DIFFERENCES IN OPTIMAL GROWTH EQUATIONS FOR WHITE OAK IN THE INTERIOR HIGHLANDS

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ABSTRACT.—Optimal growth equations are fundamental to many ecological simulators, but few have been critically examined. This paper reviews some of the behavior of the Potential Relative Increment (PRI) approach. Models for white oak were compared for Arkansas River Valley (ARV), Boston Mountains (BoM), Ouachita Mountains (OM), and Ozark Highlands (OH) ecological sections of the Interior Highlands. Noticeable divergence in equation shape was observed in the section and pooled models. PRI curves for the ARV and OM models predicted poor optimal growth, especially in the smallest size classes. The OH equation predicted high juvenile performance but limited large tree optima while the BoM model peaked at intermediate diameters. These distinctions may arise from differences in physiological potential between sections, or, more likely, from inadequate sample distributions. Our study supports pooling to improve optimal growth modeling if phenotypic conditions do not vary substantially.

Optimal growth equations are cornerstones of many ecological models (e.g., the gap models), but few existing designs have been thoroughly explored for their performance under different conditions. Without an understanding of how these equations will respond to different sampling conditions, size class distributions, or error structures, it is difficult to evaluate their quality. Recent critiques (e.g., Moore 1989, Zeide 1993, Vanclay 1994, Bragg 2001) have identified problems with some of the most commonly utilized potential growth models.

The Potential Relative Increment (PRI) approach to optimal growth modeling (Bragg 2001) has received some evaluation for behavior related to the derivation process (Bragg 2002), but there may be other fundamental issues associated with local or regional conditions that may affect this approach. Thus, using white oak (*Quercus alba* L.) as an example, this paper reviews additional PRI behavior as a function of ecological section and sample size.

STUDY AREA

The Interior Highlands of Arkansas, Missouri, and Oklahoma can be subdivided into four geographically and ecologically distinct sections (fig. 1). The northernmost section is the Ozark Highlands, which extends from south-central Missouri to northwestern Arkansas and northeastern Oklahoma. The Ozark Highlands grade into the Boston Mountains in eastern Oklahoma and west-central Arkansas. Uplifted, highly dissected limestone plateaus and deep, narrow river valleys dominate both of these sections. The Arkansas River Valley lies to the south of the Boston Mountains in central Arkansas and extends into eastern Oklahoma following the floodplain of the Arkansas River and the lower reaches of its tributaries. The southernmost section of the Interior Highlands is the Ouachita Mountains, a folded and faulted uplift of sedimentary origin characterized by east-west running ridges extending from central Arkansas to southeastern Oklahoma.

The Interior Highlands encompasses two primary ecological provinces (the Ozark Broadleaf Forest-Meadow and the Ouachita Mixed Forest-Meadow). Differences in parent materials, aspect, climate, and disturbance history have produced a mosaic of vegetation types across the study region. Presettlement vegetation

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differed markedly from one section to the next. The Ouachita Mountains were dominated by shortleaf pine (*Pinus echinata* Mill.), oak-pine, and oak-hickory communities, while the Arkansas River Valley ranged from oak-hickory or oak-pine forests on the well-drained sites to bottomland hardwoods. The Boston Mountains and Ozark Highlands were dominated by open woodlands interspersed with oak, shortleaf pine, and other hardwood cover types in sheltered coves and cedar glades on calcareous sites (Pell 1983). Many of these patterns have changed in the decades since Euroamerican settlement, with large areas cleared for agriculture, housing, industry, and mining or converted to other cover types through forest management.

PRI METHODOLOGY

The PRI methodology (Bragg 2001) involves the extraction of live tree records (those with positive growth) from the Eastwide Forest Inventory Data Base (EFIDB) (Hansen and others 1992), the selection of individuals growing at the highest rate within predetermined size classes (D_{MAX}), and the fitting of non-linear ordinary least squares regression equations to the final data using the following model form:

$$PRI = b_1 D_{MAX}^{b_2} b_3^{D_{MAX}}$$

where b_1, b_2, and b_3 are species-specific coefficients representing small tree growth potential, growth expansion factor, and the increment constraint factor, respectively. The software for this methodology is available from the primary author, and can be used for most species and state EFIDB inventories in the United States.

PRI equations for white oak in the Interior Highlands were derived to compare differences in behavior between the models for the Arkansas River Valley (ARV), Boston Mountains (BoM), Ouachita Mountains (OM), and Ozark Highlands (OH) ecological sections. White oak was chosen because of its abundance and commercial importance across the study region. Since the data in the EFIDB are presented by state or county and ecological sections were delineated without regard to these political boundaries, it was necessary to associate EFIDB plots with the appropriate ecological section. This was accomplished by translating plot locations to approximate section boundaries on a map and assigning plots to a section. For the few plots that were close to a boundary, current vegetation was used to help assign ecological section membership. Once sections were assigned, output files containing only the relevant plots were produced and then processed with the PRI methodology. A pooled model containing white oak data from across all sections was also fit for additional comparison.

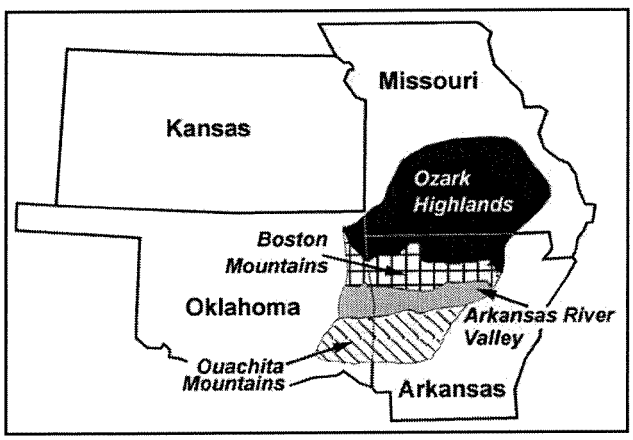

Figure 1.—*Map of the Interior Highlands, including section delineations.*

RESULTS

The ARV section contributed the fewest white oaks for PRI derivation (n = 384) compared to the other sections (fig. 2). All other sections yielded at least 1,600 individuals, with a total of 8,555 trees chosen across the Interior Highlands. Further consideration finds that not only are the samples unevenly distributed between the sections, their distributions are inconsistent within each section. Most small trees (< 15 cm diameter at breast height (d.b.h.)) and large

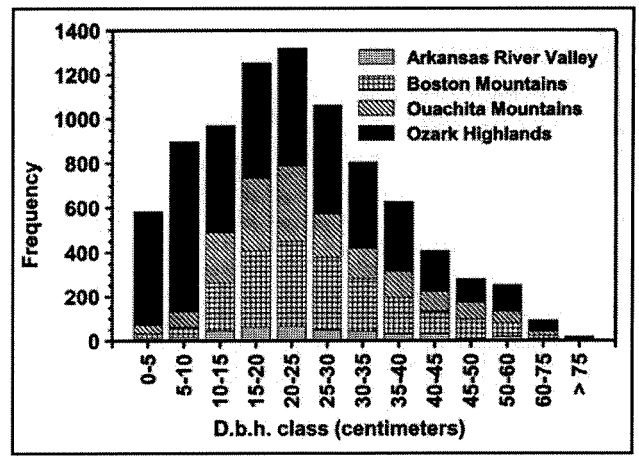

Figure 2.—*White oak sample distribution across the Interior Highlands by ecological section. Notice how trees taken from the Ozark Highlands sample dominated the smallest (< 10 cm d.b.h.) and largest (> 60 cm d.b.h.) classes, while the agriculture-dominated Arkansas River Valley contributed few individuals to any size class. Very few large trees were available, regardless of section.*

trees (> 50 cm d.b.h.) in the total sample were from the OH section, while the BoM and OM sections contributed primarily to intermediate diameters. The limited sample of the ARV section produced few representatives in any size class (especially the largest).

While there were few differences in minimum (all > 2.8 cm) and average white oak diameter (range = 21.5 to 26.8 cm) by section, considerable variation in maximum tree size was apparent (table 1). The biggest white oak by for the OM section was 74.2 cm d.b.h., compared to 85.3 cm for the ARV section, 93.7 cm in the BoM section, and 100.8 cm in the OH section.

Regression Models

Table 2 contains the fitted regression coefficients and measures of quality of model fit for each ecological section and the pooled model. The coefficients in table 2 can be roughly interpreted for their impacts on PRI models (Bragg 2001). High b_1 values suggest rapid growth in small diameter trees, which appears for both the OH and pooled models (fig. 3).

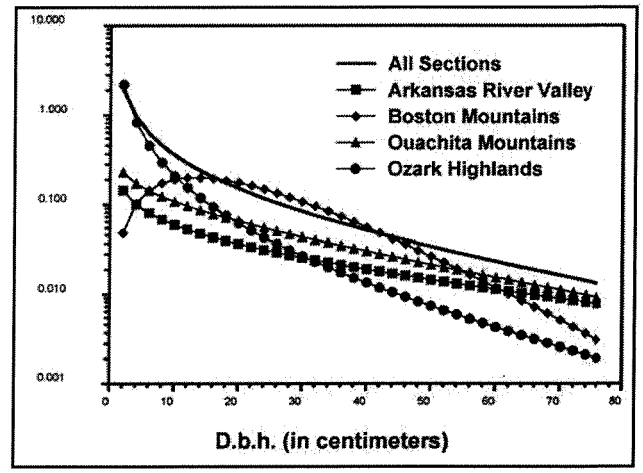

Figure 3.—*Potential Relative Increment (PRI) curves for white oak in the Interior Highlands ecoregion by ecological section and the pooled model. Note that the pooled model (solid line only) is a composite of all the section models, so its elevated performance reflects the fastest growing individual for the entire Interior Highlands.*

Table 1.—*Basic statistics on the sampled white oaks by ecological section*

Section (model abbreviation)	n	Minimum d.b.h.	Average d.b.h.	Maximum d.b.h.	Standard deviation
			cm		
Arkansas River Valley (ARV)	384	2.8	26.5	85.3	13.4
Boston Mountains (BoM)	2,012	3.0	26.8	93.7	11.7
Ouachita Mountains (OM)	1,678	2.8	25.1	74.2	12.4
Ozark Highlands (OH)	4,481	2.8	21.5	100.8	14.6
ALL SECTIONS (pooled)	8,555	2.8	23.7	100.8	13.7

Table 2.—*Regression coefficients by section*

Model	b_1	b_2	b_3	Final n[1]
OM	0.306556	-0.337021	0.973593	8
ARV	0.204727	-0.466773	0.983802	12
BoM	0.022778	1.381223	0.900305	10
OH	5.759565	-1.308236	0.969745	15
Pooled	3.817014	-0.935898	0.979100	10

[1] Final number of points used to fit optimal PRI curves.

The inconsistent nature of b_2 values translates into different curve shapes (table 2). Note how the BoM model (positive $b_2 > 1$) shows modality even in the PRI curves. This trend is further exaggerated when potential increment is calculated (fig. 4), resulting in the BoM model having the lowest potential increment at the smallest d.b.h. class but outperforming all other models from 17 to 42 cm d.b.h.

The OM and ARV models also displayed relatively high (though still negative) b_2 values, causing them to have slight modality in potential increment (fig. 4). The low negative b_2 values of the OH and pooled models limited the response of these equations, thus producing more of an exponential decline with increasing diameter. The PRI methodology requires that the b_3 be < 1, (b_3 values almost always exceed 0.90), since this parameter constrains diameter increment with increasing tree size. For example, the BoM model had a noticeably lower b_3 value, and displayed a greater reduction after its peak was reached.

Noticeable divergence in curve shape was observed between individual sections. Two of the models (ARV and OM) predicted poor optimal growth performance across the range of diameters considered, especially for the smallest size classes (fig. 4). This resulted in these models predicting annual optimal white oak increment of 0.5 to 1.0 cm, which is considerably lower performance than would be expected.

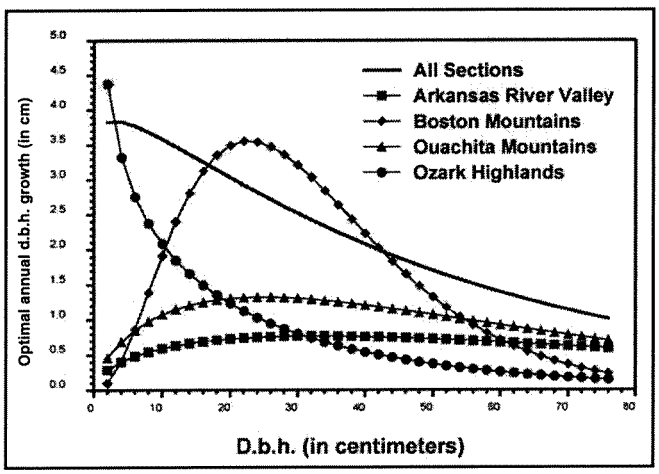

Figure 4.—*Multiplying the curves in figure 3 by their current d.b.h. yields predicted optimal annual d.b.h. growth for Interior Highland white oak. The pooled model, while generally outperforming other section models for optimal increment, was not always the highest performer.*

The OH model predicted high juvenile optimal growth (over 4 cm annually at the smallest diameters) but limited large tree performance (falling to the smallest potential increment of all models for trees 30 cm d.b.h. and larger). The BoM model peaked at intermediate sizes, with the lowest potential increment at the smallest diameters and the highest of all models from 17 to 42 cm d.b.h., followed by a decline to slow growth in big trees (fig. 4). The pooled model generally balanced all performance trends by utilizing the fastest growing individuals regardless of section. Thus, the local peaks experienced in OH and BoM models are attenuated by limited performance of other parts of the sample range.

DISCUSSION

The dissimilarity in optimal growth models by section may arise from several possible factors. One hypothesis suggests that there are innate differences between the physiological optimal growth performance of white oak growing in the ecological sections. These differences may be related to geography and topography, which could influence PRI analysis. For example, the proportion of oak or oak-pine forest types varies from 90 percent in the OH and BoM sections to 70 percent in the ARV section and 50 percent in the OM section (Guldin and others 1999).

In the OM section, white oak is more likely to occur on mesic north slopes, and thus may be found disproportionately on sites with less severe soil moisture deficits and appreciably higher productivity. Similarly, site quality increases as one goes from north to south across the Interior Highlands; thus, the better sites found in the ARV and OM sections may support oaks with inherently better growth. Management history could affect white oak growth performance. White oak was extensively cut for lumber and cooperage around the turn of the 20th Century, and the contemporary Interior Highland forests are largely a reflection of the genotypes found after these stands were high-graded. If there are inconsistencies in the age and genetics of the residual white oak timber, this could translate into the differential PRI response of this species across the ecological sections.

Another explanation of the observed disparity in optimal growth performance may be found in the differences in sample distribution. The histogram of section representation by size class (fig. 2) shows that very few small or large white oaks were sampled outside of the OH section. Therefore, the OH model dominates the

extremes of growth performance. Similarly, most intermediate size classes were dominated by the performance of the BoM section. The differential performance by section may arise from these incomplete diameter distributions. Since portions of the Interior Highland landscape have experienced shifting management and disturbance regimes, especially during the last 150 years, it is not surprising that the forests of each ecoregion have reached different developmental stages and thus would contribute differently to a regional PRI model.

The scarcity of white oaks in the largest (> 60 cm d.b.h.) size classes is typical of the maturing forests of the region, but under the PRI methodology this also means that the limited data exceeding this threshold have considerable influence on the final optimal growth models. In the original exploration of the PRI methodology, Bragg (2001) suggested that while the magnitude of error appeared highest in the intermediate size classes, the greatest potential for uncertainty lay in the biggest size classes because so few observations are found in that range.

The current age of the forests of the Interior Highlands is an unavoidable limitation on extending regional PRI models to include white oaks beyond 100 cm d.b.h. Additional flexibility may be possible if white oak from other ecoregions are incorporated, given that the phenotypic similarity between ecoregions would be acceptable (obviously different conditions should not be included if model integrity and robustness are to be preserved).

As can be seen in the pooled model, aggregating similar ecological sections provides some benefits when developing PRI models. The larger sample size ensures that fewer errors resulting from undersampled diameter classes occur in addition to supplementing the measured growth response in all classes. In this particular study, a pooled model allowed for the extension of the maximum d.b.h. from 74.2 cm if only the OM section were sampled to 100.8 cm if all sections of the Interior Highlands were included.

Broadly derived PRI models also improve regional predictability by expanding the range of sampling conditions. If adequately sampled, local (e.g., section- or compartment-based) optimal growth models can prove more accurate, but may be too site specific for regional application (Bragg 2001, 2002). A pooled model makes it theoretically possible to simulate growth performance from a dry southern or western facing slope in the Ouachita Mountains to the moist terraces along the Arkansas River or the sheltered cove forests of the Ozark Highlands.

CONCLUSIONS

Marked differences arose in white oak PRI growth models when a large ecoregion (the Interior Highlands of Arkansas, Oklahoma, and Missouri) was subdivided into four broad sections based on obvious ecological and geographic features. While it is probable that at least some of this variation may arise from genetic controls on individual trees or via section-based differences in the developmental dynamics of white oak, most of the inconsistencies can be attributed to varied sample distributions among sections. Poor representation of some (or all) size classes contributed to the widely different response curves.

This study supported pooling of regional inventory data to improve optimal growth modeling if environmental and genetics do not differ dramatically. By supplementing size classes and ameliorating local peaks (or valleys) in response curves, regional PRI fitting allows for a model capable of application across a broader range of size classes and environmental conditions.

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