



Evaluation of the FVS-CR diameter growth model in structurally-heterogeneous ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) stands in the Southern Rockies, and potential modifications

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ABSTRACT

Forest managers are increasingly focused on promoting or maintaining forest structural complexity, including the heterogeneity of forest structures within stands. However, many of the forest growth models commonly used by forest managers assume that stands are structurally homogeneous. Therefore, using these forest models to project the development of structurally complex stands may provide inaccurate results. We investigated the accuracy and precision of individual tree growth estimates from an individual tree growth model commonly used by forest managers (Central Rockies Variant of the Forest Vegetation Simulator, FVS-CR) in six structurally heterogeneous ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) stands. Furthermore, we examined whether the addition of non-spatial, semi-distance independent, or spatially explicit indices of local competition to the model improved the accuracy and precision of stand development projections over the 16-year study. We found that while the stand-scale estimates of growth were within the bounds of normal measurement precision, the estimates of individual tree diameter growth had a root mean square error (RMSE) that equated to 44% of the mean individual tree diameter growth. The addition of crown ratio to the model improved estimates more than the other investigated indices by halving the estimated bias and reducing the RMSE of the projected individual tree diameter growth by 4.8%.

1. Introduction

Forest managers are increasingly focused on mimicking natural ecosystem structures and processes to achieve landowner goals while maintaining healthy ecosystem function (Seymour and Hunter, 1999; Franklin et al., 2007). In particular, forest managers are seeking to maintain or restore forest structural complexity across a wide variety of forest types to reestablish natural ecosystem processes and function (Hansen et al., 1991; Gustafsson et al., 2012; Puettmann et al., 2012; Churchill et al., 2013). Generally, structural complexity is a combination of the abundance, relative abundance, richness, and variation in the size and spatial arrangement of ecosystem components (McElhinny et al., 2005). Here we will particularly focus on structural complexity arising from the heterogeneity of forest structures at the patch scale within forest stands, as described by Larson and Churchill (2012). However, the implications of augmenting structural complexity for a wide range of ecosystem processes and functions, including forest

growth, are not fully understood (Gustafsson et al., 2012; Bourdier et al., 2016). A clearer understanding of the influence of structural complexity on tree growth will inform forest growth models, and the modeling of stand development through time. The accurate prediction of future stand structures under a range of conditions is also necessary to understand the impact of silvicultural treatments on various ecosystem services, and inform the planning of silviculture prescriptions.

A large number of models for the prediction of forest stand development exist (Weiskittel et al., 2011). The distance-independent growth models commonly used by forest managers to plan management activities assume that the structure of forest stands are homogeneous, with little variation. These distance-independent models utilize mean stand statistics, such as tree density or basal area, to quantify competition (e.g. Forest Vegetation Simulator, FVS; Crookston and Dixon, 2005). However, contemporary silvicultural treatments that aim to maintain forest structural complexity are inconsistent with the assumption that forest stands are homogeneous; therefore, the predictions

Abbreviations: FVS-CR, Central Rockies Variant of the Forest Vegetation Simulator; DBH, diameter at breast height

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of stand development made by these forest models may be inaccurate. Although spatially-explicit tree growth models capable of modeling complex forest structures exist (e.g. TASS, Mitchell, 1975; and SORTIE, Pacala et al., 1996), these models are rarely used by forest managers due to the expense and complexity of the required inventory data.

Prior to European settlement in the 19th century, the historic frequent-fire disturbance regime of ponderosa pine (*Pinus ponderosa* Douglas ex C. Lawson) forests of the southern and central Rockies maintained a complex forest structure (Covington and Moore, 1994; Fule et al., 1997; Kaufmann et al., 2000; Allen et al., 2002). The heterogeneous nature of wildfire severity in these ecosystems resulted in a multi-aged forest distributed as a mosaic of isolated trees, groups of various sized trees, and treeless openings (Churchill et al., 2013; Reynolds et al., 2013). Since European settlement, activities such as grazing, logging, and active fire suppression has resulted in denser forests and increased fuel loads (Churchill et al., 2013; Reynolds et al., 2013). Current forest structures are now highly susceptible to uncharacteristic fire behavior and effects (Fule et al., 2004). In the last decade, the management objectives for ponderosa pine forests of the southern and central Rockies have evolved from hazardous fuels mitigation to forest restoration. Therefore, silviculture treatments have changed from thinning treatments that leave evenly-spaced, large-diameter trees, to treatments that emulate the heterogeneous, multi-aged, open-woodland structure that was typical prior to European settlement and the subsequent fire exclusion (Churchill et al., 2013).

Foresters managing ponderosa pine forests in this region typically use the Central Rockies Variant of FVS (FVS-CR, Keyser and Dixon, 2015) to inform the planning of silvicultural treatments. FVS is an empirical, individual tree, distance-independent, growth and yield model primarily developed and maintained by the US Forest Service. There are a number of geographic variants developed for forest types across the United States, and each uses a different method (or coefficients) to predict growth and mortality. While many of these variants are based on the PROGNOSIS (Stage, 1973) and TWIGS (Miner et al., 1988) models, the Central Rockies variant is based on the GENGYM model (GENeralized Growth and Yield Model) developed by Edminster et al. (1991).

While FVS-CR is relatively straightforward to parameterize and use, it assumes that the forest stand is homogeneous (i.e. spacing between individual trees does not differentially influence their growth) (Edminster et al., 1991; Crookston and Dixon, 2005). Furthermore, while the GENGYM model (which is the basis for FVS-CR) was developed using empirical data from a range of stands including managed and unmanaged; two-storied and multi-storied; even-aged, irregular and nearly-balanced uneven-aged stands; and a range of site qualities; each stand was specifically chosen to be homogeneous across the site in terms of site quality, tree density and species composition (Edminster et al., 1991). However, distance between individuals is known to influence the competitive interactions of plants (Bella, 1971; Ross and Harper, 1972; Pretzsch, 2009); therefore, it follows that heterogeneous forest structures are likely to result in large variations in growth responses among individual trees. This variation in individual tree growth may influence the prediction of forest structure development through time. Therefore, we hypothesize that FVS-CR may provide inaccurate predictions of individual tree growth if utilized for stands where silvicultural treatments have promoted heterogeneous forest structures (i.e. large variation in spacing between individuals). One approach to solving this problem may be to modify the FVS-CR model to include additional indices of local stand conditions for each tree, which may improve the accuracy and/or precision of the growth predictions.

There are a wide variety of available indices that could potentially be added to models in order to improve growth predictions, including indices of individual tree vigor, tree social status, local forest density, and spatially-explicit indices of local competition (Daniels, 1976; Lorimer, 1983; Martin and Ek, 1984; Daniels et al., 1986; Tome and Burkhart, 1989; Macdonald et al., 1990; Biging and Dobbertin, 1995;

Newton and Jolliffe, 1998; Woodall et al., 2003; Fraver et al., 2014). Indices of individual tree vigor could be considered non-spatial as they describe the condition of the tree irrespective of its location. Likewise, tree social status and local forest density indices can be considered semi-distance independent as they describe competition within a defined neighborhood. In contrast, spatially-explicit indices of local competition specifically include structural dimensions, and can be further divided into 2- and 3-dimensional indices. Two-dimensional indices describe either horizontal or vertical structural heterogeneity, while 3-dimensional indices combine the horizontal and vertical forest structure.

The addition of these indices to various models for predicting individual tree growth have had mixed success (Biging and Dobbertin, 1995). While a number of studies have reported improvements in the accuracy and/or precision of growth predictions, the best index varies among studies (Bella, 1971; Alemdag, 1978; Martin and Ek, 1984; Daniels et al., 1986; Pukkala and Kolström, 1987; Tome and Burkhart, 1989; Biging and Dobbertin, 1995; Uriarte et al., 2004). Other studies have found little improvement in model accuracy or precision with the addition of these indices (Hatch et al., 1975; Lorimer, 1983; Daniels et al., 1986; Macdonald et al., 1990). In particular, Ex and Smith (2014) evaluated the performance of FVS-CR in even- and uneven-aged ponderosa pine stands in the Black Hills of South Dakota and Wyoming, USA, and proposed the addition of a non-spatial index of tree vigor to improve the accuracy of its growth estimates. FVS-CR demonstrated bias in diameter growth estimates in uneven-aged stands, and underestimated the growth of small diameter trees particularly. The impact of this bias on predictions of stand development was potentially large, with DBH (diameter at breast height, 1.37 m) prediction errors of approximately 0.8 cm tree diameter growth over 5 years of simulated growth (Ex and Smith, 2014). They also found considerable improvements in accuracy in uneven-aged stands by adding crown ratio (the ratio of the crown length to total tree height) to the growth model.

In addition, Petrova et al. (2014) used long-term datasets from uneven-aged ponderosa pine stands from the Coconino National Forest, Northern Arizona, to validate the large tree diameter growth model of FVS-CR. Similar to Ex and Smith (2014), they also found that small tree diameter growth was over-predicted by the model, and suggested a refined model that improved growth prediction significantly. Their refined model included DBH, quadratic mean diameter, the proportion of basal area in larger trees, stem density, site index, basal area and stand top height; and omitted crown ratio, relative tree height and proportion of basal area in larger trees.

Petrova et al. (2014) and Ex and Smith (2014) focused on stands managed using conventional silvicultural systems that promote relatively homogeneous forest structures. In contrast, here we are focused on the prediction of growth in forest stands following silvicultural treatments that aim to enhance structural complexity by promoting the heterogeneity of forest structures within stands, such as those described by Larson and Churchill (2012). The specific objectives of this study were to test the behavior of a commonly used forest growth model (FVS-CR) in stands that have been treated to promote heterogeneity, and examine whether adding indices of local competition improved the prediction of individual tree diameter growth. While we will focus on tree diameter growth estimates within FVS-CR, the modeling of tree diameter in FVS-CR is integral to other routines within the model. For example, within the FVS-CR model, tree height growth and mortality are both contingent on tree diameter growth estimates. Therefore, inaccuracies in diameter growth in FVS-CR will likely result in inaccuracies in height and volume growth, and mortality rates. We hypothesize that there will be substantial improvements in the accuracy and precision of diameter growth predictions in heterogeneous stands by adding spatially-explicit indices of local competition to the model. The availability of growth data from a long-term manipulative experiment established in 1993, prior to the current focus of forest managers on increasing structural complexity, provides a unique opportunity to

investigate these current challenges in silviculture.

2. Materials and methods

2.1. Study area and field methods

The study site was located in uneven-aged ponderosa pine dominated forests located on a mesa (elevated tableland) in the Lookout Canyon area of the North Kaibab Plateau, Arizona, USA (36°32'10"N, 112°20'10"W). The topography is nearly level, and site productivity is moderately high with a ponderosa pine site index of 25.9 m (Minor, 1964). Prior to treatment, the stand was dominated by ponderosa pine with an average basal area of 24.6 m² ha⁻¹, and tree density of 384 trees ha⁻¹ over 2.54 cm DBH.

In 1993, two replicate blocks with three 4 ha treatment units in each block were established (24 ha total). Treatments were assigned randomly to units within each replicate block. One treatment unit within each of the two blocks was left untreated as a control, while the other two treatment units were harvested using group-selection with a q-ratio of 1.1 for 2.54 cm size classes (Nyland et al., 2016) to leave a total residual basal area of 14.3 m² ha⁻¹ (low residual) and 16.8 m² ha⁻¹ (high residual), respectively (Table 1). In addition, 20% of the residual basal area after the harvest treatments was left in the largest DBH size classes (> 61 cm) to ensure that there were sufficient residual large diameter trees to meet wildlife and aesthetic objectives. Following treatment, the treatment units remained highly dominated by ponderosa pine, with less than 0.29 m² ha⁻¹ basal area of other tree species across all treatment units. These minor species included *Juniperus monosperma* (Engelm.) Sarg., *Juniperus scopulorum* Sarg., *Populus tremuloides* Michx., *Quercus gambelii* Nutt., and *Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr. Harvested groups ranged in area from 0.1 to 0.2 ha, with the objective of leaving a number of small groups of residual trees consistently across the treatment unit interspersed with openings, groups of smaller trees, and occasional isolated large trees. While all treatment units were highly aggregated following treatment in 1994, the mean Clark Evans Aggregation Index for the treatments was a little higher in the low and high residual treatments compared to the control treatment (0.805 ± 0.042 [1 standard error], 0.886 ± 0.062, and 0.876 ± 0.012 for the control, low residual and high residual treatments respectively, Table 1). Therefore, both treatments were less aggregated than the control, but likely remain more aggregated than alternative silvicultural treatments, such as spacing thinning. Some improvement thinning was also undertaken within larger residual groups to achieve the desired residual basal area and favor higher quality trees by removing trees with inferior form or poor vigor. These treatments resulted in a heterogeneous forest structure (Ziegler, 2014), representing a wide range of local competitive neighborhoods well suited for assessing the accuracy of the GENGYM DBH growth model when modeling spatially heterogeneous forest stands, and the improvements that may be possible with the addition of spatially-explicit indices of local competition or crown ratio variables when simulating such stands.

Following the harvest in 1994, all trees over 2.54 cm DBH within the treatment units were tagged and mapped, and their species, DBH over bark, and height recorded. Crown base height (height of lowest live branch) was also recorded for every fifth tree (a subset of 1201 trees). These measurements were then repeated in 2001 and 2010, and all new recruitment over 2.54 cm DBH was added to the dataset. In total, 8503 trees were measured over the 16-year study period.

2.2. Data analysis

To assess the behavior of FVS-CR, the growth of each focal tree's DBH over a 16-year period was modeled based on the field data collected in 1994 using the original GENGYM model presented in Keyser and Dixon (2015) and Edminster et al. (1991) (Eq. (1)). As this model

Table 1
Summary data of treatment units for all trees greater than 2.54 cm DBH, including pre- and post-treatment basal area and tree density. Clark Evans Aggregation Index (Clark and Evans, 1954) indicates whether the spatial pattern of trees was aggregated (< 1), completely spatially random (= 1) or regularly spaced (> 1). Furthermore, * indicates that the two-tailed Clark Evans test is significant at 0.05 alpha, and therefore the pattern is not completely spatially random. Mean diameter at breast height (DBH), tree height and crown ratio are presented with standard errors in parentheses.

Treatment Unit	Pre-treatment (1991)			Post-treatment (1994)			Clark Evans Aggregation Index	DBH (cm)	Tree Height (m)	Crown Ratio (%)
	Basal Area (m ² ha ⁻¹)	Density (Trees ha ⁻¹)		Basal Area (m ² ha ⁻¹)	Density (Trees ha ⁻¹)					
1 – Control	26.0	267.6		28.3	153.6		0.848*	24.0	14.2	59.7
2 – High residual basal area	25.4	258.5		16.9	104.7		0.863*	22.7	12.9	62.2
3 – Low residual basal area	22.0	879.7		14.6	74.3		0.948*	25.8	14.4	58.0
4 – High residual basal area	24.0	257.0		16.6	72.1		0.888*	28.2	15.1	62.4
5 – Low residual basal area	24.5	238.5		14.0	64.0		0.824*	27.2	15.4	59.7
6 – Control	25.8	315.3		28.8	237.4		0.763*	17.7	10.6	59.9

projects growth of each tree in 10-year increments; growth was modeled for the initial 10-year period (1994–2004), followed by an additional 10-year period (2004–2014). The second 10-year period was then prorated to just six years (2004–2010) so that the estimated tree diameter could be directly compared with the final field measurement of tree diameter in 2010.

$$DF = 4.10552 + 0.88872 \left(\frac{DBH}{2.54} \right) + 0.1378 \left(\frac{SI}{0.3048} \right) + 0.23834 l_n \left(\frac{DBH}{2.54} \right)^2 + 0.52784 \left(\frac{\frac{BAU}{0.229568}}{\frac{BAT}{0.229568}} \right) + 0.83531 l_n \left(\frac{BAT}{0.229568} \right) \quad (1)$$

where: DF is tree diameter at breast height at the end of the period in cm; l_n is the natural log; DBH is the tree diameter at 1.37 m from the ground in cm; SI is the species site index in m; BAU is total basal area in trees above the diameter class of the subject tree at the stand scale in $m^2 ha^{-1}$; and BAT is the total stand basal area but is restricted to $\geq 4.8 m^2 ha^{-1}$.

The modeled DBH increment of these trees was then compared to their measured growth over the 16-year period from 1994 to 2010. The coefficient of determination (R^2), bias, and root mean square error (RMSE) were calculated to assess the accuracy of the model. Furthermore, to assess the original model's accuracy across the range of tree sizes, linear regression was used to test for a statistical relationship between the residuals and initial DBH , with silvicultural treatment as a covariate. Where silvicultural treatment was significant, we followed this with *posthoc* pairwise t-tests with a Bonferroni correction comparing each of the silvicultural treatments.

To assess the model accuracy at the stand scale across the range of experimental treatments, the estimates of basal area growth by treatment unit were calculated from the modeled diameter growth of individual trees. The difference between the actual and modeled basal area growth by treatment unit was calculated, and statistically significant differences among the treatments tested using an ANOVA followed by post-hoc pairwise t-tests with Holm's correction (Holm, 1979) for multiple testing to maintain a 0.05 family-wise error rate (three treatments, each with two replicates).

To examine whether adding indices of local competition improved the prediction of individual tree diameter growth in FVS-CR, 21 semi-distance independent indices and 6 spatially-explicit indices of local competition were calculated for each tree in each of the treatment units (Table 3) using ArcGIS 10.3.1 (Environmental Systems Research Institute, Redlands, CA, 2015). The semi-distance independent indices included the local basal area and local basal area excluding the focal tree ($m^2 ha^{-1}$), local sum of DBH and local sum of DBH excluding the focal tree ($cm ha^{-1}$), local sum of tree height and local sum of tree height excluding focal tree ($m ha^{-1}$), and local density of trees (trees ha^{-1}). The spatially explicit indices included Hegyi's competition index (Hegyi, 1974) and a modified Hegyi's competition index based on tree height. Hegyi's competition index is the sum of the inverse distance-weighted DBH of the neighboring trees. The modified Hegyi's competition index is the sum of distance-weighted height of the neighboring trees. Each semi-distance independent and spatially-explicit index was calculated within 6 m, 12 m and 24 m radius local neighborhoods, respectively.

There are a large number of indices of local competition that may

have potentially been investigated (Daniels, 1976; Martin and Ek, 1984; Daniels et al., 1986; Pukkala and Kolström, 1987; Tome and Burkhart, 1989; Macdonald et al., 1990; Biging and Dobberty, 1992; Biging and Dobberty, 1995; Newton and Jolliffe, 1998; Pretzsch, 2009); however, we chose to investigate a range of indices that included metrics of tree size (both diameter and height) and density across a range of neighborhood sizes, and that were conceptually simple to calculate. A gradient of neighborhood sizes were investigated, from small neighborhoods where the crowns of adjacent mature trees would likely touch (6 m radius), to large neighborhoods which were half the height of the tallest tree in the study (24 m radius). The investigated neighborhood radii are comparable to the critical neighborhood radii across a range of forest types and stands (3 to 14.7 m radii) (Moravie et al., 1999; Woodall et al., 2003; Simard and Sachs, 2004; Uriarte et al., 2004; Boyden et al., 2005; Fajardo et al., 2006; Boyden et al., 2012). In ponderosa pine specifically, Woodall et al. (2003) found that the growth efficiency of trees with $DBH < 10$ cm was most strongly correlated with neighborhoods with a radius 10.6 m, while larger trees were most strongly influenced by smaller neighborhoods with a radius of 6.1 m. In addition, Boyden et al. (2005) found regularity in the spatial patterns in older ponderosa pine in scales up to 5–7 m, while regeneration tended to occur more than 15–35 m from large canopy ponderosa pine, suggesting that competitive effects on regeneration may occur up to 35 m from mature trees. Furthermore, Fajardo et al. (2006) found some negative spatial associations between ponderosa saplings and large overstory trees at scales of 6–11 m.

To correct for edge effects, all focal trees that were closer to the edge of the treatment unit than the local neighborhood radii were removed from the dataset (Dale and Fortin, 2014), as unrecorded trees outside the treatment unit may fall within their local neighborhood. While these focal trees were excluded from the dataset as observations, they were still included as potential neighbors within the local neighborhood of other trees. Furthermore, all focal trees of species other than ponderosa pine were removed from the dataset. Any trees that died, or trees that were recruited into the dataset during the 16-year study period were also removed from the dataset (10% of all trees).

In addition to the semi-distance independent indices and spatially-explicit indices of local competition, the crown ratio (a non-spatial index of tree vigor) was also calculated for each tree where crown base height was recorded.

A correlation matrix using Pearson correlation coefficient was constructed to investigate the strength of correlations among all 28 indices and two individual tree variables already in the model (DBH and total basal area in trees larger than the diameter class of the subject tree), and to check for multicollinearity among the variables.

The resulting dataset included a total of 3635 trees, including 587 complete cases with crown ratio. This data was divided into training and testing datasets. 160 trees with all variables were randomly selected for the testing dataset, while data from all remaining trees were used to develop the revised growth models (training dataset with 3475 trees; Table 2).

Each of the 28 indices were added in-turn to the original GENGYM model to assess the potential improvements by adding these parameters to the model. Specifically, the training dataset was used to develop the 28 revised growth models using linear modeling least squares methods to calculate the coefficients for the added parameters. The coefficients

Table 2

Summary of training and testing datasets, including: number, mean, standard error and range of the diameter at breast height (DBH), height and crown ratio of trees.

Dataset	DBH (cm)				Tree Height (m)				Crown ratio (%)			
	<i>n</i>	Mean	Standard Error	Range	<i>n</i>	Mean	Standard Error	Range	<i>n</i>	Mean	Standard Error	Range
Training	3475	29.7	0.3	2.5–87.4	3472	14.03	0.15	1.22–58.83	427	60.5	0.6	15–90
Testing	160	28.9	1.4	2.5–77.2	160	12.98	0.69	1.22–35.97	160	62.3	1.1	20–91

for parameters from the original GENGym model (Eq. (1)) were held constant by specifying them as offset terms in the analysis. For the development of each model, trees in the training dataset that lacked the required indices were dropped from the analysis. The training dataset for the crown ratio model was the smallest, with 427 trees, because crown ratio was only measured on a subset of trees. However, all other models were developed using data from at least 2613 trees. For each revised model, the coefficient P-value for the added index, R^2 , bias, RMSE and Bayesian information criterion (BIC) was calculated using the testing dataset (160 trees), and compared to the original GENGym model. The testing dataset contained data from trees with all indices, and was therefore consistent across all models. In addition, Cook's distance (Cook and Weisberg, 1982) was calculated to check each model for outliers that unduly influence the model ($Di > 1$); however, no influential outliers were detected. A large R^2 , and small bias, RMSE and BIC indicate the preferred model, which is relatively simple (i.e. fewer required parameters) while maintaining high accuracy and precision. The distribution of bias among tree sizes was also assessed for the best model investigated following the same method as described above for the original FVS-CR model.

All statistical analyses were undertaken using R version 3.2.2 (R Core Team, 2015).

3. Results

The mean basal area (BA) of the treatments in 1994 following the harvest was $28.5 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.26 \text{ m}^2 \text{ ha}^{-1}$), $16.75 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.19 \text{ m}^2 \text{ ha}^{-1}$) and $14.33 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.30 \text{ m}^2 \text{ ha}^{-1}$) for the control, high residual and low residual group selection treatments, respectively. Over the 16-year study period, the mean BA of the treatments grew to $33.1 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.54 \text{ m}^2 \text{ ha}^{-1}$), $21.7 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.52 \text{ m}^2 \text{ ha}^{-1}$) and $19.4 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.77 \text{ m}^2 \text{ ha}^{-1}$), respectively. The size class and spatial distribution of trees in the treatments varied in 2010 (Fig. 1). The DBH of the 8,503 trees measured grew on average $3.29 \text{ cm decade}^{-1}$ ($\pm 0.03 \text{ cm decade}^{-1}$), with a mean diameter growth between 1994 and 2010 of $2.35 \text{ cm decade}^{-1}$ ($\pm 0.03 \text{ cm decade}^{-1}$), $4.18 \text{ cm decade}^{-1}$ ($\pm 0.05 \text{ cm decade}^{-1}$), and $4.46 \text{ cm decade}^{-1}$ ($\pm 0.06 \text{ cm decade}^{-1}$) for the control, high residual and low residual group selection treatments, respectively.

At the scale of individual tree growth, the original model (Eq. (1)) projected diameter growth with an R^2 of 0.982 (Table 3). The original model overestimated individual tree diameter growth estimates with a bias of $0.36 \text{ cm decade}^{-1}$. The RMSE of the estimates was $1.46 \text{ cm decade}^{-1}$, representing a proportionally large error in the diameter growth of individual trees equating to 44% of the mean diameter growth of the trees measured in this study. When we compared the bias across tree sizes, we found DBH was a statistically significantly related to the model's residuals ($P = 0.0055$; Fig. 2). Residuals were larger for small trees than large trees across all treatments (Fig. 2). In addition, the model's residuals varied between the treatments ($P = 0.0003$), with residuals of the control treatment significantly different from the high residual group selection treatment ($P = 0.023$; Fig. 2).

At the stand scale, the original growth model over-estimated the basal area growth in the control treatment, compared with either of the group-selection treatments ($P = 0.002$) with mean over-estimates of $1.6 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.16 \text{ m}^2 \text{ ha}^{-1}$), $0.1 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.03 \text{ m}^2 \text{ ha}^{-1}$), and $-0.01 \text{ m}^2 \text{ ha}^{-1}$ ($\pm 0.05 \text{ m}^2 \text{ ha}^{-1}$) over the 16-year study period for the control, high and low residual group selection treatments, respectively.

Correlation matrix of the 28 indices indicated that there are strong correlations within groups of indices (Fig. 3). The semi-distance independent indices within 6, 12, and 24 m radius neighborhoods were positively correlated to each other, irrespective of whether the focal tree was included or not, with all correlations greater than 0.438. While the Hegyi and modified Hegyi indices (both spatially-explicit) were positively correlated to each other (all $r > 0.550$), their correlations

with the other indices of local competition were generally weaker (ranging from -0.026 to 0.678). In contrast, crown ratio was only weakly correlated with the semi-distance independent and spatially-explicit indices of local competition, with correlations ranging from -0.173 to 0.090 . The individual tree indices already in the model (i.e. DBH and BAU) were negatively correlated to each other, and trees with larger DBH generally had smaller total basal area in larger trees at the stand scale. Furthermore, DBH was negatively correlated (-0.060 to -0.414) and BAU positively correlated (0.131 to 0.585) with the 28 indices investigated. The correlations between DBH and BAU, and local sum of DBH at 6 m (-0.076 and 0.356 , respectively), local sum of height at 6 m (-0.141 and 0.398 , respectively), and the modified Hegyi index based on tree height at 6, 12, and 24 m (-0.094 , -0.075 and -0.060 ; and 0.152 , 0.135 , and 0.131 , respectively) were weaker than with the other 20 indices.

The addition of each of the indices to the original model individually improved the R^2 of the individual tree diameter growth predictions from 0.9845 to greater than 0.9946 (Table 3). However, the effect of the additional indices on the bias, RMSE and BIC varied by index, and in some instances increased the bias, RMSE and/or BIC. Of the spatially-explicit indices of local competition, the density of trees within a 24 m radius neighborhood and the modified Hegyi with a 24 m radius neighborhood reduced the model bias the most, from $0.36 \text{ cm decade}^{-1}$ to $0.28 \text{ cm decade}^{-1}$ (Tables 3 and 4) which represents a 22% decrease in the mean overestimation of individual tree diameter growth. In contrast, sixteen of the tested indices increased the level of model bias. However, the model with the incorporation of crown ratio reduced this bias even further to just $-0.15 \text{ cm decade}^{-1}$ (Tables 3 and 4), less than half the bias of the original model. Seven of the 28 tested indices decreased the RMSE; however, these reductions were minor. In contrast, the addition of crown ratio to the model reduced the RMSE from $1.46 \text{ cm decade}^{-1}$ to $1.39 \text{ cm decade}^{-1}$ (Table 3), improving the RMSE by 4.8%. Finally, the addition of crown ratio to the model resulted in a considerably improved BIC, reducing it from 9849 to just 1184 (Table 3). The next best model in terms of BIC was the density of trees within a 24 m radius local neighborhood, with a BIC of 9413 (Table 3).

When we examined the bias for the best model (i.e. the crown ratio model) across the range of tree sizes, we found a significant relationship between initial DBH and model residual; however, the statistical significance of this relationship was weaker than the original model ($P = 0.0114$, Fig. 2). Model residuals also varied significantly among the treatments ($P = 0.0002$, Fig. 2), with residuals of the control treatment significantly different from the high residual group selection treatment ($P = 0.026$; Fig. 2).

For all of the tested spatially explicit indices of local competition, the largest neighborhood radius (24 m) demonstrated the lowest bias, RMSE and BIC (Table 3). For six of the nine spatially explicit indices tested, the RMSE increased as the neighborhood size increased from a 6 to 12 m radius, but then decreased as the neighborhood size increased further to a 24 m radius (Table 3). Finally, the BIC for all indices decreased with increasing neighborhood size; however, this decrease was much smaller for Hegyi and the modified Hegyi (Table 3). The Hegyi index weights the DBH (or tree height) of close neighboring trees more heavily than those that are further away; therefore, it could be expected that increasing the neighborhood size would have relatively little influence on these models.

4. Discussion

The overall accuracy of individual tree diameter growth estimates from the original GENGym model were comparable to the accuracy reported by Edminster et al. (1991). While the R^2 for estimates of individual tree diameter growth calculated in the present study ($R^2 = 0.982$) were a little lower than those reported during model development ($R^2 = 0.997$) (Edminster et al., 1991), the model was able to

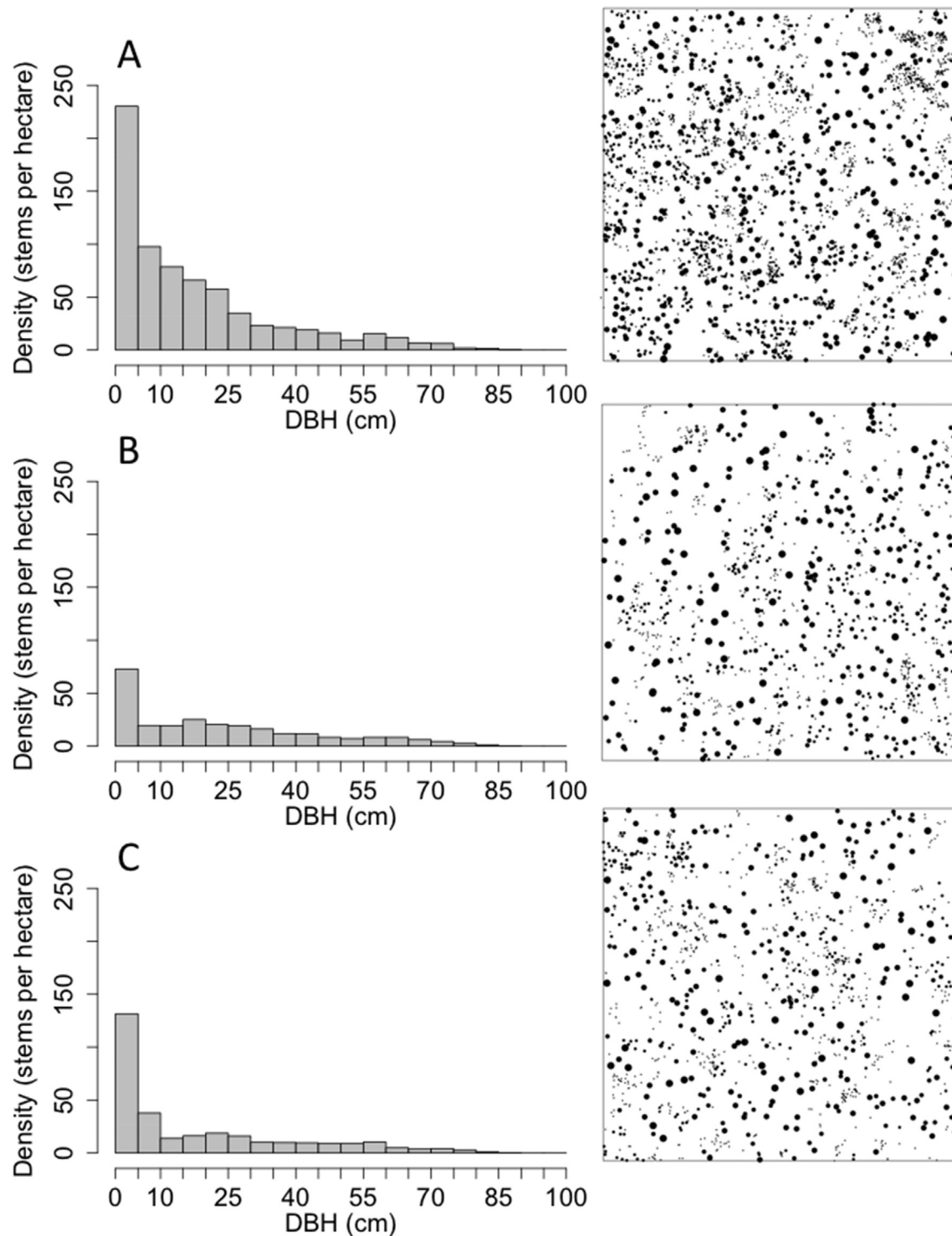


Fig. 1. An example DBH size-class distribution histogram and stem map from a (A) control, (B) high (18.4 m² ha⁻¹) and (C) low (13.8 m² ha⁻¹) residual basal area group selection plot (top to bottom) post-treatment in 2010. The size of the filled circle in the stem map is relative to the DBH.

explain considerable variation in individual tree diameter growth. Further, the estimates of stand growth in the three treatments were reasonably accurate with relatively small errors in basal area growth estimates ($< 1 \text{ m}^2 \text{ ha}^{-1} \text{ decade}^{-1}$). However, there was a significant difference among the treatments in terms of estimate accuracy, and the error in stand basal area growth of the control treatments was larger. This difference among the treatment units may be partially explained by the higher tree density and greater prevalence of small, suppressed trees in the control treatments (approximately double the tree density

of either group-selection treatment). Where tree densities are higher, errors in estimated individual tree diameter growth are likely to sum to greater errors in predicted stand basal area growth.

While the estimates made by the original model are clearly informative, the RMSE represents 44% of the mean individual tree diameter growth. Furthermore, consistent with [Ex and Smith \(2014\)](#), and [Petrova et al. \(2014\)](#) who studied stands managed for homogeneity, we found there is greater bias in the growth of small than large trees. Unfortunately, [Edminster et al. \(1991\)](#) did not report model bias;

Table 3

The coefficient P-value, correlation coefficient (R^2), bias, root mean square error (RMSE) and Bayesian information criterion (BIC) for 29 assessed models, based on data from the testing dataset (160 trees randomly selected from across all treatments and withheld during model development).

Model	Neighborhood size (m)	Coefficient P-value	R^2	Bias (cm decade ⁻¹)	RMSE (cm decade ⁻¹)	BIC
Original	N/A	N/A	0.9845	0.36	1.46	9849
BA	6	0.0006*	0.9946	0.44	1.46	9754
BA	12	0.6379	0.9946	0.38	1.46	9671
BA	24	0.0024*	0.9947	0.29	1.45	9415
BA excld focal	6	< 0.0001*	0.9946	0.45	1.46	9747
BA excld focal	12	0.4735	0.9946	0.38	1.46	9671
BA excld focal	24	0.0027*	0.9947	0.29	1.45	9416
DBH	6	< 0.0001*	0.9946	0.49	1.46	9732
DBH	12	0.1309	0.9946	0.40	1.46	9669
DBH	24	0.0016*	0.9947	0.29	1.45	9415
DBH excld focal	6	< 0.0001*	0.9946	0.50	1.46	9721
DBH excld focal	12	0.1075	0.9946	0.40	1.46	9669
DBH excld focal	24	0.0014*	0.9947	0.29	1.45	9414
Height	6	< 0.0001*	0.9946	0.50	1.46	9724
Height	12	0.0100*	0.9946	0.42	1.46	9665
Height	24	0.0237*	0.9947	0.31	1.46	9419
Height excld focal	6	< 0.0001*	0.9947	0.51	1.45	9714
Height excld focal	12	0.0075*	0.9946	0.43	1.46	9664
Height excld focal	24	0.0218*	0.9947	0.31	1.46	9419
Density	6	0.9532	0.9946	0.37	1.46	9766
Density	12	0.1133	0.9946	0.33	1.46	9669
Density	24	0.0006*	0.9947	0.28	1.45	9413
Hegyi	6	0.0051*	0.9947	0.39	1.46	9849
Hegyi	12	0.6530	0.9947	0.37	1.46	9857
Hegyi	24	0.0045*	0.9947	0.33	1.46	9849
Modified Hegyi	6	0.0214*	0.9947	0.39	1.46	9852
Modified Hegyi	12	0.8265	0.9947	0.36	1.46	9857
Modified Hegyi	24	< 0.0001*	0.9947	0.28	1.45	9835
Crown ratio	N/A	< 0.0001*	0.9954	-0.15	1.39	1184

* Statistically significant at alpha = 0.05.

therefore, we cannot compare the bias we detected with their original study. While the estimates of overall stand-scale growth (i.e. BA) are accurate, these errors in individual tree diameter growth are concerning. Foresters have traditionally used growth models to project stand growth to estimate wood volume and timber production, and the development of stand structure through time (Petrova et al., 2014). While the errors in individual tree diameter growth appear to counterbalance when scaling up to stand basal area growth, resulting in relatively accurate stand-scale estimates, errors in individual tree diameter growth are likely to produce inaccurate estimates of structural development as they compound over modelling cycles. The impact of these errors in projected stand structure are likely to be important where the objective of forest management is to create and maintain specific complex forest structures. For example, estimates of the length of time between intermediate treatments to maintain complex forest structures required for wildlife habitat (e.g. Reynolds et al. (1992)), estimates of the development of understory ladder fuels, or projections of the susceptibility to insects and disease through time may be inaccurate. Furthermore, FVS-CR estimates of tree height growth are based on estimates of tree diameter growth; therefore, errors in tree diameter growth will likely be compounded by concomitant errors in estimated height growth.

The majority of the semi-distance independent, spatially-explicit, and distance-independent tree vigor indices investigated were significant predictors of individual tree diameter growth and improved model accuracy. However, improvements from the inclusion of crown ratio surpassed those of both the semi-distance independent and spatially-explicit competition indices. The addition of crown ratio to the model halved model bias and reduced the RMSE, corroborating others who found crown ratio is positively correlated to diameter growth for a variety of tree species (Wykoff, 1990; Hann and Larsen, 1991; Hasenauer and Monserud, 1996; Lessard et al., 2001). While crown ratio does not directly quantify the local competitive neighborhood, it is likely a measure of individual tree vigor and is influenced by the

competitive interactions among trees (Wykoff, 1990). Shade intolerant ponderosa pines under strong competition from neighbors will likely be shaded, and therefore have a smaller crown ratio. However, the present study did not find a strong correlation between crown ratio and any of the indices of local competition investigated. This lack of correlation is likely because crown ratio is also influenced by past disturbances and low-severity fires (wild or prescribed) that remove low branches and raise the crown base height (Wykoff, 1990). In addition, crown ratio is an indicator of a tree's photosynthetically active surface area (Wykoff, 1990); and therefore, it is reasonable to expect that it would be a good predictor of tree diameter growth.

Our results contradict Edminster et al. (1991) who investigated the inclusion of crown ratio when developing the original GENGYM model, but found that it was not a significant predictor of individual tree diameter growth in homogeneous stands when DBH, BAU and BAT were also included, and therefore excluded it from their final model (Eq. (1)). Crown ratio may not be a significant predictor of individual tree diameter growth in stands with even-aged, homogeneous forest structures (Ex and Smith, 2014), as all trees within a stand would be subject to similar competitive neighborhoods and a stand level measure of forest structure such as BAT would be sufficient to describe the competitive environment. Likewise, our findings diverge from Petrova et al. (2014), who found that top height and quadratic mean diameter of trees were more informative than crown ratio when predicting the diameter growth of ponderosa pine. However, Petrova et al. (2014) utilized a historical long-term dataset that did not include crown ratio measurements and were therefore required to estimate crown ratio from DBH. The estimation of crown ratio in their study likely introduced an additional source of error. Therefore, the addition of crown ratio to the FVS-CR individual tree diameter growth model may be warranted where there is interest in modeling the growth and development of forest stands with complex forest structures.

Our finding that the addition of crown ratio improves the accuracy and precision of the GENGYM growth model used in FVS-CR also

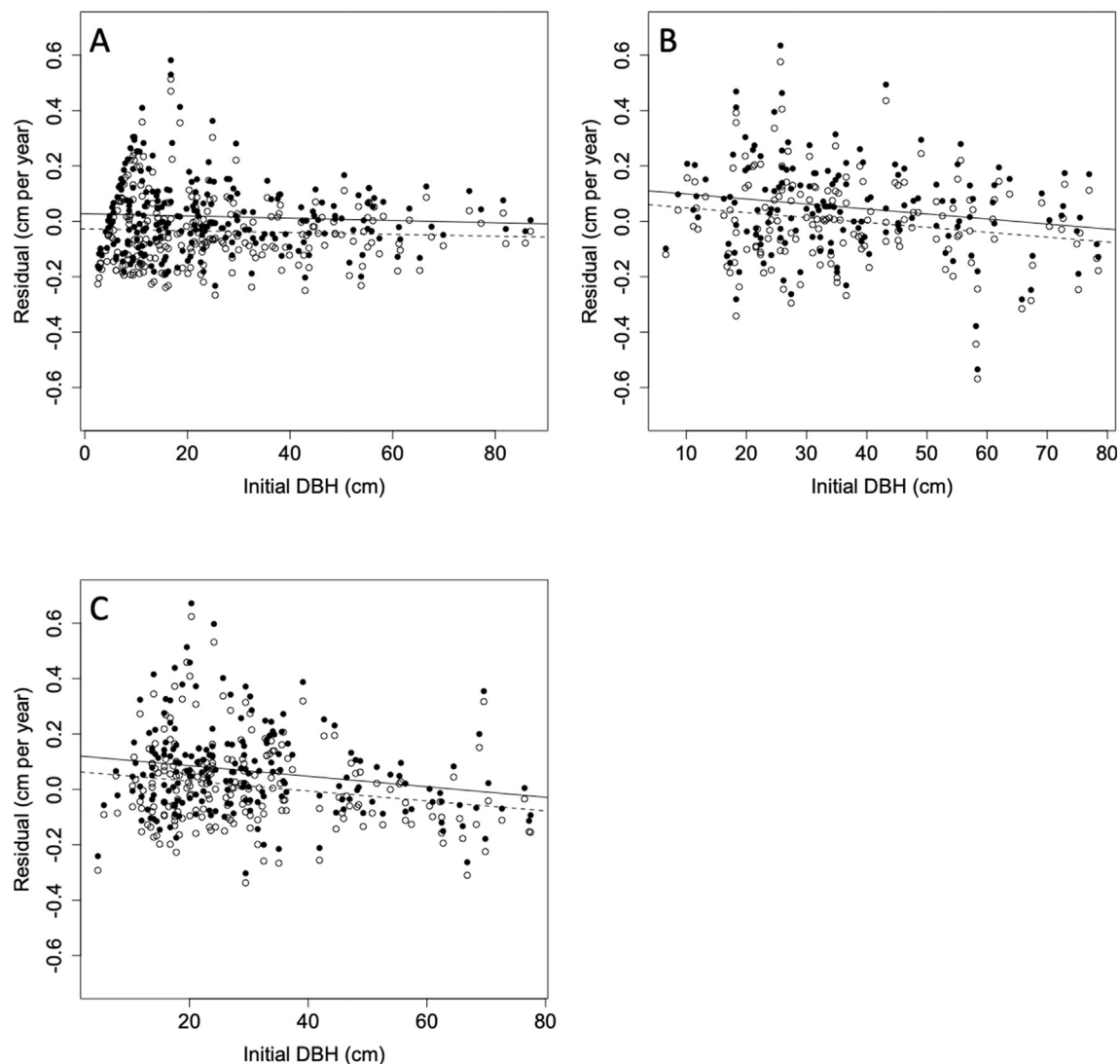


Fig. 2. Original model and crown ratio model residuals (cm per year) by initial DBH (cm) for each treatment. Filled points are residuals for original model, and open circles are residual for crown ratio model. A = control, B = low residual group selection, C = high residual group selection. Solid lines represent linear regression between initial DBH and residual for original model ($P = 0.0055$) and dotted lines for the crown ratio model, respectively ($P = 0.0114$).

corroborates the findings of [Ex and Smith \(2014\)](#). [Ex and Smith \(2014\)](#) investigated the accuracy and precision of the tree diameter growth model in FVS-CR when projecting the growth of uneven-aged ponderosa pine stands of the Black Hills, USA. While uneven-aged, the stands studied by [Ex and Smith \(2014\)](#) were not managed to promote heterogeneous forest structures. They found that the original model projected individual tree diameter growth within uneven-aged stands with a bias of $1.58 \text{ cm decade}^{-1}$, and RMSE of $2.3 \text{ cm decade}^{-1}$. Therefore, the accuracy and precision of the original GENGYM model's estimates in [Ex and Smith \(2014\)](#) were poorer than in the current study. By adding crown ratio to the model, they were able to reduce the bias and RMSE of the model to just $-0.2 \text{ cm decade}^{-1}$, and a RMSE of $1.5 \text{ cm decade}^{-1}$ which is comparable to the improvements made in the current study focused on stands managed to promote heterogeneous forest structures. It should be noted that FVS-CR uses different coefficients within the GENGYM model for projecting the growth of individual tree diameters in the Black Hills; however, the basic form of the model is the same.

The accuracy of crown ratio estimation methods should be assessed prior to adding crown ratio as a predictor of diameter growth in FVS-CR, as errors in crown ratio measurements or estimation could become a new source of error. [Leites, Robinson and Crookston \(2009\)](#)

investigated the accuracy of crown ratio estimation models used in two Prognosis-based variants of FVS (Northern Idaho, and South-Central Oregon and North Eastern California variants). Crown ratio is a predictor of tree diameter growth in Prognosis-based FVS variants, and when modeling growth beyond the initial projection cycle (when direct measurement of crown ratio at the beginning of the cycle is impossible) or in situations where crown ratio has not been directly measured, the FVS model can estimate crown ratio. [Leites et al. \(2009\)](#) found that crown ratio estimates significantly influenced the accuracy and precision of FVS growth predictions, with errors from estimating crown ratio resulting in 31% error in diameter growth predictions on average. Furthermore, FVS estimates of crown ratio in these variants over-predicted crown ratios that were $< 40\%$ and under-predicted crown ratios that were $> 60\%$ ([Leites et al., 2009](#)). Poor estimates of crown ratio would likely reduce the effectiveness of any model that includes crown ratio as an independent predictor variable.

While the addition of semi-distance independent, and spatially-explicit competition indices also resulted in improved model accuracy and precision, these improvements were smaller than those achieved with the addition of crown ratio to the model. Of the semi-distance independent and spatially explicit indices of competition, those with a large neighborhood radius of 24 m resulted in the best improvements in

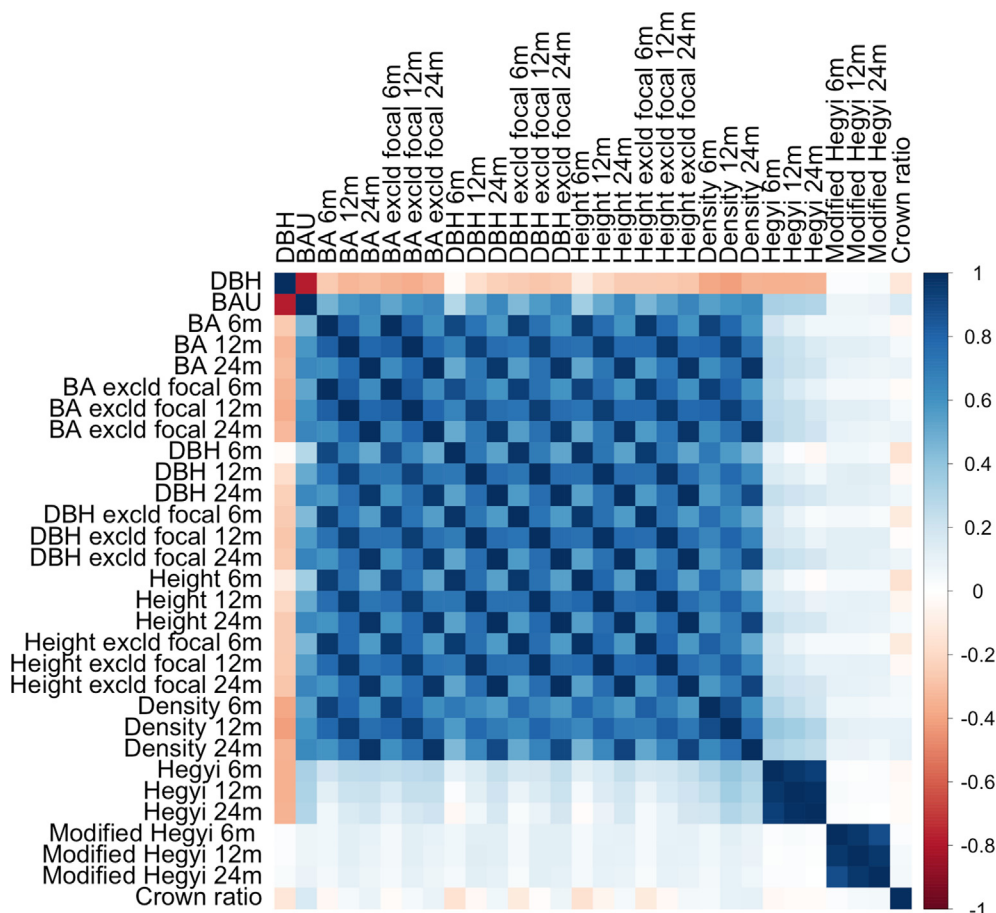


Fig. 3. Full correlation matrix of DBH, BAU, and 28 semi-distance independent and spatially-explicit indices of local competition, and tree vigor. Color of matrix indicates correlation between indices, with dark blue indicating a strong positive correlation, white no correlation, and dark red a strong negative correlation. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4

Estimated coefficients and standard error for the parameters added to Eq. (1) for the best models, including: the local density of trees in a 24 m radius neighborhood, and crown ratio models. These models had the lowest bias, RMSE and BIC and highest RMSE.

Model	Neighborhood size (m)	Estimated coefficient for added index	Standard error of the coefficient
Density	24	6.7509×10^{-4}	1.9704×10^{-4}
Crown ratio	N/A	5.3791×10^{-3}	7.401×10^{-4}

model accuracy and precision (lowest bias and RMSE). This suggests that trees competitively interact within a relatively large neighborhood of trees, and their diameter growth can be influenced by trees within a 24 m radius. Specifically, the addition of local tree density within a 24 m radius neighborhood to the model provided the best improvements of the semi-distance independent and spatially explicit indices of competition (Table 3). Our findings contrast with Woodall et al. (2003), and Boyden et al. (2005) who found competitive interactions within smaller neighborhoods. These differences may be attributed to differences in climate or site characteristics among the studies, resulting in variations among growing environments.

Crown ratio was not strongly correlated with the semi-distance independent and spatially-explicit competition indices investigated in this study. Therefore, if the available data allows, the addition of both crown ratio and one semi-distance independent or spatially-explicit competition index may provide even further improvements to model accuracy and precision beyond those achieved here, without multicollinearity problems among the predictors. Preliminary analyses of models with the simultaneous addition of both crown ratio and each of the semi-distance independent and spatially-explicit competition

indices suggest that this may further decrease model bias and the RMSE (results not shown). However, the BIC of these more complex models was somewhat increased, suggesting that the small improvement in model accuracy may not warrant the increased complexity of data input requirements. Further work is needed to more thoroughly investigate the potential advantages and disadvantages of adding multiple indices to the model.

The addition of semi-distance independent and spatially-explicit competition indices requires extensive additional data, such as the location for each tree, which may be infeasible for forest managers given current forest inventory methods. But, novel technologies being developed for forest inventory data collection, such as the use of terrestrial or aerial LiDAR (Light Detection and Ranging) may make this more feasible for forest managers in the future (Lefsky et al., 2002; Pedersen et al., 2012). In contrast, crown ratio data is already routinely available as part of current forest inventory practices for many organizations, and it is feasible for forest managers to implement the revised model.

FVS-CR is a useful simulation tool to model southwestern ponderosa pine growth in uneven-aged, spatially complex forests. Our results suggest that the addition of a crown ratio value to the growth equation would increase the accuracy and decrease the bias of diameter growth estimates for ponderosa pine stands in the southwestern United States where silvicultural treatments have increased forest structural complexity. This is particularly important as modeled height and volume growth, and mortality are contingent on the modeled diameter growth in FVS-CR, and errors in diameter growth are likely to lead to poor estimates of forest development through time. However, further evaluation of forest growth models in structurally complex forest stands is warranted, especially as these simulation models continue to be the standard of comparing silvicultural alternatives.

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