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Biometrics

Evaluating Long-Term Seedling Growth Across Densities Using Nelder Plots and the Forest Vegetation Simulator (FVS) in the Black Hills, South Dakota, USA

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Abstract

Small-tree development affects future stand dynamics and dictates many ecological processes within a site. Accurately representing this critical component of stand development is important for evaluating treatment alternatives from fuel hazard reduction to harvest scheduling. As with all forest growth, competition with other vegetation is known to regulate small-tree growth dynamics. This study uses three Nelder plots with 45 years of ponderosa pine growth to understand competition effects on seedling growth and evaluate the Forest Vegetation Simulator (FVS) Central Rockies (CR) variant's ability to represent these dynamics. Removal of herbaceous competition before planting increased tree diameters by 50–135% and height by 35–75% across a planting density gradient at age 12. However, by age 45, the effect of herbaceous competition on tree size was no longer evident. Instead, trees at the lowest planting density had diameters 2.5–3 times larger than the most densely grown trees. Forest Vegetation Simulator (FVS) simulations underpredicted diameter at breast height (dbh) by 35–50% and 0–35% for 12 and 45-year-old trees, respectively. There was an underprediction bias of 15–20% for heights at age 12 and overpredictions of 5–10% at age 45. Continuous underprediction of dbh will affect the reliability of modeled fuel treatment longevity and sustainable harvest scheduling.

Study Implications: Management and modeling of small-tree growth can affect decision-making for a range of activities, from assessing fuel treatment effectiveness to sustainable harvest scheduling. Effective small-tree density management can increase tree diameters at age 45 by 2.5–3 times the diameter of unthinned sites. FVS-CR underpredicted age 12 heights by 0–45% and age 45 diameters by 0–35% as a function of planting density, suggesting that the model fails to capture the intensity or timing of density-induced competition. These underpredictions will inflate the length of time fuel treatments remain effective and decrease projected sustainable harvest levels supported by responsible management.

Keywords: density management, forest vegetation simulator, model validation, ponderosa pine, small-tree management

Small-tree density management is a foundation of most silvicultural systems. Through most of the 20th century, small-tree management emphasized maximizing seedling growth and stocking for timber volume production (Pitt and Lanteigne 2008). Although timber production is still an essential aspect of forest management, managers increasingly recognize the importance of small-tree growth and density for nontimber services. For example, the establishment and growth of seedlings and saplings are known to affect avian habitat suitability (Mills et al. 2000), a site's resistance and resilience to drought (Gleason et al. 2017), and the length of time a fuel treatment effectively reduces crown fire hazard (Tinkham et al. 2016). The density of trees in this critical early stage of stand development affects their growth and sets the basis for future forest dynamics and informs the type of ecosystem services a site can support.

In the Black Hills of South Dakota and Wyoming, USA, favorable growing conditions and prolific seed crops often coincide, resulting in abundant natural ponderosa pine (*Pinus ponderosa* var. *scopulorum* Dougl. Ex Laws.) seedling establishment (Oliver and Ryker 1990). Because of its intermediate shade tolerance, abundant seed crops every 2–5 years, and the high summer precipitation in the Black Hills, ponderosa pine often establish at more than 5,000 seedlings ha^{-1} (Shepperd and Battaglia 2002). Before widespread timber harvesting and fire exclusion in the 20th and 21st centuries, frequent low-intensity wildfires (Brown and Sieg 1996, Brown et al. 2008) and grazing (Boldt and Van Deusen 1974) mediated seedling densities. Seedling establishment is often enhanced following timber harvesting, fuel treatments, and other disturbances such as bark beetles and fire when overstory density is reduced below 9.2 m^2 ha^{-1} (Boldt and Van Deusen 1974, Oliver and Ryker 1990, Shepperd and Battaglia 2002). Seed germination and establishment can be further enhanced by disturbances that scarify the soil. Removal of competitive herbaceous vegetation through disturbance or targeted site preparation, such as herbicide application, can often promote faster growth rates in small trees (McDonald and Fiddler 1989). In the absence of natural disturbances combined with favorable

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growing conditions in the Black Hills, competition-induced thinning is slow to occur, with many 20 to 40 year-old stands of ponderosa pine still in excess of 5,000 trees ha^{-1} with a mean diameter at breast height (dbh) < 8 cm (Boldt and Van Deusen 1974). Without intervention, many of these stands stagnate at a stocking level that reduces future resistance to fire, bark beetles, and drought (Battaglia et al. 2008, Gleason et al. 2017). These slow-growing stagnated stands remain at such a small diameter class that they are unsuitable for timber production (Boldt and Van Duesen 1974). Although most regeneration in the Black Hills occurs naturally, artificial regeneration is used as a reforestation tool following large-scale disturbances. Artificial regeneration approaches can result in a range of small-tree densities depending on management objectives and the cooccurrence of natural regeneration.

Growth and yield projection systems must account for stand dynamics from this early small-tree development through mortality to be accurate and useful for management-related applications (Rauscher et al. 2000). Within the Black Hills, forest managers commonly use the Forest Vegetation Simulator's Central Rockies (FVS-CR; Keyser and Dixon 2008) variant to project forest growth and yield for comparing silvicultural alternatives and scheduling sustainable harvests. FVS is an empirical, individual tree, distance-independent, growth and yield model primarily developed and maintained by the USDA Forest Service (Dixon 2002). The FVS-CR variant is used to simulate ponderosa pine forest systems from Arizona and New Mexico in the south, all the way north to South Dakota and Wyoming. Because of limited observations of regeneration dynamics when FVS-CR was developed, tree establishment is controlled through user inputs of species, density, size, and timing of regeneration. These parameters are often prescribed by model users or defined from inventoried estimates of seedling density, often 3–10 years after disturbance. Within FVS-CR, tree growth is modeled by aligning two separate models, a small-tree model used for trees with a dbh less than 2.5 cm and a large-tree model (Keyser and Dixon 2008).

The FVS-CR small-tree growth models were developed by blending growth equations from the Utah variant and theoretical models, as limited small-tree growth observations were available within the variant's extent (Keyser and Dixon 2008). To predict small-tree growth, FVS-CR uses a two-step process. First, FVS-CR predicts the height increment and then uses the height increment to estimate the diameter growth. Once a tree crosses into the large-tree growth model, FVS-CR predicts the diameter increment first, followed by height growth. To smooth the transition from height-based growth (small-tree model) to diameter-based growth (large-tree model), FVS-CR uses a weighted average of the small and large-tree growth model height increments for all trees with a diameter between 1.3 and 5.1 cm. Large-tree growth within FVS-CR is based on the original growth equations found in the GENGYM model (Edminster et al. 1991) that were adapted to use a broader range of regional data. Within FVS-CR, submodels have been developed for simulating large-tree growth as a function of species, site productivity, tree size, and stand competition, with a specific submodel developed for Black Hills ponderosa pine.

Previous evaluation of ponderosa pine diameter growth predictions from FVS-CR have focused on the large-tree growth model. These efforts have found a consistent underprediction of diameter increment that tended to be worse for smaller diameter trees (Ex and Smith 2014, Dickinson et al. 2019). These previous studies evaluated FVS-CR growth predictions for trees >13 cm dbh, more than 20 years old, and growing at densities <1000 trees ha^{-1}; generally lacking validation during the critical early stage of stand development represented by the small-tree growth model. Although these studies point to an underprediction bias in the large-tree model, they are limited in what they can reveal about the small-tree growth model's performance or the linkages between the small and large-tree growth models.

This study seeks to quantify the influence of planting density and site preparation on small-tree development through 45 years of ponderosa pine growth on the Black Hills Experimental Forest. Using three Nelder plots with 16 densities from 296 to 11,132 trees ha^{-1} and two site-preparation strategies, the analysis characterizes the effects of density and site preparation on average tree size at 12 and 45 years following planting. Additionally, FVS-CR simulations initiated from bare ground are used to evaluate the model's ability to represent early stand development until age 45.

Methods

Study Site

Three Nelder 1a design plots were established in 1969 in the Black Hills Experimental Forest in South Dakota, USA (Figure 1A; Nelder 1962). These designs use a circular shape with spokes radiating outward from the center that provides control of planting density as the spokes increase in separation toward the outer perimeter. Although not new, the adaptation of Nelder plot designs from agriculture provides a spatially compact way of observing a wide range of planting densities with a high level of replication for studying small-tree density dynamics in forestry (Parrott et al. 2012). Such designs have been used to refine our understanding of small-tree dynamics throughout the world (Krieger 1998, Peracca and O'Hara 2008, Van Clay et al. 2013, Gadow and Kotze 2014, Sevillano-Marco et al. 2015).

The study area is located on Virkula-Pactola complex soils with an average summer temperature of 16.3°C and receives 515 mm of annual precipitation, with nearly 80% occurring during spring and summer. In 1969, the three sites were clearcut within circular 61 m radius areas (1.17 ha), and all merchantable wood was removed, and nonmerchantable material >2.54 cm diameter was chipped and spread with smaller diameters lopped and scattered in pieces <1.2 m long. Within adjacent sites, the average clearcut understory vegetation biomass has been shown to increase from ~1000 to 2500 kg ha^{-1} at 8 and 15 years postharvest (Uresk and Severson 1989). Additionally, the graminoid/forb contribution to biomass from species like bearded wheatgrass (*Agropyron subsecundum*) and western yarrow (*Achillea lanulosa*) shifted from ~70% to 50% over the same time period as shrubs species like bearberry (*Arctostaphylos uva-ursi*) increased in their contribution. Similar trends appear to have been present for the current study at planting and age 12 by comparing Figure 1A and B.

The three sites were randomly divided into two site-preparation treatments, half being 'judiciously sprayed with herbicide' (hereafter Herbicide) and the other left natural with 40–46 cm planting scalps (hereafter Scalped). Each site was established with 52 spokes radiating out from the center. Each spoke contained 18 positions at decreasing planting density the further from the center one gets (Figure 1A). To maintain control of growing conditions, guard trees at the inside and outside position of each spoke and spokes on the border between ground treatments were removed from the study ana-

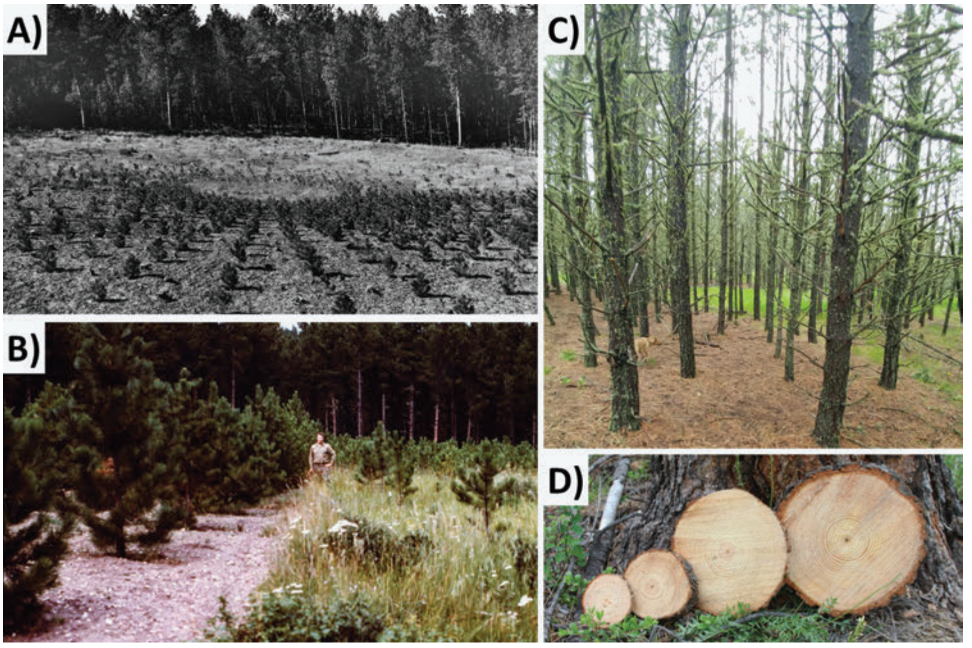

Figure 1. Images depicting Black Hills Nelder plot, including (A) conditions at planting, (B) contrasting the herbicide (left side) and scalping (right side) site-preparation treatments 12 years after planting (C), age 45 view along the site-preparation boundary (C), and (D) dbh cross-sections at 45 years after planting for 8,755, 3,322, 612, and 296 trees per hectare from left to right.

lysis. The remaining 16 positions in the 48 remaining spokes corresponded to planting densities ranging from 296 to 11,132 trees per hectare (TPH; or 0.9 to 5.8 m spacing; Table 1). This density range represents common density levels seen from mature stands ready for harvest and regenerating stands following disturbance in the Black Hills (Battaglia et al. 2008). Two-year-old bare-root ponderosa pine seedlings were sourced and planted from the Black Hills. In order to replace any seedling that might die within the first two growing seasons, additional seedlings were planted at a square spacing of 1.22 × 1.22 m adjacent to the study site and maintained for transplanting. Each site was inventoried 12 and 45 years after planting for dbh and tree height (Figure 1B and C). Although all trees were inventoried, trees were only included in analysis if they were originally planted in 1969 and their four immediate neighbors were alive during subsequent inventory periods.

FVS Simulations

FVS simulations were completed using the Black Hills ponderosa pine growth allometries of the Central Rockies variant (version 2614; Keyser and Dixon 2008). Based on regional observations, the maximum stand density index was set to 450 (10-inch diameter trees per acre; Long and Shaw 2005). Additionally, record tripling was turned off, as there were enough replicates being simulated at each density to assume stability of the Gaussian distributions used to introduce randomness to the FVS growth process (Dixon 2002). For each Nelder plot, site index was estimated for a 100-year breast height base age using Meyer (1961) based on the average height of the most open-grown trees at age 45 to be 20.2, 21.8, and 22.7 m (based on field observations, it was assumed that it took six to eight years to reach breast height). To evaluate FVS's ability to simulate seedling growth following disturbance, we initialized bare ground simulations of ponderosa pine seedlings using the PLANT Keyword. Bare ground simulations were initiated for each of the 16 planting densities and three site indices using 0.30 m tall seedlings and 100% survival for the first six years. Because FVS-CR does not account for site preparation, this was ignored in these simulations, resulting in a total of 48 bare ground simulations. The simulated quadratic mean diameter (QMD) and height for each planting density and site combination was compared against the QMD and height from each of the field observed site preparation techniques at 12 and 45 years following planting.

Analysis

To evaluate the influence of planting density, site preparation, and the interaction of these parameters on QMD and height at 12 and 45 years after planting, generalized linear mixed-effects models were fit. Because of the truncated lower distributional bounds of QMD and height, these models used a Gamma distribution with identity link and treated site as a random effect. Treating site as a random effect was necessary to remove the influence of local abiotic and biotic factors not captured in the Nelder design. Additional linear mixed-effects models were fit to the percent error (Equation 1) associated with FVS's predicted QMD and height at age 12 and 45 to evaluate how well these dynamics are captured in the model form, again site was treated as a random effect. Fixed-effect significance was calculated using the Satterthwaite (1941) approximation for degrees of freedom as it conservatively reduces the occurrence of Type I errors when the sample size is sufficiently large (Luke 2017). For the linear mixed-effect models, R^2 was derived using the method explained by Nakagawa and Schielzeth (2012). Additionally, Cohen's f^2 was calculated to standardize parameter effect sizes. All modeling and significance testing was completed using the lme4, lmerTest, and sjstats packages (Bates et al. 2015, Kuznetsova et al. 2017, Lüdecke 2020) and lmer regression function of R version 3.5.3 (R Core Team 2019). Fine scale variations within Nelder studies are known to potentially cause spa-

Table 1. Summarization of mean (standard deviation) for observed QMD and height across the planting densities within each site preparation treatment at 12 and 45 years after planting.

TPH	Spacing (m)	Age 12 QMD (cm)			Age 45 QMD (cm)		
		Herbicide	*Scalped*	*FVS-CR*	*Herbicide*	*Scalped*	*FVS-CR*
296	5.8	6.8 (2.0)	3.6 (2.2)	2.0 (0.82)	29.1 (4.3)	26.3 (4.6)	19.7 (1.5)
377	5.1	7.4 (3.1)	3.9 (2.3)	2.0 (0.82)	28.0 (4.1)	27.5 (4.2)	19.1 (1.5)
480	4.6	7.6 (3.1)	3.6 (1.8)	2.0 (0.82)	26.4 (3.9)	26.2 (4.6)	18.6 (1.5)
612	4.0	8.3 (2.9)	3.5 (1.9)	2.0 (0.82)	24.1 (4.0)	24.8 (4.4)	18.0 (1.4)
779	3.6	7.8 (3.2)	3.7 (1.5)	2.0 (0.82)	23.4 (4.5)	23.7 (3.5)	17.4 (1.4)
991	3.2	7.2 (3.0)	3.3 (1.6)	2.0 (0.82)	20.8 (3.3)	21.8 (3.6)	16.8 (1.3)
1263	2.8	7.1 (2.6)	4.0 (1.9)	2.0 (0.81)	19.9 (4.0)	20.2 (5.0)	16.2 (1.3)
1607	2.5	6.8 (2.5)	3.6 (1.7)	2.0 (0.81)	18.2 (3.9)	19.0 (4.4)	15.7 (1.3)
2046	2.2	6.6 (2.1)	3.5 (1.7)	2.0 (0.81)	17.3 (3.4)	16.8 (3.4)	15.0 (1.2)
2606	2.0	5.9 (2.2)	3.5 (1.3)	2.0 (0.80)	16.0 (3.8)	16.1 (3.6)	14.4 (1.2)
3322	1.7	5.7 (1.9)	3.9 (1.6)	2.0 (0.80)	14.8 (3.5)	15.1 (3.2)	13.8 (1.1)
4229	1.5	5.7 (1.7)	3.5 (1.8)	2.0 (0.81)	14.2 (3.7)	13.3 (3.5)	13.3 (1.1)
5388	1.4	5.7 (2.1)	3.5 (1.4)	2.0 (0.81)	12.7 (2.9)	14.1 (3.7)	12.7 (1.1)
6866	1.2	4.9 (1.6)	3.3 (1.3)	2.0 (0.81)	12.2 (3.2)	11.1 (3.3)	12.1 (1.1)
8755	1.1	4.4 (1.4)	3.0 (1.1)	2.0 (0.81)	11.1 (2.2)	10.1 (2.9)	11.6 (1.0)
11,132	0.9	4.5 (1.1)	3.0 (1.2)	2.0 (0.81)	10.7 (2.6)	10.2 (3.6)	11.1 (1.0)
TPH	**Spacing (m)**	**Age 12 Height (m)**			**Age 45 Height (m)**		
		Herbicide	*Scalped*	*FVS-CR*	*Herbicide*	*Scalped*	*FVS-CR*
296	5.8	3.1 (0.8)	2.1 (0.9)	1.9 (0.3)	11.8 (2.0)	10.7 (1.3)	10.5 (1.5)
377	5.1	3.3 (1.0)	2.2 (0.9)	1.9 (0.3)	11.4 (2.0)	10.6 (1.3)	10.5 (1.4)
480	4.6	3.4 (1.0)	2.2 (0.8)	1.9 (0.3)	10.3 (1.2)	10.5 (1.3)	10.5 (1.4)
612	4.0	3.6 (1.1)	2.1 (0.8)	1.9 (0.3)	10.1 (1.0)	10.8 (1.7)	10.5 (1.5)
779	3.6	3.6 (1.2)	2.2 (0.8)	1.9 (0.3)	11.8 (1.9)	10.7 (1.4)	10.5 (1.5)
991	3.2	3.5 (1.1)	2.0 (0.8)	1.9 (0.3)	10.9 (1.3)	10.6 (1.2)	10.5 (1.5)
1263	2.8	3.5 (1.0)	2.2 (0.8)	1.9 (0.3)	10.6 (1.2)	10.8 (1.4)	10.5 (1.6)
1607	2.5	3.4 (0.9)	2.2 (0.8)	1.9 (0.3)	10.3 (1.3)	10.1 (1.3)	10.5 (1.6)
2046	2.2	3.3 (0.8)	2.1 (0.8)	1.9 (0.3)	10.3 (1.2)	9.9 (1.4)	10.5 (1.5)
2606	2.0	3.3 (0.8)	2.2 (0.7)	1.9 (0.3)	10.5 (1.1)	10.3 (1.4)	10.5 (1.5)
3322	1.7	3.3 (0.7)	2.4 (0.8)	1.9 (0.3)	9.7 (1.1)	9.9 (1.5)	10.5 (1.5)
4229	1.5	3.3 (0.7)	2.3 (0.8)	1.9 (0.3)	9.9 (1.1)	9.6 (1.0)	10.6 (1.5)
5388	1.4	3.3 (0.8)	2.4 (0.6)	1.9 (0.3)	9.8 (0.8)	10.4 (1.2)	10.6 (1.5)
6866	1.2	3.1 (0.7)	2.3 (0.6)	1.9 (0.3)	10.2 (0.8)	10.0 (1.1)	10.6 (1.5)
8755	1.1	3.1 (0.7)	2.3 (0.5)	1.9 (0.3)	10.1 (0.9)	9.8 (1.1)	10.7 (1.6)
11,132	0.9	3.1 (0.5)	2.3 (0.7)	1.9 (0.3)	10.7 (0.9)	10.1 (1.6)	10.8 (1.7)

tial autocorrelation that violates the assumptions of generalized linear modeling and potentially biases estimates of model parameters and their variance. This was tested by developing a model to account for spatial correlation between neighbor rings within plots by adding a compound symmetry term that accounts for any remaining residual autocorrelation relating to proximity of rings within plot. As no significant autocorrelation effects were found, only the generalized linear model results are reported.

$$error\,(\%) = \frac{Predicted - Observed}{Observed} \times 100 \qquad (1)$$

Given the wide range of applications associated with FVS growth predictions, there are no agreed-upon accuracy standards. As an additional estimate of model accuracy, we calculated the proportion of FVS-CR QMD and height predictions at age 12 and 45 that were within the USDA Forest Service Region 2 Common Stand Exam measurement accuracy requirements (USDA 2014) of the true measured values. Diameter at breast height predictions within 0.25 cm and tree height predictions within 10% accuracy for the Common Stand Exam intensive protocol or 20% accuracy for the extensive protocol were considered acceptable. This approach explicitly assumes that in lieu of a standard criterion, an acceptable prediction is one that is within measurement standards. The metrics of height and QMD are also first order factors being predicted by FVS, and so quality assessment of predicted height and QMD accuracies can be extrapolated to other management decision criteria commonly derived from these metrics, like crown biomass for fuel hazard assessment or merchantable volume for harvest planning.

Results

Initial site preparation had the largest effect, according to Cohen's f^2, on the diameter and height of trees at age 12 (Table 2). Trees in the Herbicide treatment had larger tree diameters at age 12 by 1.5–4.8 cm compared to trees in the Scalped treatment, with the largest differences occurring for the most open-grown planting densities (Table 1 and Figure 2). This gradient of differences only exists because planting density had no effect on QMD at age 12 in the Scalped treatment (Table 2). Site preparation also significantly affected height at age 12, with trees in the Herbicide treatment tending to be taller on average by 1.1 m (Table 1). However, at age 45, site preparation no longer influenced the diameter or height of trees (Figure 2).

With increasing coefficient magnitudes, the influence of planting density on tree diameter strengthened over time, whereas the effect of site preparation was eliminated by age 45 (Table 2). Both treatments followed the same trend at age 45 of lower planting densities resulting in larger diameters (Figure 2). By age 45, diameters for the most open-grown planting densities were an average of 16.9 cm or ~165% larger than the most densely grown trees (Table 1 and Figure 2). Although density affected height at age 12 (Table 2), the small effect size represents ~10% variation in height in both treatments (Figure 2). Interestingly, the age 12 increase in height with decreasing density seen in the Herbicide treatment is reversed for the Scalped treatment, where height decreases for the most open-grown trees. By age 45, the effect of planting density had weakened, but represents ~10% taller trees at the lowest density levels for both treatments compared to the most densely grown trees.

Both diameter and height at age 12 were underpredicted by FVS-CR with the Herbicide treatment, producing greater errors (Table 3). Although QMD underprediction was high (35–75%) for both treatments at age 12, the Scalped treatment tended to have a third less error compared to the Herbicide treatment. Similarly, height underprediction at age 12 increased with planting density from 5–20% in the Scalped treatment, but this trend reversed for the Herbicide treatment, with underpredictions of 35–45% as planting density increased (Figure 3). These density effects also extended to the FVS-CR predictions of diameter. In the Herbicide treatment at age 12, diameter underpredictions ranged from ~75% at lower densities to ~60% for the greatest densities. These underpredictions correspond to an 8.0 and 2.5 cm negative bias of the observed QMD for the Herbicide treatment moving from lower to greater planting densities, respectively (Figure 3). Scalped treatment diameter biases were all ~45%, corresponding to a 2.9 and 0.8 cm underprediction for the sparsest and greatest planting densities, respectively.

At age 45, the FVS-CR prediction accuracies of QMD and height were no longer significantly influenced by site preparation (Figure 3). However, the effect of planting density on FVS-CR's underprediction of QMD had strengthened compared to outputs at age 12 (Table 3). For both treatments, diameter estimates varied from a 35% underprediction at the lowest density to less than 5% when densities exceeded ~6,000 seedlings ha^{-1} (Figure 3). At age 45, this means underpredicting QMD in the 296 seedlings ha^{-1} density by 9.2 and 10.2 cm for the Scalped and Herbicide treatments, respectively, when these trees were observed to average 26.3 and 29.1 cm (Table 1). Although planting density significantly influenced height prediction accuracy at age 45, the effect size was relatively small (Table 3). For both treatments, age 45 height accuracies varied from no bias at the lowest planting densities and increasing to ~10% overprediction for the greatest planting densities (Figure 3).

When evaluated against the USDA Forest Service Region 2 Common Stand Exam accuracy standards at age 12, none of the Herbicide treatment projections met either the intensive or extensive criteria for height or diameter (Table 4). However, in the Scalped treatment, 43.8% of projected tree heights met the intensive requirement (<10% error) and 72.9% of trees met the extensive requirement (<20% error). At the same time, only 2.1% of trees in the Scalped treatment met the diameter requirement (<0.25 cm error). For the age 45 assessment, 53.3 and 64.6% of trees met the intensive height accuracy requirement for the Herbicide and Scalped treatments, respectively. These numbers increased to 93.3 and 97.9% of projected heights meeting the extensive requirement. For the diameter estimates, 12.5 and 8.3% of trees in the Herbicide and Scalped treatments met the requirement, respectively.

Table 2. General linear mixed-effects model analysis of covariance in observed QMD and height at 12 and 45 years following planting. TPH, site-preparation with Herbicide as the base treatment, and the interaction of the parameters were modeled as fixed effects and site as a random effect. Models were fit using a Gamma distribution with identity link to account for the lower bound truncation of the distribution of QMD and height values.

	Age 12				Age 45			
Parameter	Coefficient	Std. Error	*p*-value	Cohen's f^2	Coefficient	Std. Error	*p*-value	Cohen's f^2
Observed QMD (cm)								
Intercept	13.908	1.146	<0.001	-	55.834	0.959	<0.001	-
ln(TPH)	−0.918	0.094	<0.001	0.129	−4.909	0.108	<0.001	4.517
Scalped	−9.864	0.828	<0.001	2.427	−0.141	0.227	0.535	0.063
ln(TPH): Scalped	0.918	0.105	<0.001	0.917	-	-	-	-
Observed Height (m)								
Intercept	4.0446	0.478	<0.001	-	11.868	0.694	<0.001	-
ln(TPH)	−0.0704	0.029	0.0144	0.565	−0.197	0.069	0.004	0.297
Scalped	−2.388	0.256	<0.001	3.047	−0.081	0.153	0.598	0.055
ln(TPH): Scalped	0.1696	0.0337	<0.001	0.518	-	-	-	-

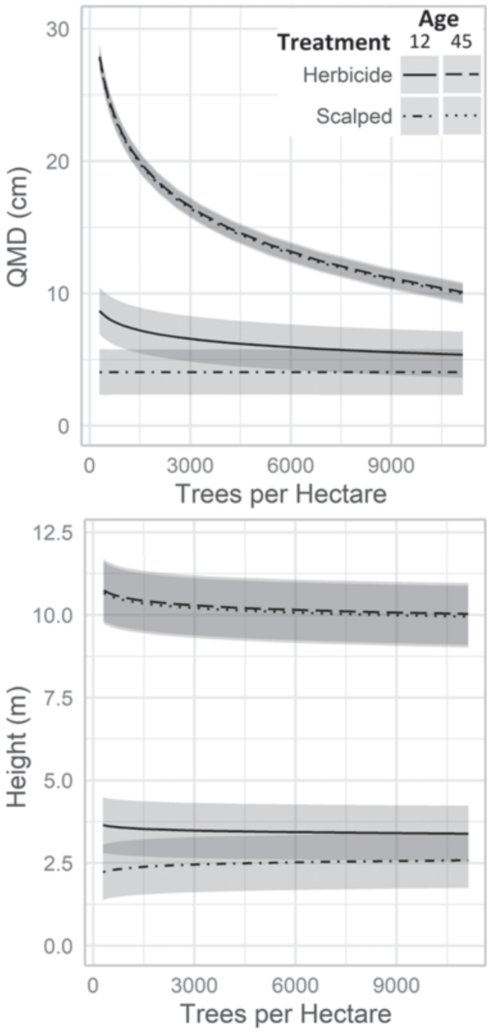

Figure 2. General linear mixed-effects model prediction of Nelder plot observed QMD (top panel) and height (bottom panel), with lines distinguishing age and treatment. Shaded bands represent 95% confidence intervals.

Discussion

Controls on Tree Size

Our results demonstrate that both herbaceous vegetation and tree density affect tree size, but the influence of these factors varied with tree development stage. Through the first 12 years of field observations, site preparation had the strongest effect on diameter and height growth (Figure 1B), with a much weaker effect from planting density. By age 12, trees in the Herbicide treatment were 47–137% larger in diameter and 35–75% taller than trees in the Scalped treatment (Table 1). These differences in tree size between treatments is attributed to the suppressing effects of herbaceous vegetation in the Scalped treatment. Although not specifically documented, it can be seen in the photography of Figure 1B that the understory plant community at age 12 had not recovered in the Herbicide treatment but there is healthy and dense understory vegetation in the Scalped treatment. At neighboring sites in the Black Hills, herbaceous understory production in clearcuts has been observed to exceed 2,000 kg ha^{-1} annually (Uresk and Severson 1989). This suggests that competition between herbaceous vegetation and seedlings is critical for both height and diameter growth during the first 12 years. These findings are supported by McDonald and Fiddler (1989), who found ponderosa pine growth was suppressed through competition with shrub and herbaceous vegetation for 18 years following planting. At age 12, the largest impact of planting density was on diameter growth for the Herbicide treatment. The reduced background competition due to herbaceous vegetation in the Herbicide treatment allowed trees to achieve a more rapid growth rate at a younger age, inducing density-dependent competition sooner.

By age 45, the effect of planting density strengthened (Figure 1D), with the trees at the lowest planting density ~2.5–3 times larger in QMD than the most densely grown trees (Table 1). Density-dependent growth is generally thought of as a standing rule of small-tree management and has been widely seen in other studies (Pitt and Lanteigne 2008). Similar density effects on growth have been anecdotally observed to cause stand stagnation within the Black Hills when young trees are not sufficiently thinned (Boldt and Van Deusen 1974). Additionally, by age 45, site preparation no longer influences QMD or height. This lack of residual site preparation influence on tree size for all densities was surprising given the strength of effect it had at age 12. However, most studies evaluating site preparation effects look at less than 10 years (Lanini and Radosevich 1986), with longer studies evaluation 20 year responses (McDonald and Fiddler 1989); our results suggest that revisiting these studies could be warranted. Instead, the small variation in height (<0.5 m) was explained as a function of planting density (Figure 2). The relatively small effect size of planting density on height we observed at age 45 is supported by empirical observations (Peracca and O'Hara 2008) and theories of plant physiology (Koch et al. 2004) that suggest height growth is less sensitive to stand density than diameter growth.

FVS-CR Bare Ground Simulations

Growth and yield simulations provide a framework to support management decisions. To ensure their reliability, these systems need to capture forest dynamics starting from tree establishment through growth, maturation, and mortality. The FVS-CR bare ground simulation predictions of height at age 12 suggest the adapted theoretical models used in FVS-CR for small-tree height growth provide a reasonable accuracy (0–15% error) in describing height in the Scalped treatment and a substantial underprediction for the Herbicide treatment (~40% bias; Figure 3). The study's Scalped treatment provides a close approximation of the herbaceous competition that natural regeneration faces (McDonald and Fiddler 1989) in the Black Hills following harvest or bark beetle infestation. Trees within our scalped planting appear to have reached breast height around eight years after planting, and natural regeneration following disturbance in the Black Hills reaches breast height at an age of 7 to 18 years. Although our scalped treatment appears on the faster end of this growth rate, it still makes for a reasonable approximation. Therefore, the relatively small errors in height for the Scalped treatment hold promise for applications dependent on models representing this dynamic.

When it comes to FVS-CR simulated diameters, the modeled trees reached 2 cm QMD at age 12 regardless of density. This substantially differs from the observed QMDs, which varied between low and high densities from 4.5–8.3 cm in the Herbicide treatment and 3.0–4.0 cm in the Scalped treatment (Table 1). These differences correspond to QMD underpredictions of 56–76% in the Herbicide treatment and 33–50% in the Scalped

Table 3. Linear mixed-effects model analysis of covariance in FVS QMD and height prediction errors (%) from simulations initiated using bare ground planting. TPH, site-preparation with Herbicide as the base treatment, and the interaction of the parameters were modeled as fixed-effects and site as a random-effect.

	Age 12				Age 45			
Parameter	Coefficient	Std. Error	*p*-value	Cohen's f²	Coefficient	Std. Error	*p*-value	Cohen's f²
FVS-CR QMD Error (%)	$R^2_{Cond} = 0.89$		$R^2_{Marg} = 0.65$		$R^2_{Cond} = 0.84$		$R^2_{Marg} = 0.67$	
Intercept	−107.31	7.23	<0.001	-	−93.19	5.18	<0.001	-
ln(TPH)	5.07	0.73	<0.001	0.593	10.32	0.52	<0.001	2.074
Scalped	58.25	7.81	<0.001	0.786	0.85	1.162	0.466	0.077
ln(TPH): Scalped	−4.35	1.03	<0.001	0.445	-	-	-	-
FVS-CR Height Error (%)	$R^2_{Cond} = 0.89$		$R^2_{Marg} = 0.72$		$R^2_{Cond} = 0.57$		$R^2_{Marg} = 0.05$	
Intercept	−51.87	7.88	<0.001	-	−14.83	7.20	0.0678	-
ln(TPH)	1.41	0.83	0.0933	0.256	2.29	0.70	0.0016	0.347
Scalped	74.57	8.93	<0.001	0.880	0.43	1.56	0.7837	0.029
ln(TPH): Scalped	−5.68	1.18	<0.001	0.508	-	-	-	

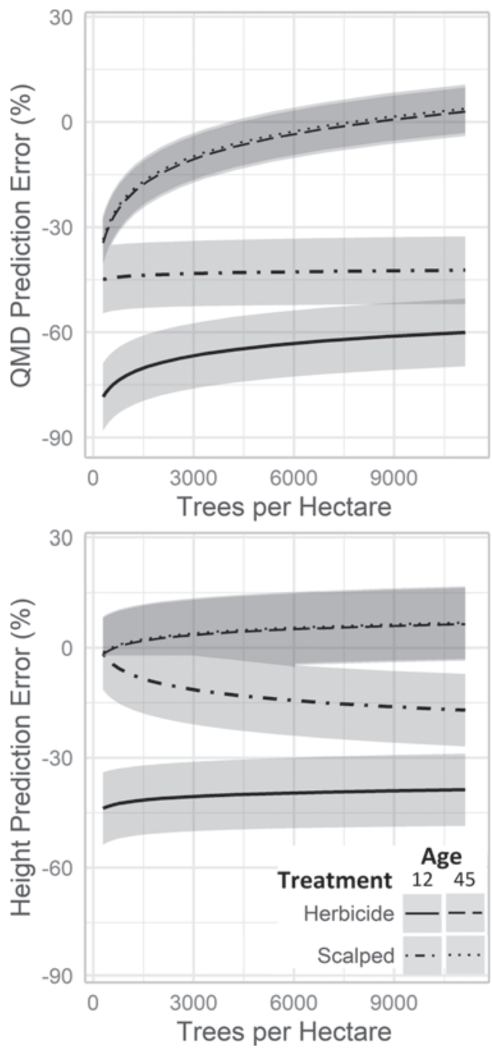

Figure 3. Linear mixed-effects model predictions of FVS-CR bare ground simulation prediction errors in QMD (top panel) and height (bottom panel), with lines distinguishing age and treatment. Shaded bands represent 95% confidence intervals.

treatment. Although our analysis points to underpredictions in even-aged forest systems, similar trends of underprediction have been observed in validation of multiaged forest stands (Ex and Smith 2014). Because diameter is predicted as a function of height in the FVS-CR small-tree growth model, the presence of 2–3 times more underprediction bias in diameter predictions than height predictions points to an issue with the models underlying height-to-diameter relationship. This inequity in diameter and height prediction bias occurred for all densities but was closer to being balanced in the Scalped treatment.

At age 45, FVS-CR resulted in an overprediction of height by 0 to 10% regardless of the site preparation treatment (Figure 3). This shift from 10–40% underprediction at age 12 to a slight overprediction at age 45 indicates that the FVS-CR height growth increment from age 12 to age 45 is greater than was seen in the Nelder plots. QMD accuracies for both treatments followed similar trends at age 45, from less than 5% error for trees grown at the greatest planting densities to 35% underprediction for the most open-grown condition (Figure 3). FVS-CR's underprediction ranges from 0 to 35% as a function of planting density suggest that the model fails to capture the intensity or timing of density-induced competition in these even-aged growth trials. This underprediction bias we found for even-aged systems is greater than previously reported for FVS-CR by Ex and Smith (2014) and Dickinson et al. (2019). The presence of relatively small errors in FVS-CR estimates of height across densities 45 years into the simulation but QMD underpredictions that are dependent on planting density suggests that the Black Hills large-tree growth equation underrepresents the effect of stand density on diameter growth. Recent assessments have significantly improved accuracy in FVS-CR diameter increment projections by adding crown ratio as an additional parameter to the large-tree model (Dickinson et al. 2019). Further work is needed to corroborate how these findings translate to natural regeneration where local variation and herbaceous competition may shift the observed growth rates and FVS-CR prediction accuracies.

Implications on Small-Tree Management and Modeling

Growth and yield models are tasked to represent and inform a wide range of forest dynamics and management considerations

Table 4. Percentage of FVS-CR projected QMD and height observations meeting USDA Forest Service Common Stand Exam accuracy requirements.

Treatment	Age	All Exams	Intensive	Extensive
		QMD (<0.25 cm error)	Height (<10% error)	Height (<20% error)
Herbicide	12	0.0	0.0	0.0
Scalped	12	2.1	43.8	72.9
Herbicide	45	12.5	53.3	93.3
Scalped	45	8.3	64.6	97.9

from timber management to fuel treatment design. Interpretation of model validation results is often easier in the context of an application with a defined precision criterion (Rykiel 1996). However, across most ecological modeling applications, there is seldom a single agreed-upon criterion and the degree of precision needed for supporting decisions is rarely reported (Hoffman et al. 2016). Despite these limitations in model validation, it is possible that using expected human observation accuracies can provide a context for interpretation. Generally, FVS-CR projections at age 12 captured most heights in the Scalped treatment within the USDA Forest Service's Common Stand Exam expectations, and QMD values have a much lower fidelity rate (Table 4). By age 45, the model's predictions nearly meet the human observation standard for height on every tree in the Scalped treatment. However, there remain substantial departures from the human expected accuracy for diameters.

Modeling small-tree growth has implications for management decision-making regarding a range of activities, such as assessing fuel treatment effectiveness and sustainable harvest scheduling. In modeling crown fire potential, the most important fuel parameter is arguably the distance between surface and aerial fuels (Van Wagner 1977). In postfuel treatment effectiveness assessments, this distance is responsive to crown recession and regeneration density (Tinkham et al. 2016). Additionally, it is widely understood that young ponderosa pine seedlings and saplings have high mortality rates during fire (Battaglia et al. 2008, 2009) and that increased establishment densities and growth rates of these young trees can significantly reduce the longevity of fuel treatments (Ex et al. 2019). FVS-CR's underprediction of height and QMD for 12-year-old trees will propagate through to affect the distance between surface and aerial fuels, ultimately reducing crown fire hazard. This will occur through underpredictions of small-tree height growth, increasing the distance between mature overstory canopy and regenerating ladder fuels. In contrast, underpredictions of diameter will result in reduced ladder fuel biomass estimates. These underpredictions will lead to FVS-CR predicting longer posttreatment periods of effective fuel hazard reduction efforts (Tinkham et al. 2016). Such errors could be most consequential in the wildland-urban interface, where potential impacts could be minimized through integration of effectiveness monitoring and adaptive management.

FVS is the most widely applied tool for USDA Forest Service planning activities from stand to forest levels, but the CR variant's underrepresentation of how stand density affects small-tree growth through time has significant implications. All National Forests are required to maintain and follow short- to moderate-term (10–20 year) planning horizons for guiding both stand improvement activities and commercial harvests. The underprediction of tree height and diameter growth rates in stands with high regeneration densities during the first 12 years could delay scheduling of precommercial thinning and lead to loss of growth or stand stagnation, a situation seen anecdotally within the Black Hills (Boldt and Van Deusen 1974). Similarly, the QMD underpredictions we observed until age 45 propagate through volume estimates and affect modeling of forest-wide sustainable yields and commercial harvesting rates. Such underpredictions will cause projected sustainable harvest levels to be reduced from what the land base and responsible management could support.

Several options exist to overcome model prediction bias and improve the reliability at both local and broader scales. FVS was designed for local tuning of the model through automated growth calibration from user-provided observations and multipliers that can be used to increase or decrease growth rates based on locally observed values (Dixon 2002). Given our observed underestimation, these growth multipliers could allow users to increase growth rates in the small-tree growth model such that diameters and heights might be unbiasedly predicted by the time they enter the large-tree growth model. However, because prediction bias varied across planting density, it is unlikely that calibration through FVS's multipliers would be able to improve growth rate predictions for more than a small range of densities at a time. More aggressive options exist to refit parameters in the existing FVS-CR growth algorithms to more reliably represent local growing conditions without completely changing the model (Russell et al. 2013). Alternatively, if these biases exist more broadly across the CR variant, it may be necessary to explore alternative model forms and parameters to improve model performance. To overcome the inconsistent diameter underprediction rates observed through time and across densities, larger model development efforts could be undertaken to use data within the CR variant geographic extent instead of an adaptation of growth relationships from other regions. Model refitting and parameter alterations in the FVS Southern variant resulted in a 5% reduction in prediction bias and 5% improvement in prediction reliability (Radtke et al. 2012). Through a combination of long-term forest observations established over the last 40 years across the United States and improved continuity in the US Forest Service Forest Inventory and Analysis network (Tinkham et al. 2018), datasets exist to enable improved representation of local forest growth dynamics.

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