

biometrics

Evaluating Forest Vegetation Simulator Performance for Trees in Multiaged Ponderosa Pine Stands, Black Hills, USA

Seth A. Ex and Frederick W. Smith

Increasing emphasis on ecological objectives such as biodiversity in forestry has precipitated interest in multiaged silvicultural methods that create and maintain more complex stand structures than simpler even-aged methods. Foresters often use the Forest Vegetation Simulator (FVS) growth model to compare competing silvicultural alternatives, which can include multiaged structures. For models such as FVS to be useful for this task, they must realistically simulate structural dynamics in multiaged stands. We evaluated FVS performance for trees in even-aged and multiaged stands of ponderosa pine (*Pinus ponderosa* C. Lawson var. *scopulorum* Engelm.) in the Black Hills, USA, by comparing FVS predictions of dbh increment to measurements from increment cores. Dbh change is the primary element of tree growth estimated by the regional FVS variant used in the Black Hills and is the basis for all other aspects of tree growth. We found that the dbh growth model used by FVS was more biased and less accurate for trees in multiaged stands than for trees in even-aged stands and that residual error varied systematically with tree size class in multiaged stands, which could affect stand dynamics simulation. Performance improved for trees in multiaged stands when predictions were adjusted with a model that included crown ratio (CR), which is related to photosynthetic capacity and tree growth. A CR-based adjustment did not improve model predictions for trees in even-aged stands, presumably because CR was less variable than in multiaged stands and because stand structures were more similar to those used for model development. This study illustrates the potential for empirical forest growth models such as FVS to behave in unexpected ways when they are used for stands and trees that are dissimilar from those used for model development. It also highlights the importance of continued model testing because growth models are increasingly used to develop silvicultural alternatives for structurally complex stands.

Keywords: Central Rockies Variant, uneven-aged, model evaluation, GENGYM, multistoried

Forests are increasingly managed for diverse suites of objectives such as wildlife habitat, water quality, and aesthetics, in addition to wood production. Foresters often use multiaged silvicultural methods to accommodate multiple objectives because structurally complex stands are typically better suited to meet multiple objectives than simpler even-aged structures (Maguire 2005). Forest growth models such as the Forest Vegetation Simulator (FVS; Crookston and Dixon 2005) can be used to design and evaluate silvicultural alternatives that encompass a variety of stand structures. For growth models to be useful in this capacity, they must perform satisfactorily for both even-aged and multiaged structures. It is particularly important that growth is not systematically over- or underestimated for different size classes of trees in multiaged stands, because this would preclude realistic stand dynamics simulation. In the FVS Central Rockies Variant (FVS-CR), predicted change in

dbh (breast height = 1.37 m) over time is the primary element of tree growth estimated by the growth model (Keyser and Dixon 2008). Other aspects of tree growth are derived from dbh increment. FVS “grows” trees in ponderosa pine (*Pinus ponderosa* C. Lawson var. *scopulorum* Engelm.) stands in the Black Hills of South Dakota and Wyoming, USA, using separate dbh prediction procedures for even-aged and multiaged stands (Keyser and Dixon 2008). This has the effect of reducing dbh estimates for small size classes of trees in multiaged stands compared with similar trees in even-aged stands. It makes intuitive sense that small size classes of trees in multiaged stands grow slowly relative to their larger neighbors, because they face overhead light competition. However, it does not necessarily follow that FVS overestimates dbh for these trees, thus necessitating a growth reduction procedure. The growth model used by FVS-CR relies on variables that index potential acquisition and

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Affiliations: Seth A. Ex (seth.ex.442@gmail.com), Colorado State University, Department of Forest and Rangeland Stewardship, Fort Collins, CO. Frederick W. Smith (frederick.w.smith@colostate.edu), Colorado State University, Department of Forest and Rangeland Stewardship.

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allocation of resources (measures of tree size) and competition from other trees (measures of stand density; Keyser and Dixon 2008); it may perform well without adjustment if these variables adequately represent the forces driving stand dynamics in multiaged stands. In this work, we assess FVS-CR dbh estimation performance for trees in multiaged stands and then offer a biologically defensible explanation for observed patterns in residual error with respect to tree size.

FVS is descended from the Prognosis Model for Stand Development (Stage 1973), which was originally developed for mixed-conifer forests in the interior northwestern United States. Prognosis was adopted as a national forest growth-and-yield model platform in the early 1980s and later renamed FVS (Crookston and Dixon 2005). There are numerous regional FVS variants, most of which estimate tree growth using the Prognosis basal area (stem cross-sectional area at breast height) growth model (Stage 1973). However, some variants incorporate alternative growth models into the FVS framework. FVS uses separate growth estimation approaches for large and small trees. Trees are classified as large or small using a predefined dbh threshold (Dixon 2002). All aspects of large tree growth estimation are driven by predicted basal area increment, whereas small tree growth estimation is driven by predicted height increment (Crookston and Dixon 2005).

In FVS-CR, the first step in estimating large tree growth for most species is to predict future dbh using a version of the GENeralized Growth and Yield Model (GENGYM) (Edminster et al. 1991), originally developed for southwestern mixed-conifer stands. Basal area is then calculated from predicted dbh for use in successive growth routines in the FVS framework (Keyser and Dixon 2008). GENGYM model coefficients are specific to species and locality. One of several versions of the GENGYM model used by FVS-CR is tailored to Black Hills ponderosa pine. However, under certain conditions, FVS reduces growth estimates for small size classes of large trees in multiaged Black Hills ponderosa pine stands by predicting dbh using either a version of the GENGYM model tailored to southwest ponderosa pine or as a weighted average of Black Hills and southwest model predictions (Keyser and Dixon 2008).

One potentially important characteristic of the GENGYM model with respect to its performance in multiaged stands is the absence of a parameter accounting for crown size (i.e., foliage area) of trees. Upper canopy tree density in multiaged stands is typically low compared with that of comparably stocked even-aged stands, which allows more light to penetrate to small trees, presumably letting them maintain more foliage area than they would under deeper shade (Oliver and Larson 1996, p. 293). Dbh increment growth is inherently related to foliage area because foliage area is fundamentally related to photosynthetic capacity and thus stemwood production (Maguire and Bennett 1996). One index of foliage area commonly used in growth models is crown ratio (CR), calculated as the vertical live crown length of a tree divided by total tree height. Data for CR calculation are relatively easy to obtain during inventory, and CR is regarded as an integrative measure of tree vigor and stand management history (Wykoff 1990). Evaluations of tree growth models have shown that CR can be an influential variable in diameter growth prediction models (e.g., Lessard et al. 2001, Leites et al. 2009).

Our primary objective in this work was to evaluate the performance of FVS-CR in predicting future dbh for different size classes of trees in multiaged Black Hills ponderosa pine stands. To this end, we compared predicted dbh increment from FVS with measured values from increment cores. Close correspondence between pre-

dicted and measured values for all size classes of trees would suggest that the model adequately represents the forces driving stand dynamics in multiaged stands. Conversely, unequal performance for different size classes of trees could indicate the influence of important variables missing from the model. We used scatterplots of residual error to identify biologically relevant variables that potentially affected model performance. This procedure, along with the absence of a foliage area term in the GENGYM model, led us to conduct a post hoc analysis, for which we developed a CR-based model to adjust dbh predictions for trees in multiaged stands.

Methods

Study Area

The Black Hills comprise uniquely rugged terrain within the predominantly flat topography of the American Great Plains. These small mountains formed several million years ago when underlying granite was forced upward through sedimentary rock, creating a landscape composed variously of limestone, shale, sandstone, sandy clay, siltstone, dolomite, and granite, among other substrates (Hoffman 1986). Winter temperatures in the Black Hills are typically freezing, whereas summers are warm (Shepperd and Battaglia 2002). Most precipitation falls during the growing season as rain and on average exceeds 50 cm annually (Shepperd and Battaglia 2002). About one-third of the Black Hills is administered by the Black Hills National Forest (BHNF), which covers approximately 5,000 km² (DeBlander 2002). Of the 92% of the BHNF that is forested, 85% is primarily ponderosa pine, whereas the remainder consists of white spruce (*Picea glauca* [Moench] Voss), quaking aspen (*Populus tremuloides* Michx.), paper birch (*Betula papyrifera* Marsh), and burr oak (*Quercus macrocarpa* Michx.) (DeBlander 2002). Many decades of management for commercial timber production have simplified ponderosa pine stand structures in much of the BHNF (Brown and Cook 2006). Consequently, stands with more than two canopy strata are now uncommon, although pre-settlement stand structures varied widely (Brown and Cook 2006). The BHNF is currently managed for myriad competing priorities, including biological diversity (USDA Forest Service 2005). This has generated interest in multiaged silvicultural methods that not only are compatible with commercial timber harvesting but also enhance biological diversity by creating structural complexity.

Sampling Protocol

We collected data used in this work from 1,483 trees in 21 multiaged stands and 325 trees in 10 even-aged stands of pure ponderosa pine located in the BHNF. Data were initially collected for a study of wood production efficiency of different size classes of trees in multiaged stands (S.A. Ex and F.W. Smith, *For. Sci.*, in review, 2013). Because there are currently few examples of managed multiaged stands in the BHNF, we sought out discrete areas in managed stands (hereafter “multiaged stands”) for which structural characteristics that might be created intentionally using multiaged silvicultural methods had developed accidentally (e.g., after advance regeneration was allowed to mature beneath a two-storied canopy). All multiaged stands met the following criteria: fully stocked (basal area >13.77 m² ha⁻¹ [>60 feet² acre⁻¹]); no evidence of fire, disease, or timber harvest within the previous 20 years; and trees in three discrete canopy strata, with at least as many trees ha⁻¹ in the smallest stratum as in the largest, and pure ponderosa pine. Isolated paper birch and white spruce were present in a few stands, but at

Table 1. Summary data.

	Stands	Mean <i>n</i>	SDI	TPH	QMD (cm)	Mean age (yr)	SI (m)
Stand structure							
Even-aged	10 (317)	32 (28, 44)	549 (329, 823)	595 (170, 900)	26.3 (17.1, 41.2)	91 (54, 128)	16.6 (13.4, 20.4)
Multiaged	21 (1483)	71 (49, 96)	422 (262, 600)	NA	NA	NA	19.4 (16.5, 25.0)
Size class							
Small	21 (619)	29 (15, 45)	90 (27, 162)	222 (60, 410)	14.4 (12.3, 18.0)	37 (20, 60)	NA
Medium	21 (559)	27 (13, 42)	163 (74, 335)	140 (52, 400)	28.4 (22.6, 32.1)	81 (59, 126)	NA
Large	21 (305)	15 (10, 23)	164 (85, 332)	56 (26, 95)	49.4 (42.8, 57.8)	148 (86, 285)	NA

Size classes correspond to canopy strata in multiaged stands (i.e., trees in the large size class were in the uppermost canopy stratum in their stand, and so on). For the stands column, the total number of sampled trees follows the number of sampled stands in parentheses. For all other columns, mean values are followed by minimums and maximums in parentheses. Mean *n* is average number of trees sampled in each stand or size class within a stand. SDI is average metric stand density index, TPH is average trees ha⁻¹, QMD is average quadratic mean diameter (cm), mean age is average breast height age (yr), and SI is average base age 100 site index. Summary statistics are omitted where they are not meaningful for multiaged stands or size classes within stands (NA).

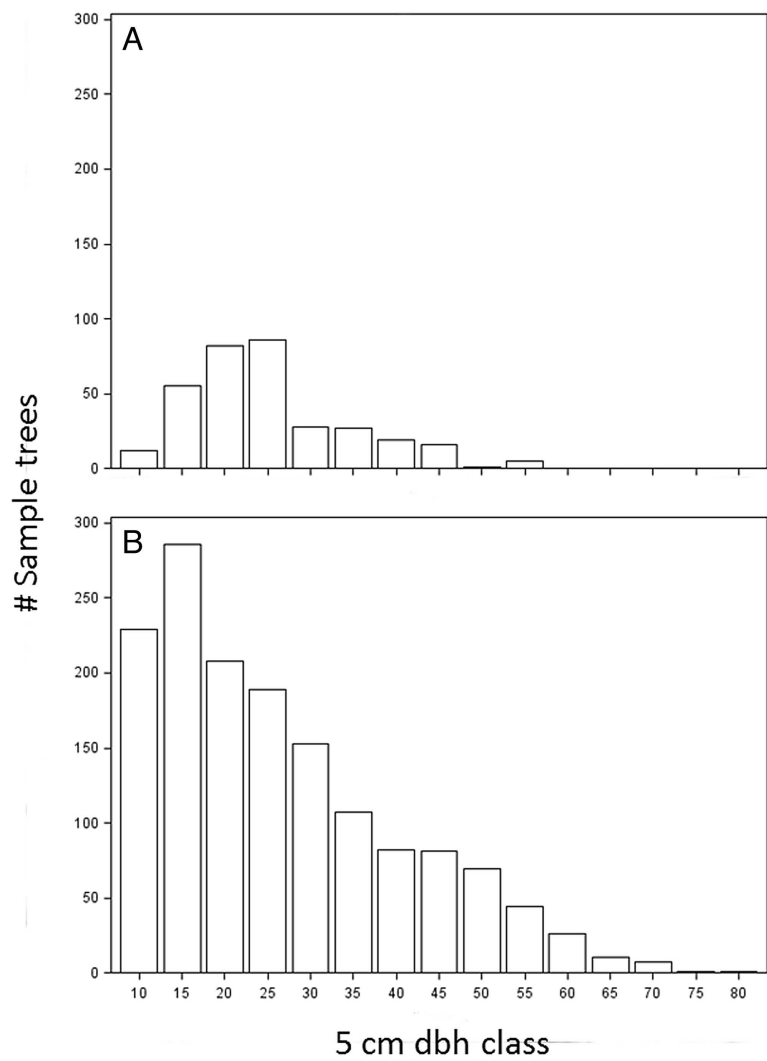


Figure 1. Histogram of sample trees for even-aged (A) and multiaged (B) stands. Trees are grouped by dbh into 5-cm size classes for display.

least 95% of sample trees in each stand were ponderosa pine. Multiaged stands were invariably three-storied, with a good representation of trees in all canopy strata (Table 1) and were generally ~1 ha in size. Given the management history of the area, we assumed that discrete canopy strata represented cohorts that regenerated after thinning. We also sampled even-aged stands across a range of average tree sizes and ages to facilitate comparison with multiaged stands that had trees of varying size and age (Figure 1). Even-aged stands

had only one canopy stratum but otherwise met all criteria used for multiaged stand selection.

Our field methodology was designed to sample a relatively large number of trees from each canopy stratum in multiaged stands. In each stand, we attempted to measure approximately 10 trees from the uppermost stratum and approximately 30 trees from each lower stratum using a single set of nested, circular fixed-radius plots with a common center point. Plot centers were subjectively chosen to

sample the dominant stand structure. Plots in nested sets were sized individually to capture the target number of sample trees in each stratum. We sampled fewer trees in the large size class than in other classes because trees were widely spaced; larger samples would have necessitated unfeasibly large plots. Because all multiaged stands were three-storied, trees in each stand were sampled with a set of three nested plots. Plots ranged from 0.08 to 0.50 ha in size, and combinations of plot sizes were generally different for each stand. We assigned trees to plots using the observed dbh range of trees in each stratum to define dbh boundaries between “small,” “medium,” and “large” size classes of trees, where size classes corresponded to canopy strata. In even-aged stands, we used a single circular fixed-radius plot sized to sample approximately 30 trees. We did not measure trees <10 cm dbh. Four sample trees in each of two even-aged stands of much larger trees were advance regeneration that barely exceeded the 10-cm dbh cutoff and were clearly not part of the main canopy. These eight trees were excluded from analysis.

We collected increment cores and measured dbh, tree height, and crown base height for all ponderosa pine trees in our plots. We defined crown base as the base of the compacted live crown as described in Keyser and Smith (2010). One breast height increment core was collected from each tree. When trees leaned or grew on appreciable slopes, cores were collected perpendicular to lean or slope. A subset of trees was cored to the pith to determine mean tree age for even-aged stands and size classes of trees within multiaged stands (Table 1). We multiplied number of sample trees by the inverse of fixed plot size to calculate trees ha^{-1} in each size class in multiaged stands and total trees ha^{-1} in even-aged stands (Table 1). We also calculated the metric stand density index (SDI) for each size class in multiaged stands and total SDI for even-aged stands (Table 1). SDI calculation is described in Ex and Smith (2013). Base age 100 site index (m; Hann 1975) was obtained for each stand from USDA Forest Service inventory data (B. Cook, pers. comm., USDA Forest Service, May 11, 2011; Table 1). Finally, we calculated CR for each sample tree to permit comparison of mean values across size classes and stand structures.

GENGYM Model

We evaluated GENGYM model performance by comparing model predictions for our sample trees with the 5-year dbh increment obtained from increment cores. Input dbh for the GENGYM model was obtained by backdating 2010 dbh to 2005 as described by Wykoff et al. (1982) using model 1

$$\text{dbh}_{i,t-5} = \text{dbh}_{i,t} - 1.128 (\text{inc})$$

where $\text{dbh}_{i,t}$ is dbh of the i th tree at time t , $\text{dbh}_{i,t-5}$ is estimated dbh of the i th tree at time $t - 5$ years, inc is the 5-year dbh increment for the i th tree, and the estimated parameter is from the literature. We used the 5-year increment spanning 2004–2009 because 2010 rings were not completely formed at sampling. The GENGYM model is model 2

$$\begin{aligned} \text{dbh}_{i,t+10} = & \beta_0 + \beta_1 (\text{dbh}_{i,t}) + \beta_2 (\text{SI}) + \beta_3 (\ln(\text{dbh}_{i,t}))^2 \\ & - \beta_4 \left(\frac{\text{bau}}{\text{bat}} \right) - \beta_5 (\ln(\text{bat})) \end{aligned}$$

where $\text{dbh}_{i,t}$ is dbh (in.) of the i th tree at time t , $\text{dbh}_{i,t+10}$ is predicted dbh (in.) of the i th tree at time $t + 10$ years, SI is site index (ft), bau is basal area (ft^2) in larger diameter classes, bat is total stand

basal area (ft^2), and the β s are estimated parameters (Keyser and Dixon 2008). FVS-CR uses different versions of model 2, with unique parameter values, for ponderosa pine in the Black Hills (hereafter the BH model) and the southwest United States (hereafter the SW model). Parameter values can be found in Keyser and Dixon (2008). Under some circumstances, FVS-CR uses the SW model for small trees in multiaged Black Hills stands (see below).

To permit comparison of model predictions with available measurements of 5-year dbh increment, we first converted the estimated 10-year dbh increment from the BH and SW models to basal area increment, halved the basal area increment, and then converted back to dbh increment. This procedure yielded a better estimate of the 5-year dbh increment than simply halving the 10-year dbh increment because basal area increment is more linear over time than dbh increment (Wykoff 1990).

We evaluated BH model performance for even-aged and multiaged stands and for individual size classes of trees in multiaged stands by assessing average bias and accuracy (Walther and Moore 2005) using measured dbh increment as a “true” reference value. We used scatterplots to identify trends in residual error with respect to tree size. Bias (systematic error [SE]) was calculated using Equation 1

$$\text{SE} = \frac{1}{n} \left(\sum_{i=1}^n (\text{dbh}_i - \text{dbh}_i) \right) \quad (1)$$

where dbh_i is the observed dbh of the i th tree, dbh_i is the expected dbh of the i th tree, and i ranges from 1 to n where n is number of observations. Accuracy (root mean square error [RMSE]) was calculated using Equation 2

$$\text{RMSE} = \sqrt{\frac{1}{n} \left(\sum_{i=1}^n (\text{dbh}_i - \text{dbh}_i)^2 \right)} \quad (2)$$

We also used scatterplots of residual error (cm, $\text{dbh}_i - \text{dbh}_i$) over relative tree size (within-stand percentile dbh) to identify patterns in error distribution that could potentially affect stand dynamics simulation by systematically over- or underestimating growth for different size classes of trees. We used relative instead of absolute tree size to avoid confounding tree size with stand-level factors such as SI and SDI.

FVS-CR in Multiaged Stands

To assess the effect of predicting future dbh for some trees in multiaged stands using the SW model or a weighted average of predictions from the BH and SW models, as is the current procedure in FVS, we first determined which trees in our data set would be affected using methods described in Keyser and Dixon (2008), applied the appropriate model for each tree, and then evaluated performance using the procedure described above for the BH model. Three criteria must be met for an individual tree to qualify for an alternative dbh prediction procedure: first, the stand must be uneven-aged (defined as age of 95th percentile tree – age of 5th percentile tree >40 years); second, the tree must be overtopped (defined as $\text{bau} \geq 30\%$ of bat); and third, $\text{dbh}_{i,t+10}$ from the BH model > $\text{dbh}_{i,t+10}$ from the SW model. If all three conditions are met and $\text{bau} \geq 30\%$ of bat but $\text{bau} < 50\%$ of bat, a weighted average of predictions from the BH and SW models is used. If all conditions

Table 2. AIC values used to compare models for adjusting GENGYM dbh predictions.

Structure	Model 4	Model 5	Model 6
Even-aged	435.8	437.7	436.8
Multiaged	3579.8	3411.9	3408.5

are met and trees are severely overtopped (bau $\geq 50\%$ of bat), the SW model is used (Keyser and Dixon 2008).

CR-Based Adjustment for Multiaged Stands

After evaluating predictions of future dbh from different versions of the GENGYM model, we conducted a post hoc analysis of CR as a basis for model adjustment in multiaged stands, instead of using the SW model. Our approach was to first make statistical comparisons of CR across stand structures and size classes of trees in multiaged stands. Then, we used scatterplots to identify relationships between CR, stand structure, and BH model dbh prediction error. Next, we developed a CR-based adjustment for model predictions using these patterns as guides. Finally, we evaluated performance of the adjusted model using the procedure described above for the BH model.

We started the post hoc analysis by testing whether mean tree CR was different in even-aged and multiaged stands using Satterthwaite's approximate *t*-test to account for unequal variance. Then, we tested for differences in mean CR between size classes of trees in multiaged stands using a Tukey-adjusted least significant difference means comparison in an analysis of variance. Finally, we used multiple linear regression to test whether there was significant interaction between stand structure and CR when these variables were used to predict residual dbh prediction error. These tests (results below) led us to develop CR-based adjustments separately for even-aged and multiaged stands.

We compared three model forms for adjusting BH model predictions. The most basic version was a linear model based on $\hat{dbh}_{i,t+10}$ that we used to assess whether more complicated models that incorporated CR outperformed an adjustment based on predicted values alone. The simplest model was model 3

$$\hat{a}_{i,t+10} = \hat{\beta}_0 + \hat{\beta}_1 (\hat{dbh}_{i,t+10})$$

where $\hat{a}_{i,t+10}$ is the adjusted model prediction of dbh and the β s are parameters estimated from the data. A second, more complicated, model estimated $\hat{a}_{i,t+10}$ from $\hat{dbh}_{i,t+10}$ and CR using a linear model form. The linear CR adjustment is model 4

$$\hat{a}_{i,t+10} = \hat{\beta}_0 + \hat{\beta}_1 (\hat{dbh}_{i,t+10}) + \hat{\beta}_2 (CR)$$

Finally, the most complicated model form we evaluated estimated $\hat{a}_{i,t+10}$ from $\hat{dbh}_{i,t+10}$ and CR using a model with an exponent on CR. The exponential CR adjustment is model 5

$$\hat{a}_{i,t+10} = \hat{\beta}_0 + \hat{\beta}_1 (\hat{dbh}_{i,t+10}) + \hat{\beta}_2 (CR)^{\hat{\beta}_3}$$

For each stand structure, the model with the lowest Akaike information criterion (AIC) (Akaike 1974) was deemed the best. For even-aged stands, model 3 had the lowest AIC (Table 2), so we did not develop a CR-based adjustment for even-aged stands. For multiaged stands, model 5 had the lowest AIC (Table 2), leading us to adjust BH model dbh predictions for trees in multiaged stands using model 6

Table 3. Model performance statistics for even-aged and multiaged stands and for different size classes of trees in multiaged stands.

Model and group	<i>n</i>	ME (cm)	RMSE (cm)
BH			
Even-aged	317	0.13	0.54
Multiaged	1,483	0.79	1.15
Multiaged: small	619	0.93	1.31
Multiaged: medium	559	0.79	1.11
Multiaged: large	305	0.51	0.81
BH and SW			
Multiaged	1,483	0.81	1.16
Multiaged: small	619	0.97	1.34
Multiaged: medium	559	0.79	1.11
Multiaged: large	305	0.51	0.81
BH + 6			
Multiaged	1,483	< -0.01	0.76
Multiaged: small	619	-0.05	0.85
Multiaged: medium	559	0.04	0.72
Multiaged: large	305	0.03	0.63

Model is the dbh prediction model used. Group is the set of stands or size classes for which model predictions of tree dbh were evaluated. *n* is number of sample trees. Model formulations and calculation of bias (ME, cm) and accuracy (RMSE, cm) measures are described in Methods.

$$\hat{a}_{i,t+10} = 0.9935 (\hat{dbh}_{i,t+10}) + 1.8856 (CR)^{1.6285}$$

The intercept term ($\hat{\beta}_0$ in model 5) was not significant and was dropped. All remaining parameters were significant at $\alpha = 0.05$.

Results

BH Model Performance

The BH model underestimated future dbh on average regardless of stand structure. However, underestimation was much more severe for multiaged stands. Average model bias for trees in multiaged stands was more than six times greater than that for trees in even-aged stands (Table 3). The model was also less accurate (Table 3). Within multiaged stands, predictions from the BH model were worse than those in even-aged stands for each individual size class of trees, and performance was variable across size classes. BH model predictions were best for large size classes of trees and worst for small size classes (Table 3). Graphical analysis of trends in residual prediction error with respect to relative tree size showed no patterns for predictions in even-aged stands (Figure 2A) and a weak negative relationship for predictions in multiaged stands (Figure 2C). Graphical analysis of trends in residual prediction error with respect to CR showed no relationship for predictions in even-aged stands (Figure 2B) and a positive relationship for predictions in multiaged stands (Figure 2D).

FVS-CR Performance in Multiaged Stands

In total, 244 trees from our multiaged stands qualified for dbh prediction using the SW model according to criteria outlined in the FVS-CR documentation (Keyser and Dixon 2008). We assumed that all multiaged stands would qualify as uneven-aged (defined as >40 years age difference between 5th and 95th percentile trees), because trees in the largest size class in multiaged stands were on average 111 years older than trees in the smallest size class (Table 1). The vast majority (1,299) of trees in multiaged stands were overtopped as defined by FVS (bau >30% of bat) and consequently met the second criterion. Of these, 1,139 were severely overtopped (bau >50% of bat). However, only 244 trees met the third criterion (\hat{dbh}_i from the BH model > \hat{dbh}_i from the SW model). All of these

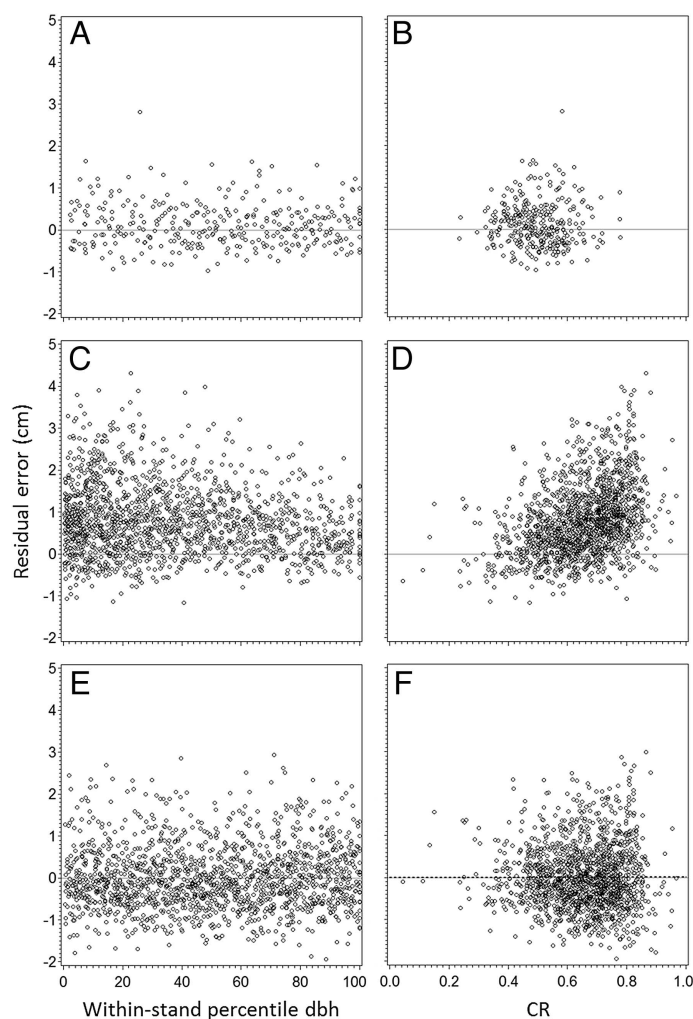


Figure 2. Residual error (cm, $dbh_i - \hat{dbh}_i$) of predictions with respect to relative tree size and CR. A. Residual error of BH model predictions with respect to within-stand percentile dbh for trees in even-aged stands. B. Residual error of BH model predictions with respect to CR for trees in even-aged stands. C. Same relationship for trees in multiaged stands. D. Same relationship for trees in multiaged stands. E. Residual error with respect to within-stand percentile dbh for trees in multiaged stands after adjustment using model 6. F. Same relationship with respect to CR. For all panels, circles represent individual trees ($n = 317$ for even-aged stands; $n = 1,483$ for multiaged stands), and horizontal lines reference zero deviation from dbh_i .

trees were severely overtopped. Consequently, \hat{dbh}_i was estimated for all trees in multiaged stands using either the BH model or the SW model, and a weighted average of predictions from the two models was never used. Of the trees that qualified for dbh prediction using the SW model, 240 were from the smallest size class of trees. The remaining four trees were from the medium size class.

Application of the SW model slightly worsened FVS dbh prediction performance for multiaged stands (Table 3). Performance declined because, on average, the BH model underestimated \hat{dbh}_i for trees in multiaged stands (especially for trees in the smallest size class, for which the SW model was most often used), and the third criterion for application of the SW model ensured that its use invariably reduced \hat{dbh}_i further. There was no appreciable effect of using the SW model on trends in residual error with respect to relative tree size and CR. Because plots were essentially identical to those in Figure 2C and D, they are not shown here.

Trends in CR and Model 6 Performance

Mean tree CR was on average 15% larger in multiaged stands than in even-aged stands (Figure 3A) (Satterthwaite's approximate

t -test, $df = 595.45$, $t = -22.50$, $P < 0.01$; means: even-aged = 0.51; multiaged = 0.65). Within multiaged stands, average CR was largest for trees in the smallest size class and smallest for trees in the largest class (Figure 3B). Differences in mean CR between all size classes were significant ($P < 0.05$; means: small = 0.67, medium = 0.61, and large = 0.57). Multiple linear regression of residual error on stand structure, CR, and their interaction revealed a significant ($P < 0.01$) interaction between predictor variables, leading us to assess potential forms of CR-based adjustment to predictions from the BH model separately for even-aged and multiaged stands.

We found no justification for use of a CR-based adjustment to GENGYM model predictions for trees in even-aged stands (see Methods). However, for trees in multiaged stands, use of model 6 to adjust predictions from the BH model reduced model bias and improved accuracy when it was evaluated for both stands and individual size classes of trees within multiaged stands (Table 3). Graphical analysis of residual prediction error with respect to relative tree size showed that the weak negative trend evident for predictions from the BH model (Figure 2C) disappeared after they were

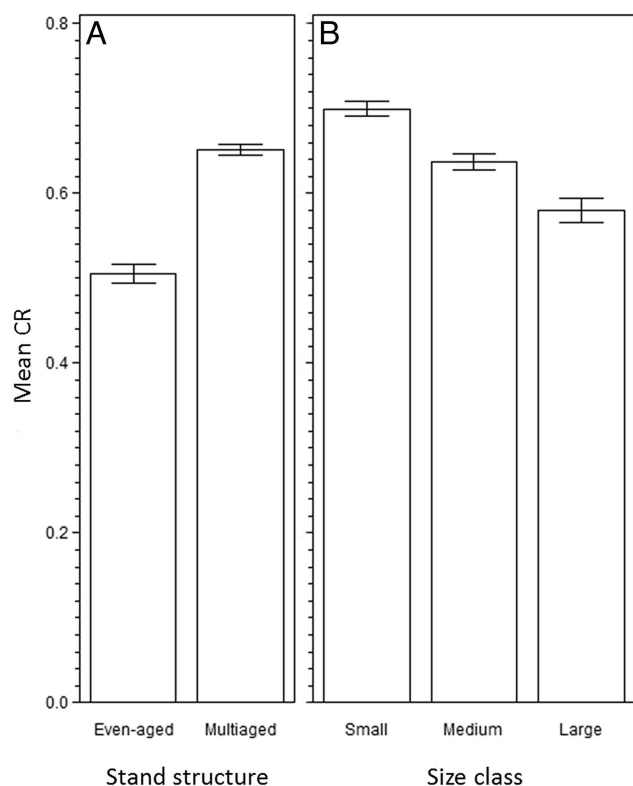


Figure 3. Mean CR for even-aged ($n = 10$) and multiaged ($n = 21$) stands (A) and for individual size classes of trees in multiaged stands (B) ($n = 21$ for all size classes). For both panels, all differences between groups are significant at $\alpha = 0.05$ (statistical comparisons of means are described in Methods). Error bars are 95% confidence intervals of means.

adjusted using model 6 (Figure 2E). The positive trend in residual prediction error with respect to CR apparent for predictions from the BH Model (Figure 2D) similarly disappeared when model 6 was used to adjust values (Figure 2F).

Discussion

This work shows that FVS-CR dbh estimation is biased in a way that could reduce its capacity to realistically simulate stand dynamics in multiaged Black Hills ponderosa pine stands (Figure 2C and D). The GENGym dbh prediction model used by FVS-CR systematically underestimated future dbh for all size classes of trees in multiaged stands (Table 3). It is notable that underestimation was more severe for small size classes of trees than for large size classes (Table 3), which could make small trees grow unrealistically slowly in FVS simulations for multiaged stands. We found that the dbh estimation procedure used by FVS-CR in multiaged stands slightly worsened model performance compared with that for the procedure used in even-aged stands (Table 3). Accordingly, we developed an alternative procedure for use in multiaged stands that adjusts GENGym model predictions using a CR-based model. Our CR-based adjustment reduced model bias and improved accuracy of dbh prediction (Table 3) and eliminated patterns in residual prediction error with respect to tree size (Figure 2E). This result suggests that adjustment with a CR-based model has the potential to improve the capacity of FVS-CR to realistically simulate structural dynamics of multiaged stands. In stark contrast with the poor performance of the GENGym model in multiaged stands, the model was much less biased and more accurate for trees in even-aged stands, and there

were no trends in residual error with respect to relative tree size or CR (Figure 2A and B; Table 3). We found no justification for using a CR-based model to adjust GENGym model predictions for trees in even-aged stands.

Performance of empirical tree growth models such as GENGym depends to a large degree on the data from which estimated parameters were derived. Models generally yield the best predictions for trees and stands that are similar to those used during development; however, models with biologically meaningful parameters can perform well even for dissimilar trees and stands (Wyckoff 1990). The GENGym model was developed using data that included a high proportion of trees from managed, even-aged ponderosa pine stands (Edminster et al. 1991). Managed even-aged stands are typically structurally simple, which limits differentiation and thus variation in tree morphology, including crown size (Oliver and Larson 1996, p. 217). Consequently, biologically relevant variables such as CR are sometimes unimportant for tree growth prediction in even-aged stands simply because they are relatively invariant. This result probably explains why the GENGym model performed better for trees in even-aged stands than for trees in multiaged stands and why a CR-based adjustment improved predictions in multiaged but not in even-aged stands. Although CR or other indices of photosynthetic capacity are biologically relevant regardless of stand structure, only in our multiaged stands was CR sufficiently variable within stands for it to be a useful basis for model adjustment. The multiaged stands we sampled had higher average SI and lower average SDI than even-aged stands (Table 1), which raises the question of whether these factors could account for differences in model performance between structures. However, exploratory analysis of scatterplots showed no relationship between average residual error and stand-level factors for either stand structure, so we did not pursue this line of inquiry.

Our CR-based adjustment to BH model predictions outperformed the current procedure for modeling tree growth in multiaged stands, which presupposes that the BH model overestimates dbh increment for small size classes of trees. Our data suggest that the opposite is true (Table 3). Because the current procedure in effect reduces estimates of dbh increment for small trees in multiaged stands, it is particularly ill-suited to compensate for the underestimation of small tree dbh increment we observed in this work. A CR-based adjustment improved predictions from the BH model (Figure 2E; Table 3) and has a clear biological basis. In theory, adjustment using a CR-based model such as model 6 would improve FVS performance in any circumstance in which CR is variable within stands and the BH model is used, which could include irregularly spaced even-aged stands (Oliver and Larson 1996, p. 219). However, it is important to point out that the real world utility of a CR-based adjustment for GENGym model predictions probably depends to a large degree on the availability of CR data. In many situations, FVS simulations are based on inventory data that do not include CR values for all trees (Leites et al. 2009). Adjustment using a CR-based model may be substantially less effective when CR values are themselves estimated from inventory data. This is an argument for estimating crown base height (necessary to calculate CR) of sample trees in inventories, particularly in multiaged stands.

Conclusions

Realistic stand dynamics simulation is crucial for forest growth models such as FVS to be useful for management of complex, multiaged stands. Whereas an in-depth analysis of GENGym model

bias on stand dynamics simulation was beyond the scope of this study, the magnitude of dbh prediction error (~ 0.8 cm on average for trees in multiaged stands after only 5 years of simulated growth) suggests a potentially large effect. This is of practical importance to end users. Unrealistically slow growth of small size classes of trees in FVS-CR simulations could lead users to select silvicultural alternatives based on faulty assumptions about the rate of ladder fuel development, the length of time between commercial entries, or the number of large trees that can be retained without encumbering the growth of smaller neighbors, to offer only a few examples. Our CR-based adjustment potentially improves FVS-CR performance for multiaged stands, making it more useful for silviculturists.

In a broader sense, this work highlights the importance of continual reevaluation of established forest growth models as they are used in increasingly complex ways. This need has been identified in the scientific literature (Peng and Wen 2006), and model testing is considered a high priority by the FVS Steering Team (Cawrse et al. 2010). Although this particular study focused on GENGYM and multiaged Black Hills ponderosa pine, our results point to wider-reaching issues. GENGYM is used to estimate dbh for most tree species in FVS-CR. If other versions of the GENGYM model behave like the BH model, it could mean that FVS-CR performs poorly for multiaged stands as a rule, although our results could be unique to ponderosa pine and only further testing with other species will say for sure. More fundamentally, this work shows the potential for empirical growth models, whatever their form, to behave unexpectedly when used to predict growth of trees and stands that are dissimilar from those used for model development. Contemporary emphasis on ecological forestry, heterogeneous stand structures, and multiaged silvicultural methods means that models such as FVS will increasingly be used to evaluate silvicultural alternatives that include complex stand structures. Ongoing model evaluation using data from multiaged stands is key to improving model performance for complex structures.

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