediate stems; upper canopy = dominant and codominant stems.

TABLE 4 Competitive Rankings for Common Species Following Clear-cut on Xeric and Subxeric Sites in the Central Appalachians

Rank	Xeric	Subxeric
1	Chestnut oak Sp, scarlet oak Sp, sourwood Sp, Virginia pine L	Black locust Sp, chestnut oak Sp, e. white pine L, red maple Sp, scarlet oak Sp, sweet birch Sp, yellow-poplar Sp
2	Black oak Sp, chestnut oak L, e. white pine L, pitch pine L, red maple Sp, shortleaf pine L, Table Mt. pine L	Black cherry Sp, black locust L, black oak Sp, cucumbertree Sp, e. white pine M, fire cherry Sp, sweet birch L, white oak Sp, yellow-poplar L
3	Black locust Sp, black oak L, blackgum Sp, e. white pine M, hickory Sp, n. red oak Sp, sassafras Sp, scarlet oak L, sourwood L, Table Mt. pine M, Virginia pine S, white oak Sp,	Black locust M, chestnut oak L, cucumbertree L, fire cherry L, hickory Sp, n. red oak Sp, scarlet oak L, sweet birch M, yellow-poplar M
4	Black locust L, chestnut oak M, e. white pine S, pitch pine S, red maple L, scarlet oak M, shortleaf pine S, sourwood M, Table Mt. pine S, Virginia pine G, white oak L	Black cherry L, black locust S, black oak L, e. white pine S, fire cherry M, red maple L, sourwood Sp, sweet birch S, Virginia pine L, yellow-poplar S
5	Black locust M, black oak M, blackgum L, chestnut oak S, e. white pine G, hickory L, ironwood Sp, n. red oak L, pitch pine G, red maple M, sassafras L, scarlet oak S, serviceberry Sp, shortleaf pine G, sourwood S, Table Mt. pine G, white oak M,	Ash Sp, black cherry M, black locust G, chestnut oak M, dogwood Sp, e. white pine G, fire cherry S, ironwood Sp, n. red oak L, pitch pine L, scarlet oak M, shortleaf pine L, sweet birch G, Table Mt. pine L, white oak L, yellow-poplar G
6	Black cherry Sp, black locust S, black oak S, blackgum M, chestnut oak G, dogwood Sp, hickory M, n. red oak M, red maple S, sassafras M, scarlet oak G, sourwood G, white oak S, yellow-poplar Sp	Basswood Sp, beech Sp, black cherry S, black oak M, cucumbertree M, fire cherry G, Fraser magnolia Sp, hickory L, ironwood L, sassafras Sp, serviceberry Sp, sourwood L, striped maple Sp, Virginia pine M
7	Ash Sp, beech Sp, black cherry L, black oak G, blackgum S, dogwood L, fire cherry Sp, hickory S, ironwood L, n. red oak S, red maple G, sassafras S, serviceberry L, sweet birch Sp, white oak G	Ash L, basswood L, beech L, blackgum Sp, buckeye Sp, dogwood L, Fraser magnolia L, hemlock L, ironwood S, pitch pine M, sassafras L, serviceberry L, shortleaf pine M, striped maple L, sugar maple Sp, Table Mt. pine M
8	Ash L, basswood Sp, beech L,black cherry M, black locust G, blackgum G, buckeye SP, cucumbertree Sp, dogwood M, fire cherry L, Fraser magnolia Sp, hemlock L, hickory G, ironwood M, n. red oak G, sassafras G, serviceberry M, striped maple Sp, sugar maple Sp, sweet birch L, yellow birch Sp, yellow-poplar L	Ash Sp, basswood Sp, black cherry G, black oak S, blackgum L, buckeye L, chestnut oak S, cucumbertree S, dogwood M, Fraser magnolia M, hemlock M, hickory M, ironwood S, n. red oak M, red maple M, scarlet oak S, serviceberry M, sourwood M, striped maple M, sugar maple L, Virginia pine S, white oak M, yellow-birch Sp

Note. Sp = stump-sprout; L = large seedling; M = medium seedling; S = small seedling; G = germinant.

TABLE 5 Competitive Rankings for Common Species Following Clear-cut on Submesic and Mesic Sites in the Central Appalachians

Rank	Submesic	Mesic
1	Basswood Sp, black cherry Sp, black locust Sp, fire cherry Sp, sweet birch Sp, yellow-poplar Sp	Basswood Sp, black cherry Sp, fire cherry Sp, sweet birch Sp, yellow-poplar Sp
2	Basswood L, black cherry L, black locust L, e. white pine L, fire cherry L, n. red oak Sp, sweet birch L, yellow-poplar L	Ash Sp, black cherry L, black locust Sp, cucumbertree Sp, e. white pine L, fire cherry L, sugar maple Sp, sweet birch L, yellow birch Sp, yellow-poplar L
3	Black locust M, black oak Sp, e. white pine M, fire cherry M, red maple Sp, yellow-poplar M	Ash L, basswood L, black cherry M, fire cherry M, red maple Sp, sweet birch M, yellow-poplar M
4	Ash Sp, basswood M, black cherry M, black locust S, chestnut oak Sp, e. white pine S, fire cherry S, scarlet oak Sp, sweet birch M, white oak Sp, yellow-poplar S	Beech Sp, black cherry S, black locust L, black oak Sp, buckeye Sp, cucumbertree L, dogwood Sp, e. white pine M, fire cherry S, Fraser magnolia Sp, hemlock L, hickory Sp, n. red oak Sp, striped maple Sp, sugar maple L, sweet birch S, yellow birch L, yellow-poplar S, ash M, basswood M, beech L
5	Ash L, black locust G, cucumbertree Sp, e. white pine G, fire cherry G, hickory Sp, n. red oak L, striped maple Sp, sweet birch S, yellow birch Sp, yellow-poplar G	Black cherry G, black locust M, buckeye L, chestnut oak Sp, cucumbertree M, dogwood L, fire cherry G, red maple L, scarlet oak Sp, sugar maple M, sweet birch G, white oak Sp, yellow birch M, yellow-poplar G
6	Ash M, basswood S, beech Sp, black cherry S, black oak L, blackgum Sp, Fraser magnolia Sp, red maple L, sassafras Sp, scarlet oak L, serviceberry Sp, sourwood Sp, sweet birch G, white oak L, yellow birch L	Beech M, black locust S, black oak L, buckeye M, e. white pine S, Fraser magnolia L, hemlock M, hickory L, n. red oak L, serviceberry Sp, sourwood Sp, striped maple L, sugar maple S, yellow birch S
7	Ash S, basswood G, chestnut oak L, cucumbertree L, Fraser magnolia L, ironwood Sp, serviceberry L, sugar maple Sp, yellow birch M	Black locust G, blackgum Sp, chestnut oak L, cucumbertree S, dogwood M, e. white pine G, Fraser magnolia M, hickory M, ironwood Sp, red maple M, sassafras Sp, scarlet oak L, serviceberry L, striped maple M, white oak L, yellow birch G
8	Ash G, beech L, black cherry G, black oak M, blackgum L, buckeye Sp, cucumbertree M, dogwood Sp, hemlock L, hickory L, ironwood L, n. red oak M, pitch pine L, red maple M, sassafras L, scarlet oak M, serviceberry M, shortleaf pine L, sourwood L, striped maple L, sugar maple L, Table Mt. pine L, Virginia pine L, white oak M, yellow birch S	Ash S, basswood S, beech S, black oak M, blackgum L, buckeye S, cucumbertree G, dogwood S, Fraser magnolia S, hemlock S, hickory S, ironwood L, n. red oak M, pitch pine L, red maple S, sassafras L, serviceberry M, shortleaf pine L, sourwood L, striped maple S, sugar maple G, Table Mt. pine L, Virginia pine L, white oak M

Note. Sp = stump-sprout; L = large seedling; M = medium seedling; S = small seedling; G = germinant.

nonparametric tests. These analyses were conducted in SAS® v. 9.2 software using the UNIVARIATE procedure. REGEN predicts the future upper canopy species composition; therefore, only the upper canopy measurements from the regenerating clear-cut stands were included in these analyses. To assess the overall performance of the model, values of predicted species composition from the REGEN model (which were based on advance reproduction inventories from mature stands) were compared to values of measured species composition (based on upper canopy measurements from regenerating clear-cut stand inventories) for each paired stand in each data set. For example, if the model predicted that black cherry will make up 25% of the future upper canopy stems following harvest based on the advance reproduction inventory, but only 20% of the upper canopy stems measured in the regenerating clear-cut stand were black cherry, then the difference (or model error) at that sample site was 5 percentage points. The Wilcoxon Signed Rank test, a nonparametric alternative to a paired *t* test, was conducted to test for differences between measured and predicted sample distributions for each species group across all paired stands (Ott & Longnecker, 2001).

Simple linear regression was employed on each data set to evaluate the ability of the model to explain the variability in future species composition. To conduct this analysis, paired values of species composition (predicted vs. measured) were analyzed without regard to their associated stands using the REG procedure in SAS™ v. 9.2 statistical software. For example, in the model calibration data set, there were paired values of species composition for eight different species groups in 48 paired stands. Because no regard was given to the individual stand in this analysis, a total of 384 data points (8 species groups × 48 paired stands = 384 data points) were used to evaluate the model's overall ability to explain future species composition. Assessment of performance was based on the coefficient of determination from the regression analysis. To evaluate the model performance for each species group individually, a regression analysis was conducted for the measured and predicted proportions of each species group separately across all paired stands in each data set. Regression analysis was also conducted on the paired values of species composition for individual stands.

The range and standard deviation of the model error (predicted–measured) were calculated for each species group using data from all paired stands in each data set to assess the variation in model predictions. One standard deviation of model error was both added and subtracted from the mean error for each species group to evaluate the spread and frequency of model error.

RESULTS

Model Calibration

The rankings and results presented in this article represent the best fit achieved for the initial model calibration data set after several iterative trials

with the revised RKBs. Using the final RKBs, REGEN appeared to reasonably describe the species composition of regenerating stands following clear-cutting in the 48 paired stands of the model calibration data set that was used to calibrate the RKBs (Fig. 2A). Across all 48 paired stands, mean species composition predicted by REGEN was within 4 percentage points of the measured species composition for all eight species groups used in this
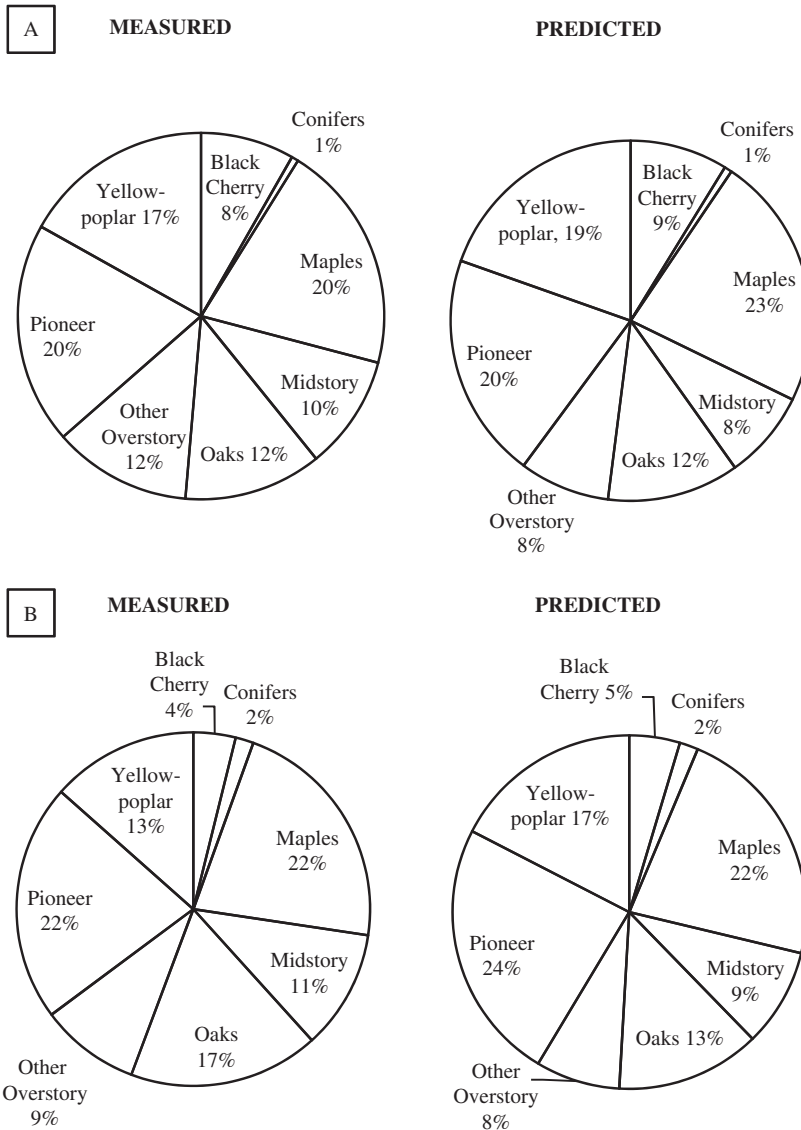

FIGURE 2 Comparison of mean values for measured and predicted species composition in regenerating clear-cut stands from paired stands in the Central Appalachians. Graph A depicts the model calibration dataset, Graph B depicts the model validation data set.

study. Mean differences between measured and predicted samples indicated that black cherry, maples, and yellow-poplar species groups were generally slightly overpredicted. Midstory, and other overstory species groups were generally underpredicted. Tests for differences in sample distributions indicated that among species groups, only the other overstory and yellow-poplar measured distributions were statistically different than their predicted distributions at an α level of .1 (Table 6). Across all 48 paired stands used to build the RKBs, one standard deviation of model error for any species group was no more than about ±20 percentage points from the measured value (Figure 3A). The error for the maples, midstory, pioneer, and yellow-poplar species groups tended to be greater as each had a standard deviation between 15 and 20 percentage points for model error.

The predictions on the 10 subxeric sites were, on average, within about 6 percentage points of the measured values, with the greatest discrepancies observed for the maples, other overstory, and yellow-poplar species groups (Figure 4A) The predictions for the 38 submesic sites were within about 4 percentage points of the measured values on average (Figure 4B). The range of model error from the subxeric RKB appeared to be smaller than the submesic on average, with the exception of yellow-poplar on subxeric sites, which tended to be underpredicted to a greater extent (Figure 5). However, it is possible that this reduced error spread may be due to fewer subxeric sample sites rather than superior performance. On average, one standard deviation of the model error for a species group was not more than ±20 percentage points for both RKBs, except for subxeric yellow-poplar which was typically within about ±24 percentage points.

The overall regression analysis for the 48 paired stands used to build the RKBs indicated a significant linear relationship between predicted and

TABLE 6 Comparison of Mean Measured and Mean Predicted Species Composition of All Sample Stands in the Central Appalachians

Species group	Model calibration data set			Model validation data set		
	Measured	Predicted	*p* value	Measured	Predicted	*p* value
	. . . .(%)			. . . .(%)		
Black cherry	8	9	.3797	4	5	.2661
Conifers	1	1	.7819	2	2	.6250
Maples	20	23	.4060	22	22	1.0000
Midstory	10	8	.9419	11	9	.6777
Oaks	12	12	.8012	17	13	.4037
Other overstory	12	8	.0397	9	8	.7119
Pioneer	20	20	.1460	22	24	.8209
Yellow-poplar	17	19	.0466	13	17	.0413
Total	100	100		100	100	

Note. The *p* values < .1 are considered significant differences between measured and predicted samples as calculated by the Wilcoxon Signed Rank test.
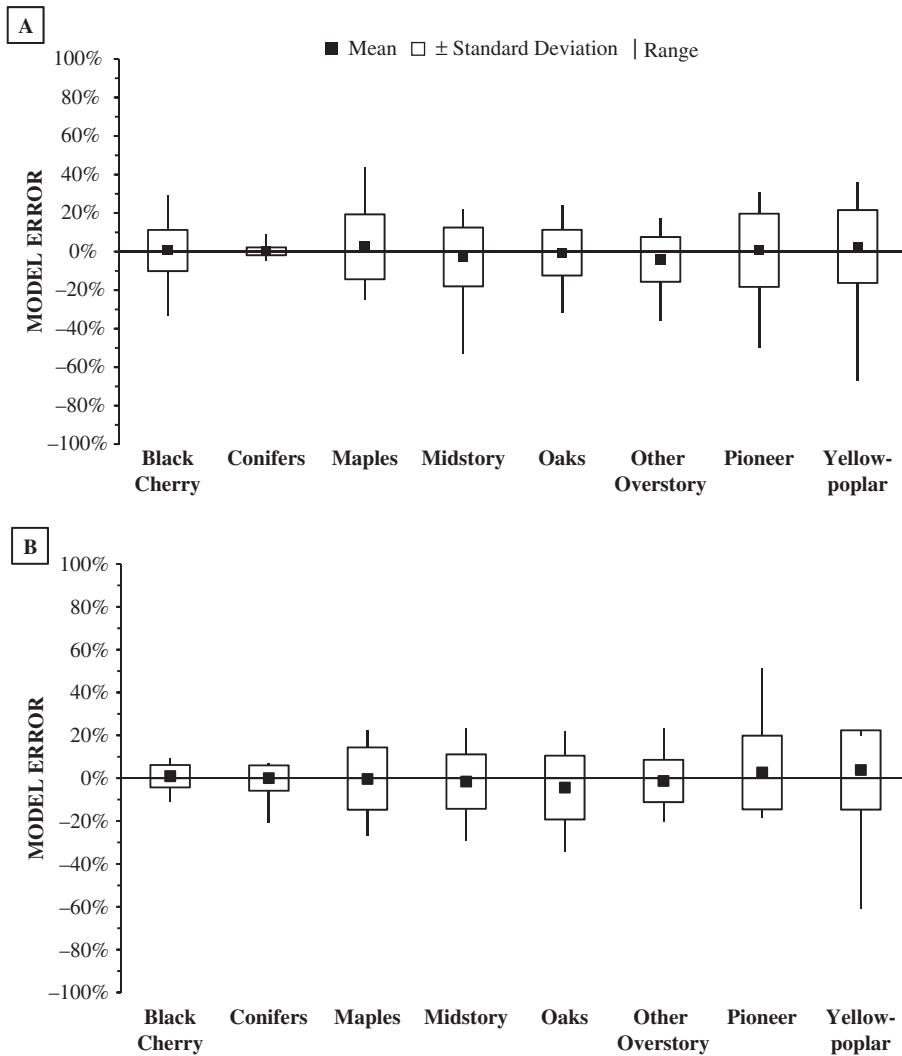
FIGURE 3 Mean model error spread for each species group from paired stands in the Central Appalachians. Model error was calculated as predicted–measured. Data points = mean species group model error, boxes = mean species group model error ± one standard deviation, vertical lines = species group model error range. Graph A depicts the model calibration data set, Graph B depicts the model validation data set.

measured species composition (Figure 6A). The coefficient of determination indicated that the REGEN predictions explained 32% ($R^2 = .32$) of the variation in species composition in regenerating clear-cut stands across both site classes. The subxeric RKB explained 42% ($R^2 = .42$) and the submesic RKB explained 29% ($R^2 = .29$) of the variation in species composition in regenerating clear-cut stands on those sites, respectively. In this data set, 86% of the individual predictions were within ±20 percentage points of their
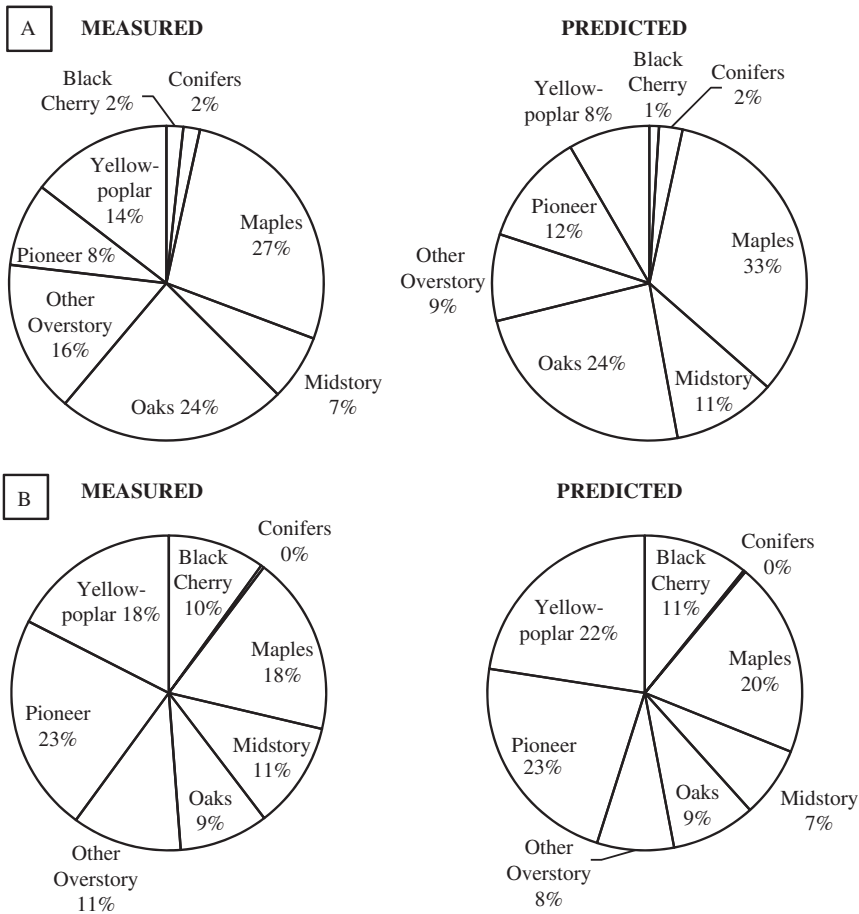
FIGURE 4 Comparison of mean values for measured and predicted species composition by site class in regenerating clear-cut stands from paired stands in the Central Appalachians used for model calibration. Graph A depicts the subxeric stands, Graph B depicts the submesic stands.

paired measured values, 66% of the predictions were within 10 percentage points, and about half were within 5 percentage points.

The analysis of the model residuals, which plotted the model error (predicted–measured) against the measured values, suggested that the model consistently underpredicted future composition when a measured group was greater than about 30% of total stand composition (Figure 7A). In both the regression and residual plots, the subxeric and submesic data points appeared to be randomly distributed. In the model calibration data set, there were 46 instances where a species group comprised at least 35% of stand composition. Early successional species reached this level in 23 of the 46 instances (black cherry 3, pioneer 11, yellow-poplar 9). Maples were the next most frequent group, attaining a composition of at least
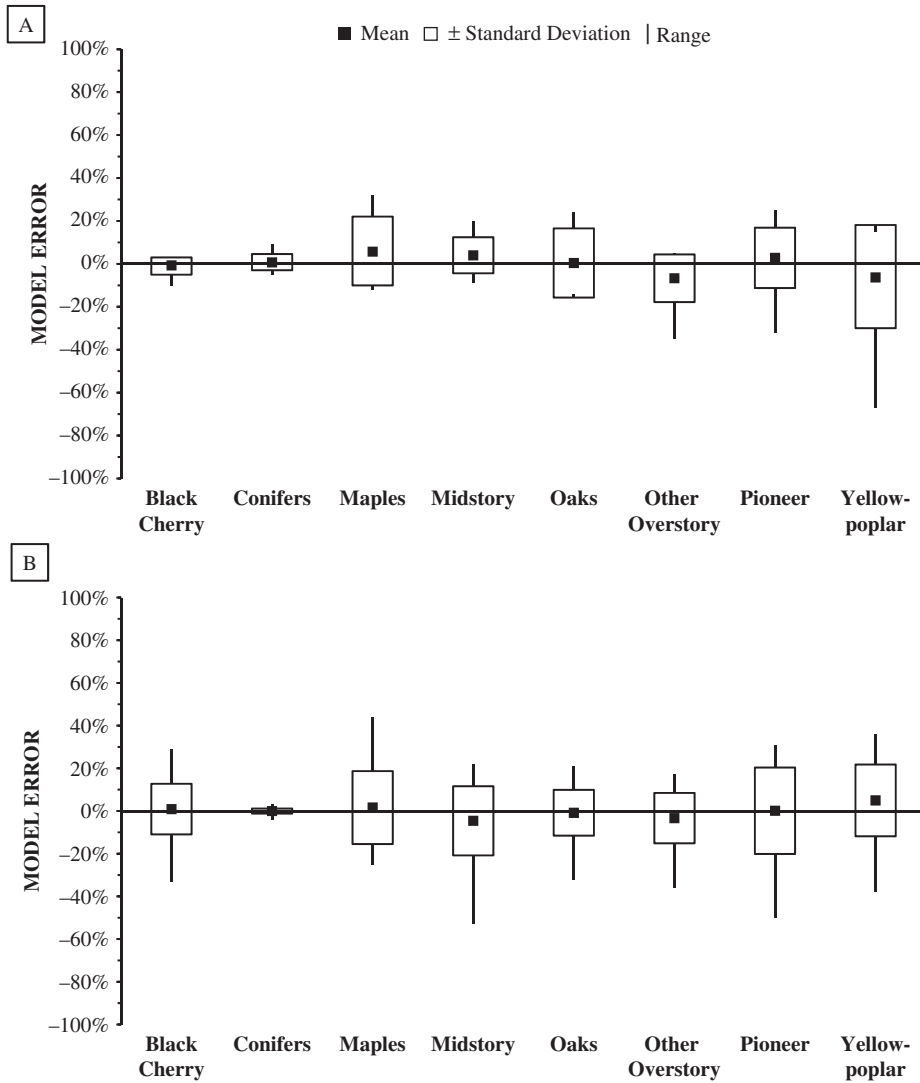
FIGURE 5 Mean model error spread for each species group by site class from paired stands in the Central Appalachians used for model calibration. Model error was calculated as predicted – measured. Data points = mean species group model error, boxes = mean species group model error ± one standard deviation, vertical lines = species group model error range. Graph A depicts the subxeric stands, Graph B depicts the submesic stands.

35% in 11 instances. The remaining 12 instances were by the midstory (3), oaks (4), and other overstory (5) groups. Although this level of stand occupancy was somewhat encouraged by grouping species, instances where individual species attained this level of composition were nearly as frequent (31 instances). Forty of the total 48 regenerating clear-cut stands had at least one group that occupied 35% or more of total composition, and 6 of the
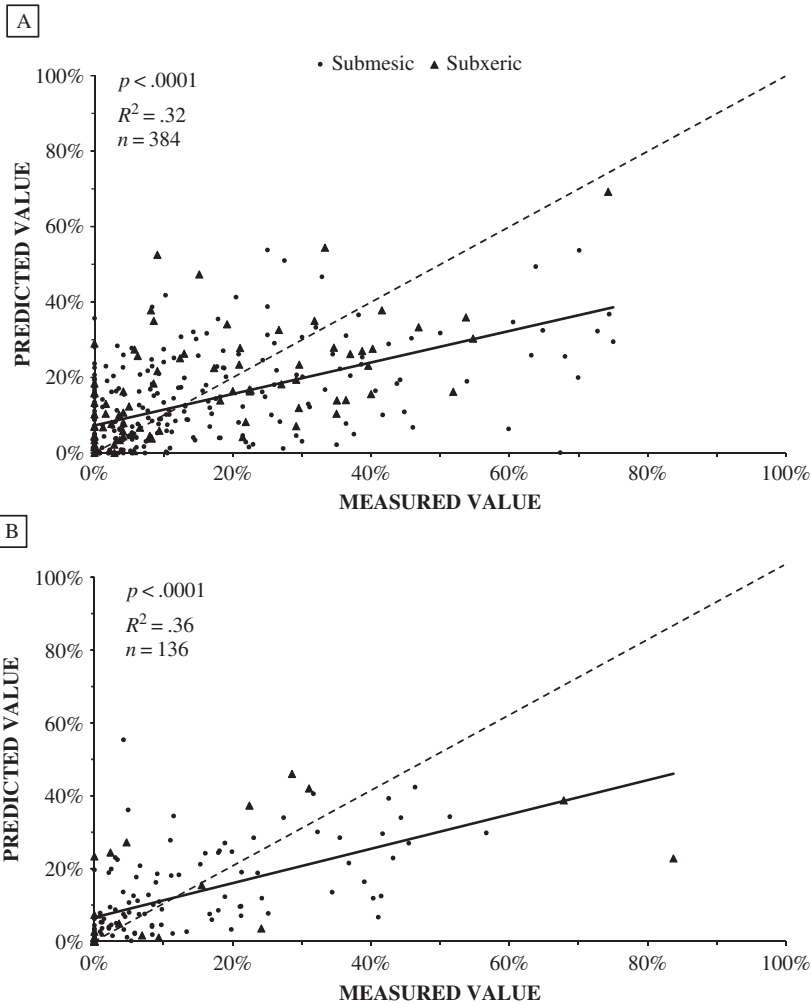
FIGURE 6 Regression analysis comparing measured and predicted values for each species group from paired stands in the Central Appalachians. Y-axis = predicted values, X-axis = measured values. Graph A depicts the model calibration data set, Graph B depicts the model validation data set.

40 stands had two different groups reaching this threshold. In all but one of the stands where two different species groups made up at least 35% of the species composition maples was one of those groups.

Individual regression analysis for each species group indicated significant regressions for all species groups except midstory at an α level of .1 (Figure 8). The model explained the greatest amount of variation for black cherry ($R^2 = .45$), and over 25% of the variability in individual species composition in the regenerating clear-cut stands for three other species
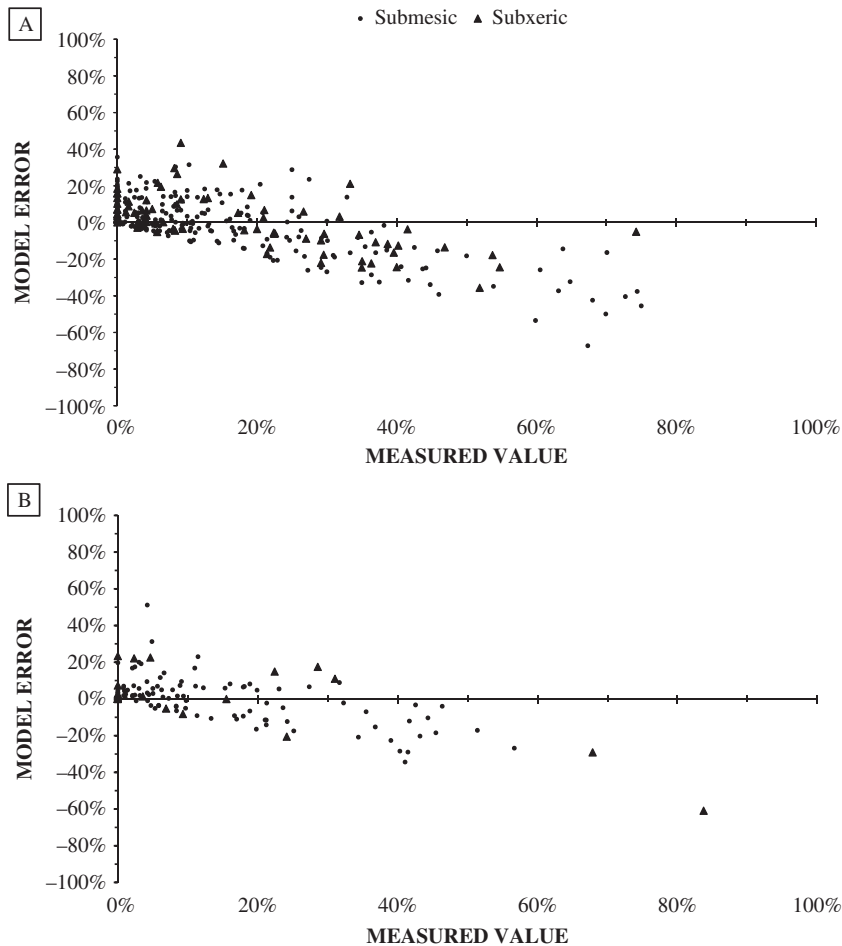
FIGURE 7 Residual analysis for each species group from paired stands in the Central Appalachians. Y-axis = model error (predicted–measured), X-axis = measured values. Graph A depicts the model calibration data set, Graph B depicts the model validation data set.

groups: 39% (R^2 = .39) for oaks, 30% (R^2 = .30) for other overstory, and 28% (R^2 = .28) for the pioneer species group.

Along with the overall stand summary of species composition output, REGEN also reports the original source size (sprout, large, medium, small, germinant) of each winning stem at each plot. The ratio for winning stems of sprout origin in the predicted samples was compared to the sprout ratio in measured regenerating clear-cut stands across all 48 paired stands used to build the RKBs. Tests indicated that the distribution of the proportion of predicted stems of sprout origin were significantly different from measured distributions for the black cherry, midstory, oaks, and pioneer species groups at an α level of .1 (Figure 9A).
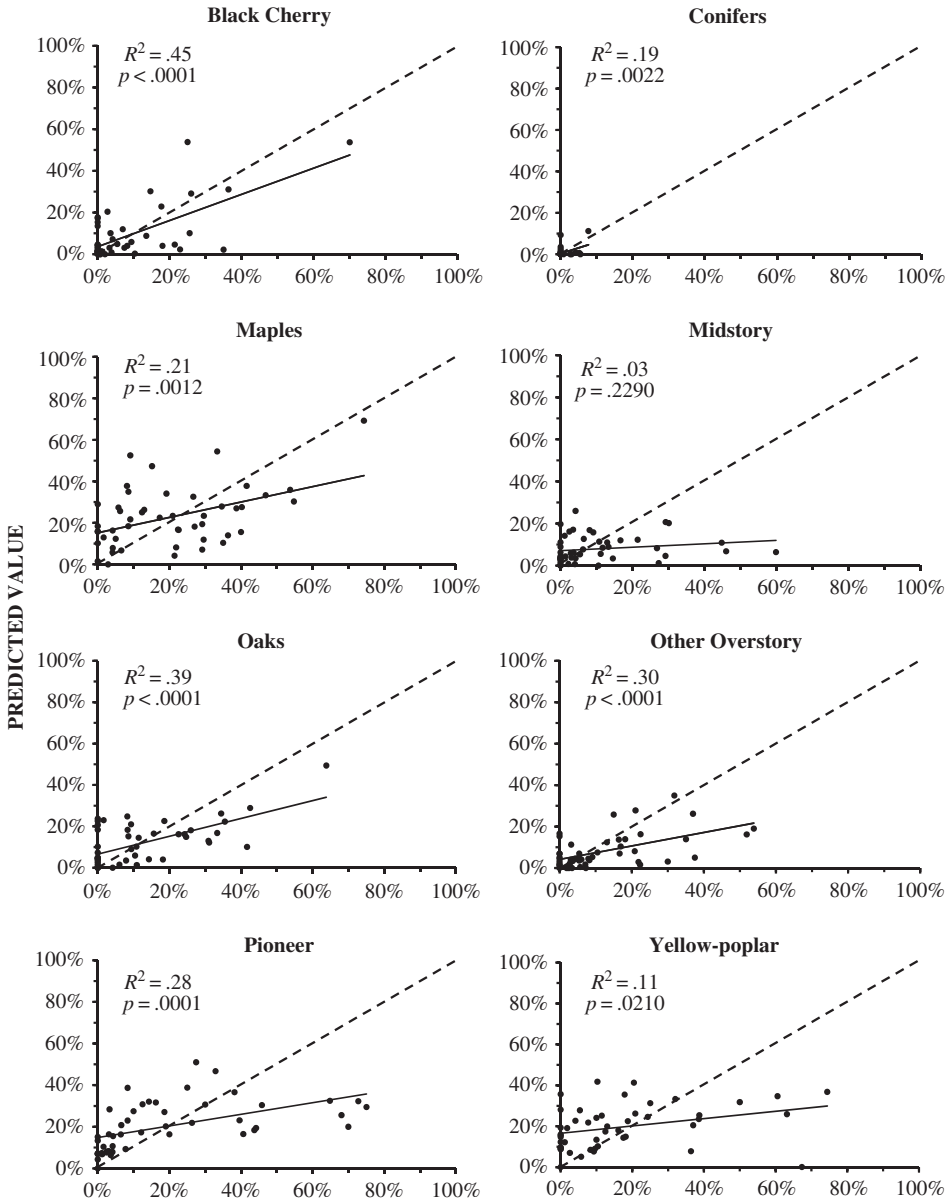
FIGURE 8 Regression analysis comparing measured and predicted values for each species group individually from paired stands in the Central Appalachians used for model calibration. Y-axis = predicted values, X-axis = measured values.

Model Validation

When the final RKBs in REGEN were applied to the 17 paired stands collected to serve as an independent validation data set, the performance of the
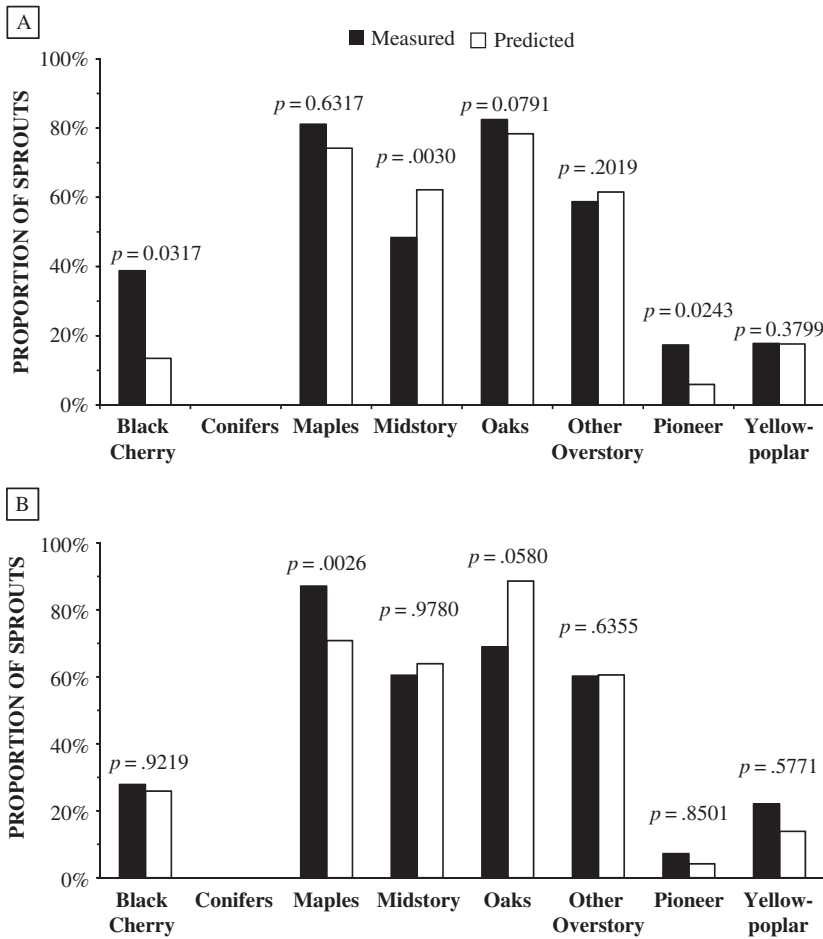
FIGURE 9 Comparison of measured and predicted stump-sprout proportion of upper canopy stems for each species group individually from regenerating clear-cut stands in the Central Appalachians. Y-axis = % of dominant and codominant stems of sprout origin. The *p* values < .1 indicate significant differences between measured and predicted samples as calculated by the Wilcoxon Signed Rank test. Graph A depicts the model calibration data set, Graph B depicts the model validation data set.

model in general was on par with its ability to explain the data used to calibrate the RKBs. Across all 17 paired stands in the validation data set, mean species composition predicted by the REGEN model was within 4 percentage points of the measured species composition for all eight species groups used in this study (Figure 2B). Mean differences between measured and predicted samples indicated that black cherry, pioneer, and yellow-poplar species groups were generally overpredicted on average. Midstory, oaks, and other overstory species groups were generally underpredicted on average. Tests for differences in sample distributions indicated that, among species groups, only the yellow-poplar measured distribution was statistically different than

its predicted distribution at an α level of .1 (Table 6). Across all 17 paired stands in the validation data set, one standard deviation of the model error for any species group was not more than about ± 20 percentage points (Figure 3B).

The overall regression of predicted versus measured species composition for the paired stands in the validation data set was highly significant (Figure 6B). The coefficient of determination indicated that REGEN predictions explained 36% ($R^2 = 0.36$) of the variation in species composition in regenerating clear-cut stands across both site classes. About 89% of the predictions were within $\pm$ 20 percentage points of their paired measured values in this data set. About 71% of the predictions were within 10 percentage points, and about half were within 5 percentage points.

The analysis of the model residuals for the validation dataset suggested that the model consistently underpredicted future species composition when a measured species group reached greater than about 30% of total stand composition (Figure 7B). In the validation data set, a species group reached this level of site occupancy in 16 instances. In eight of these instances, early successional species groups (pioneer and yellow-poplar) were responsible. The maples and oaks species groups each reached this level three times, and the other overstory and midstory groups each reached this level once. Fourteen of the total 17 stands in the validation data set contained at least one species group that comprised at least 35% of total stand composition. Two stands had two different groups to reach this level. REGEN slightly overpredicted future species composition when a measured species group made up less than about 5% of total stand composition.

Individual regression analyses for each species group in the validation data set indicated significant regressions for all groups except conifers and midstory at an α level of .1 (Figure 10). The model explained the greatest amount of variation in individual species composition in the regenerating clear-cut stands in the validation data set for oaks ($R^2 = .36$), and over 25% for two other species groups: 34% ($R^2 = .34$) for other overstory, and 26% ($R^2 = .26$) for the pioneer species group. Tests on the validation data set indicated that mean predicted distributions for proportion of winning stems of sprout origin were significantly different from measured distributions of sprout origin regeneration for only the maples and oaks species groups using $\alpha = .1$ (Figure 9B).

Although the model performed well on average, and individual predictions were often reasonable, there were considerable inconsistencies in the ability of the model to predict species composition for individual stands. Regression analyses conducted on each paired stand revealed that the amount of variation explained by the model for individual stands ranged from 0 to 98% ($R^2 = .00–.98$) in the model calibration dataset and 0 to 93% ($R^2 = .00–.93$) in the model validation data set. Further exploration into this condition did not reveal any obvious discrepancies in stand characteristics
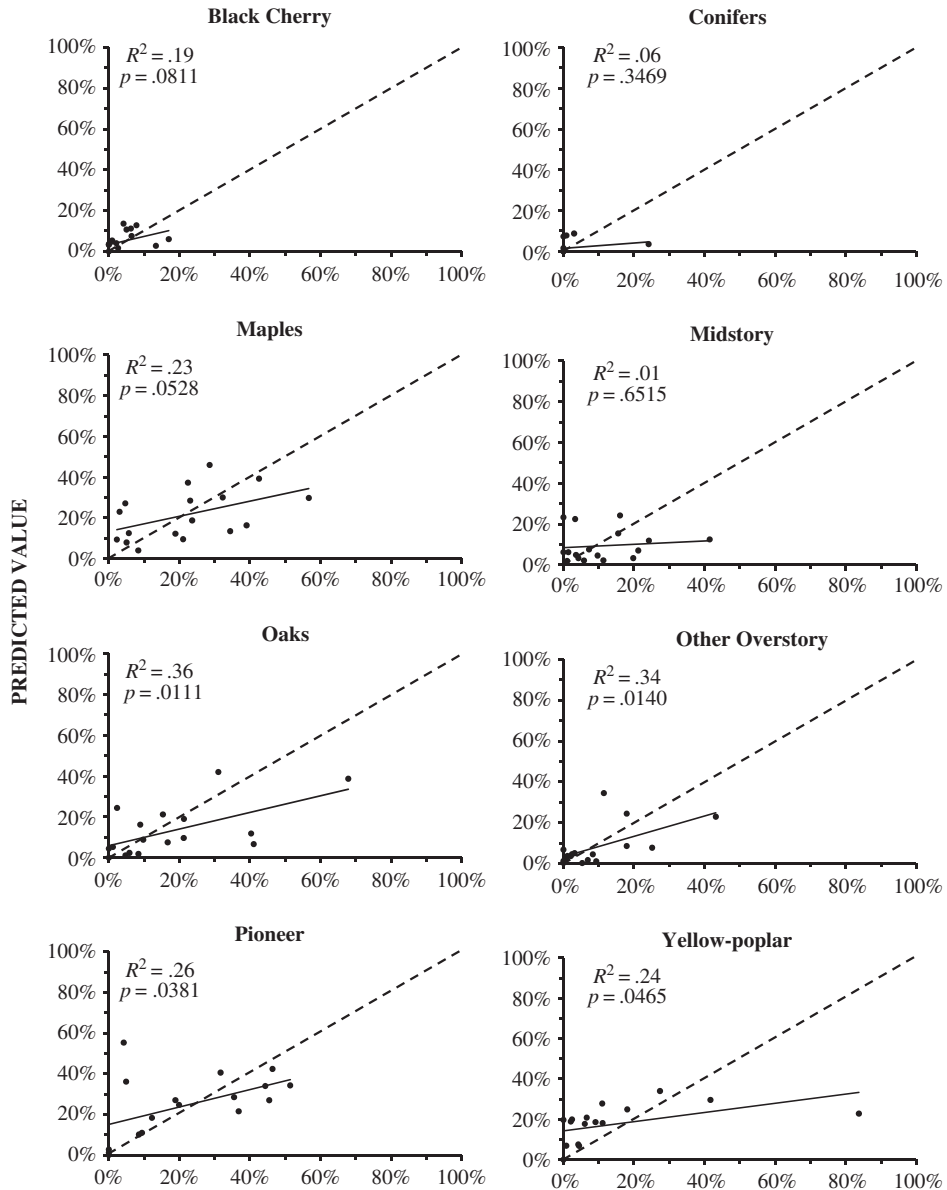
FIGURE 10 Validation regression analysis comparing measured and predicted values for each species group individually from paired stands in the Central Appalachians used for model validation. Y-axis = predicted values, X-axis = measured values.

between those stands that were predicted with at least average results (from the overall regression analysis) and those that were below average. In the mature stands, mean basal area and composition, mean overstory density and composition, mean advance reproduction density and composition, site

quality, aspect, slope, and topographic position were all seemingly of similar distribution between stands that were predicted with at least average results and those that were below average. There were also no discernible major differences found in stand age, mean density and composition, site quality, aspect, slope, or topographic position between the regenerating clear-cut stands that were predicted with at least average results and those that were below average.

DISCUSSION

Rather than solely a collection of regression equations and probabilistic parameters, REGEN is more explanatory in design. It was built on a foundation of fundamental ecological and silvicultural concepts that acknowledge certain species possess characteristics that allow them to flourish following certain disturbances (Egler, 1954). The successes of REGEN in predicting the species composition following clear-cutting was likely attributable to its design and emphasis on local competition. Unlike many models, REGEN actually attempts to model the species competition for dominance in a stand. The often made assumption that competition can be considered a uniform, constant variable is likely too broad in many cases. Regeneration and subsequent stand development is driven by local influences and microsite conditions (Oliver & Larson, 1996). During early stand development in Appalachian hardwoods, the composition of surrounding competition on a plot-sized scale likely influences the success or failure of individual stems to the greatest degree. This is evident in studies of precommercial crop-tree release (Trimble, 1974; Smith & Lamson, 1983; Heitzman & Nyland, 1991) that show increased levels of competition for site resources on some plots more than others.

Previous research on regeneration dynamics in the Appalachians on stands of similar site quality and disturbance history (Trimble, 1973; Brashears, Fajvan, & Schuler, 2004; Gould, Steiner, Finley, & McDill, 2005), along with accepted theories of stand development (Egler, 1954; Oliver & Larson, 1996) enabled the development of rankings of species competitiveness. These rankings are a qualitative approximation of the ability of a species to capture growing space following disturbance and attempt to describe competitive relationships amongst species. In a similar manner, numerical points have also been used successfully to evaluate regeneration of red oaks and green ash (*Fraxinus pennsylvanica* Marsh.) in bottomland hardwood ecosystems (Johnson, 1980; Johnson & Deen, 1993; Belli et al., 1999). The consideration of the advantages that more mature root systems typically provide to larger advance reproduction and stump-sprouts by incorporating competitive rankings for different size classes of reproduction within a species in REGEN likely increased the potential accuracy

of predictions of future species composition. The regeneration models developed for bottomland hardwoods (Johnson, 1980; Johnson & Deen, 1993; Belli et al., 1999), as well as those for upland oak by Sander et al. (1976, 1984), Steiner, Finley, Gould, Fei, and McDill, (2008), and Loftis (1990) all give a competitive advantage to larger stems of advance reproduction. These stems have greater ability to capture site resources (Larsen & Johnson, 1998), and are the most competitive forms of regeneration for a given species following harvest (Sander, 1972).

The competitive rankings and site quality delineations that were incorporated into RKBs performed surprisingly well on the model calibration data set (Figures 2A, 3A) and warranted further investigation into the adoption of REGEN as a regeneration prediction model for the Central Appalachians. That performance was subsequently confirmed on an independent validation data set (Figures 2B, Figure 3B) collected a year later. As was expected, the model did not always perform as well for the validation data set as it did for the model calibration data set (Figures 8, 10). Nonetheless, the results were encouraging due to a lack of statistical difference for all species groups except yellow-poplar (Table 6). Difficulties predicting yellow-poplar was likely due to its successful reliance on buried seed in the forest floor as a regeneration strategy which is difficult and possibly impractical to quantify. In addition, many of the paired stands were located in the northern portions of the range of yellow-poplar where it occurs more sporadically than farther south in the Appalachians. The forests in this region tend to be transitional between central, Allegheny, and northern hardwoods (Braun, 1950; Stout, 1991) and as a result, may have made it more difficult to assess REGEN competitiveness compared to other regions. Waldrop et al. (1986) also experienced difficulty modeling early successional species, particularly yellow-poplar, on the Cumberland Plateau of Tennessee. Although the results indicate that yellow-poplar was slightly overpredicted on average (Table 6), the model error graph (Figure 3) shows potential for drastic underprediction if the ranking for yellow-poplar was reduced. Any change in rank for yellow-poplar could also adversely affect the model performance for other species as well. This type of scenario was encountered numerous times during the model calibration process.

The poor results in the regression analyses for the midstory group (Figures 8, 10) was likely due to the developmental stage of the regenerating stands rather than geography. As found in Table 3, the canopy position of this species group was in a state of flux as many stems were already being relegated to lower canopy positions, which made it difficult to assign competitive rankings to those species.

Although species groups were used in analyses to simplify data presentation, REGEN provides predictions for individual species. The model performance for individual species within groups was often similar. For

example, within the maples group, the model appeared to predict the regeneration of sugar maple slightly better than red maple. On average, predictions for sugar maple were within about 1 percentage point of the measured values while red maple was within about 2 percentage points in the model calibration data set. However, depending on ecological characteristics, some individual species within a group may exhibit more variation in their predictions than others. This may be the result of differences in the magnitude of regeneration across a landscape or a greater innate variation in regeneration occurrence for a particular species. For example, one standard deviation of model error for sugar maple, which is more of a specialist in the Appalachians and is often confined to mesic environments, was typically within about ±6 percentage points in the model calibration data set. Whereas for red maple, which is more of a generalist and occurs with varied prevalence across the Appalachian landscape, one standard deviation of model error was ±17 percentage points in the model calibration data set. Species groupings were composed of species that were expected to occupy similar ecological and structural niches in a mature forest where they occur. In most cases, individual species within these groupings probably have similar commercial value as well. Even within a group such as the other overstory group, which contains a more miscellaneous assortment of species, all species should occupy similar positions in the canopy of a mature Appalachian hardwood stand when they occur and should collectively regenerate similarly to these results in spite of the variation for individual species predictions.

Other regeneration prediction models for Appalachian hardwoods have performed better than the results from REGEN in this study (Loftis, 1990; Gould et al., 2006). However, these models were focused solely on oak regeneration and were developed from more extensive, long-term data sets that target only certain components of natural regeneration. While these more narrowly focused models serve as useful tools when the primary species of interest is oak, they do not provide a complete stand assessment of regeneration species composition. In contrast, REGEN provides a broad quantitative estimate of future species composition for a stand rather than an evaluation of regeneration adequacy for an individual species or species group. Consequently, REGEN could potentially provide greater insight into future stand dynamics and how species such as oak will compete with other species during the initial portion of the stem exclusion stage (Loftis, 2004).

REGEN likely provides a more accurate portrayal of regeneration following clear-cutting across a region than for a single stand. Although this phenomenon is to be expected with any effort to apply generalized population trends to an individual, particularly given the natural variation in forest ecosystems, it is of particular interest in this line of research since managers most often prescribe silvicultural treatments to individual stands

rather than across regions. Certainly poor model performance for a single species negatively impacted predictions for other species given their proportional relationship in some cases, but that explanation more appropriately describes an outcome of poor performance for a single species rather than an underlying cause. Part of the variability found in the results of individual stand predictions could be due to the sampling approach taken and the use of paired stands. While there was no visible reason that the assumptions of this paired stand approach were unwarranted, it is likely that some preharvest stand conditions in the regenerating clear-cut stands were different than those found in the mature stands. Because the selection of sites was based on the best available knowledge of the local forest manager, factors such as drought, frost, ice, browsing, or any other stochastic events that may have impacted species composition in the regenerating clear-cut stands cannot be accounted for. Considering this, it is possible that if the development of these mature stands were to be monitored following a clear-cut harvest to the onset of stem exclusion, the performance of REGEN may prove different from the results reported from this study. For this reason, proposed silvicultural treatments based on model predictions for any given stand must always be subject to the scrutiny of an experienced forester prior to implementation.

While there is room for improvement in the accuracy of REGEN predictions, the potential to improve these RKBs without additional data is limited. For modeling purposes, long-term trials conducted across the study region would be needed. In spite of the large amount of literature detailing the effects of clear-cutting on regeneration, there are few works that follow the progress of stand development to stem exclusion and include detailed characteristics of preharvest advance reproduction. This information would likely contribute a measurable improvement to the current model. However, species that are often the most successful immediately following clear-cutting have limited reliance on advance reproduction. Therefore, the greatest potential for improvements could come from modeling efforts to establish the probability for early successional species to attain upper canopy status from seed origin reproduction. An exception to this potential for improvement would likely be red maple. Red maple can function as a pioneer species in this region, but is most often regenerated from advance reproduction (Oliver & Larson 1996). Regeneration from seed sources tend to be highly stochastic events, and modeling attempts would likely be complex and inconsistent given the transitional tendency of the forests in much of this study region. Nonetheless, empirical results from such studies often can, and should be incorporated into the REGEN model as they become available. Insights from these types of efforts may begin to provide a more quantitative estimate of the competitive relationship amongst species and explain greater amounts of the seeming stochastic variation that is observed in regeneration dynamics.

Improvements in modeling seed origin regeneration could perhaps also remedy much of the lack of sensitivity in the RKBs for species occupying greater than 30% of future species composition and improve the accuracy of yellow-poplar and pioneer predictions. A suitable explanation for the consistent underprediction of species groups occupying greater than 30% of stand composition by REGEN was not apparent. Species groups reached this level of site occupancy about a third of the time in both data sets. Although a majority of these occurrences were by early successional species that can become established from seed sources following a major disturbance, the frequency of the maples group to reach this level discounts that trend as a comprehensive explanation.

CONCLUSION

Results of this study indicate that the REGEN model can be adapted to predict regeneration of hardwood stands across the Appalachians. REGEN can be adapted quickly based on expert knowledge of local regeneration ecology and gradually improved as research becomes available. The detailed description of advance reproduction required by REGEN is likely more time-consuming in the field compared to other regeneration evaluations that utilize simpler metrics. Still, the REGEN methodology is straightforward and could likely be implemented into periodic stand evaluations with limited increases in labor, especially if an advance reproduction tally is already included in assessments of stands nearing rotation age. REGEN has the potential to be a useful tool in regeneration silviculture and should assist managers by identifying stands that may be candidates for preharvest manipulation or future ameliorative treatments necessary to meet management objectives. Further research is needed to fully realize that potential. REGEN should provide insight into regeneration trends to managers in the Central Appalachians of Virginia and West Virginia. However, any management decisions based on REGEN predictions should be subject to the judgment of an experienced forester.

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