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Assessing and modeling total height and diameter increment of ponderosa pine planted in Minnesota, USA

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Abstract

Forest managers are increasingly planting non-native tree species that are adapted to anticipated future conditions such as increased droughts. This work quantified individual tree growth patterns of ponderosa pine (*Pinus ponderosa* P. & C. Lawson), a western US species, planted outside of its natural range in Minnesota, USA. After 50 years, survival was as high as 69% for some ponderosa pine seed sources, and individuals from the Black Hills, Eastern High Plains, and South and East Montana regions of the western US were some of the tallest and largest diameter trees grown in Minnesota. Predictions of total tree height and diameter increment displayed the lowest bias when equations for ponderosa pine in the western US were used rather than equations for red pine (*Pinus resinosa* Ait.) in Minnesota, a species that occupies a similar ecological niche. These results indicate that using existing growth and yield equations from a species' native range may provide a suitable representation of growth and yield patterns if observations from outside the species' native range are lacking. Historical data from provenance trials such as these can provide a long-term record to quantify the growth potential of non-native species in anticipation of future climate scenarios.

Keywords *Pinus ponderosa* · Growth and yield · Seed source · Provenance trial · Climate adaptation

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Introduction

As shifting climatic conditions continue to influence the distribution and range of tree species, natural resource managers are increasingly considering adaptation and mitigation strategies aimed at increasing resistance, promoting resilience, or facilitating transition in forest ecosystems (Millar et al. 2007). Facilitating transition may include the promotion of future adapted species through range expansion or the use of assisted migration by humans (Park and Talbot 2018). An ongoing scientist-manager partnership, the Adaptive Silviculture for Climate Change (ASCC) study, is exploring this concept by planting ponderosa pine (*Pinus ponderosa* P. & C. Lawson), a western US species, as an alternative to the native red pine (*Pinus resinosa* Ait.) due to its increased tolerance to drought in northern Minnesota (Nagel et al. 2017). Red pine is widely distributed across central and northeastern North America (Burns and Honkala 1990). It is hypothesized that ponderosa pine would maintain key ecological characteristics and provide a high value economic product. The western border of Minnesota is approximately 600 km from the closest native range of ponderosa pine in the Black Hills region of southwestern South Dakota, but early research indicates that specific seed sources of ponderosa pine may show adequate levels of growth and survival in Minnesota (Muller et al. 2019; Nagel et al. 2017; Radsliff et al. 1981).

As information on the growth of novel and non-native species in new areas is limited, managers are restricted to using existing models from their native range to describe allometric and growth relationships for trees planted in new areas. The implementation of these existing models may not be suitable since current models may not capture conditions outside of the species native range and/or how the species respond to new and changing climatic conditions (Crookston et al. 2010). Long-term data (i.e., tree measurements up to 50 years) and modeling tools that describe the allometry and growth of species planted in non-native areas (e.g., ponderosa pine in Minnesota) are often lacking and may be of limited use by forest managers, complicating decisions to implement adaptive management strategies to solve forestry problems.

Essential components in understanding forest growth and yield is the association between tree diameter, height, and diameter and height increment, all of which are quantitative relationships required to accurately determine stem volume (Weiskittel et al. 2011). Species-specific models of total height and diameter increment are often developed and suggested for use in a specific region, such as the geographical variants inherent to the Forest Vegetation Simulator, a semi-distance-independent growth model developed by the US Forest Service that forecasts individual trees through time (Crookston and Dixon 2005). In provenance or genetic trials, models are typically developed that incorporate seed sources or genetic varieties as random effects that influence tree allometry or growth (e.g., Leites et al. 2012b; Sabatia and Burkhart 2013). Despite the fact that recent advances in modeling techniques capture the variability of growth across different geoclimatic gradients, equations are lacking that can be used to describe the growth of species planted in regions outside of their native range. One alternative is to instead use equations for a species in the region that has similar stature and ecological traits for a species outside of its native range, e.g., substituting red pine growth and yield equations to quantify ponderosa pine. In other words, should forest managers use an existing equation for a similar species in the non-native range, or should they adapt existing growth equations of a similar species in the native range?

The objective of this study is to quantify individual tree growth patterns of ponderosa pine grown outside of its natural range in Minnesota, USA. Specific objectives are to (1)

examine the performance of seed sources on the height and diameter growth of ponderosa pine up to 48 years after field planting, (2) develop models of total tree height and diameter increment of ponderosa pine grown in Minnesota, and (3) compare height and diameter increment observations with predictions from models in regions where ponderosa pine is native and for models for a similar species.

Methods

Study area

Ponderosa pine is the most wide-ranging pine species across North America (Critchfield and Little 1966) and in the United States has a native range that spans 17 western states. There are two main varieties of ponderosa pine: *P. ponderosa* var. *ponderosa* and *P. ponderosa* var. *scopulorum*. However, there continues to be research on the classification of *P. ponderosa* var. *arizonica.* The two main varieties have distinct ranges with limited overlap in west-central Montana. *P. ponderosa* var. *scopulorum* extends generally from southern California north to southern British Columbia, while *P. ponderosa* var. *scopulorum* ranges from northern Mexico north to Montana and east to central Nebraska (Rehfeldt et al. 2014).

Minnesota's landscape is characterized by four ecological provinces: the prairie parkland, tallgrass aspen parkland, eastern broadleaf forest, and Laurentian mixed forest (Minnesota Department of Natural Resources 2018). The total area of forest land in Minnesota occupies 7.07 million hectares and red pine is the second largest contributor to live-tree volume across the state (Miles and VanderSchaaf 2015). There are three pine species native to Minnesota: red pine, eastern white pine (*Pinus strobus* L.), and jack pine (*Pinus banksiana* Lamb.). Minnesota pine forests occupy approximately 400,000 ha of land (Miles et al. 2016). With this land base, the red pine cover type is the most abundant in terms of area and provides the majority of softwood sawtimber harvested annually (greater than $13 million US dollars in stumpage) in Minnesota.

Forest inventory and analysis data

Forest Inventory and Analysis data were used to examine the current range distribution of ponderosa pine. The FIA program monitors forests by establishing permanent sample plots across the US using a three phase inventory (Bechtold and Patterson 2005). If the FIA program identifies an area as forested, field personnel establish an inventory plot at that location. These inventory plots consist of four 7.32-m fixed radius subplots for a total plot area of approximately 0.07 ha where standing tree and site attributes are measured, and plots are sampled at an intensity of approximately 1 plot per 2400 ha. All live and standing dead trees with a diameter at breast height (DBH) of at least 12.7 cm are measured on these subplots. Within each subplot a 2.07-m microplot is established where live trees with a DBH between 2.5 and 12.7 cm are measured.

A total of 59,183 inventory plots were compiled across 17 western US states throughout the native range of ponderosa pine. In addition, 6707 inventory plots were examined from Minnesota, a state known to exist outside the range of the species. In the western US states 19% of plots contained at least one ponderosa pine tree whereas no plots in Minnesota contained an observation of the species. Each FIA plot was summarized to determine whether or not ponderosa pine occurred on the plot (Fig. 1). Recurring plot measurements began in
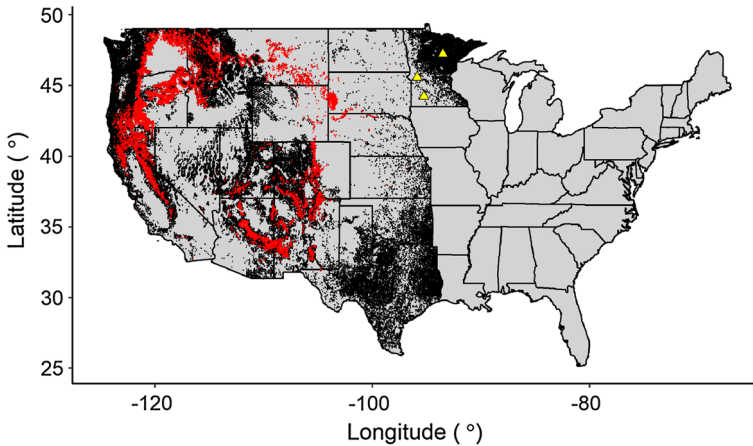
Fig. 1 Current distribution of ponderosa pine occurrence (red; $n=11{,}090$ plots) and absence (black; $n=54{,}800$ plots) at approximate locations of Forest Inventory and Analysis plots across the native range of the species and locations of plantings in Minnesota, USA (yellow; $n=3$). (Color figure online)

1999 with remeasurements occurring approximately every ten and 5 years in western states and Minnesota, respectively, with the final measurement occurring in 2016. Only the most recent measurement of a plot was employed in this analysis.

Tree data

As early as 1914 and as late as 1970, several ponderosa pine trials with *P. ponderosa* var. *scopulorum* were established with various provenances across Minnesota (Fig. 1). The purpose of these trials was to assess the suitability of various seed sources for planting across the state, notably as a component of protection plantings in the prairie region of Minnesota (Tauer et al. 1974). The survival of ponderosa pine at the sites was mixed, as many sites experienced low initial survival. Others were likely affected by droughts in the late 1960s and mid 1970s (Alm et al. 1972; Radsliff et al. 1981; Schantz-Hansen 1932; Schantz-Hansen and Hall 1952; Tauer et al. 1974).

Measurements of survival, total tree height (HT), and diameter at breast height (DBH) were collected periodically at three sites from ages 12 through 48 years. Trees planted at these sites were a component of a larger provenance trial of ponderosa pine and were planted from 1968 through 1970 at a spacing of 2.4 × 2.4 m. In total, 72 different seed sources were examined across these sites in a randomized complete block design (Radsliff et al. 1981; Tauer et al. 1974). Two of these sites were located in the prairie parkland (Morris and Lamberton) and another in the Laurentian mixed forest ecological province (Grand Rapids).

In 2016, survival, HT and DBH were collected on all living trees (representing 70 surviving seed sources) at the Morris and Lamberton sites when trees were 48 years old in the field. At the Grand Rapids site HT and DBH measurements were used that were collected in 1982 when trees were 12 years old in the field due to limited survival (Table 1). There was no evidence of forest management activities at any of the sites; however, stand edges were affected over time due to unrelated anthropogenic activities such as road construction and agricultural field expansion. We tested for significant differences in HT and

Table 1 Number of surviving trees (n), survival percentage (Surv [%]), mean height (HT; m), and diameter at breast height (DBH; cm; standard deviations in parentheses) for ponderosa pine measurements by regional seed source group at three locations in Minnesota, USA

Regional group	Grand Rapids (age = 12 years)				Lamberton (age = 48 years)				Morris (age = 48 years)			
	n	Surv (%)	HT	DBH	n	Surv (%)	HT	DBH	n	Surv (%)	HT	DBH
Black Hills[a]	77	71.3	3.2 (0.8)	6.2 (2.3)	141	47.2	13.1 (1.8)	23.2 (5.7)	97	53.0	12.9 (1.4)	23.0 (4.9)
Central High Plains	60	45.5	3.1 (0.7)	6.1 (2.2)	175	45.8	12.4 (1.8)	23.5 (5.3)	103	46.4	12.3 (1.3)	21.9 (4.1)
Central Montana	16	57.1	3.4 (0.8)	7.4 (2.6)	20	29.4	11.8 (2.1)	19.8 (3.5)	10	22.2	12.4 (1.5)	24.9 (5.7)
Central Rockies and Plains	94	41.2	2.8 (0.6)	5.1 (2.1)	176	27.5	11.8 (1.9)	22.4 (6.0)	100	25.9	11.7 (1.7)	20.1 (5.4)
Eastern High Plains[a]	22	50.0	3.5 (0.5)	7.0 (1.9)	75	54.7	13.9 (1.6)	26.5 (4.6)	54	69.2	13.7 (0.9)	26.1 (5.5)
Far West[b]	3	7.5	–	–	2	2.9	–	–	0	0.0	–	–
North Central Montana	33	68.8	3.6 (0.5)	7.6 (2.0)	65	52.4	12.5 (2.1)	22.8 (6.1)	48	54.5	12.4 (1.4)	23.1 (4.8)
South and East Montana[a]	88	66.7	3.7 (0.7)	7.5 (2.2)	174	52.9	13.0 (2.0)	24.0 (5.2)	107	55.2	13.3 (1.1)	25.6 (5.1)
Southern Rockies[b]	3	5.4	–	–	13	5.7	–	–	4	2.8	–	–
SW N Dakota; NW S Dakota	30	62.5	3.1 (0.8)	5.8 (2.4)	72	56.3	12.6 (2.1)	24.3 (6.4)	41	51.2	12.3 (1.7)	23.0 (5.0)
All trees	426	49.3	3.3 (0.8)	6.4 (2.3)	913	37.9	12.7 (2.0)	23.5 (5.6)	564	38.7	12.6 (1.5)	23.1 (5.3)

[a] Trees from these regions were subsequently cored and analyzed for diameter growth at Lamberton and Morris

[b] Means for these regions not shown due to few observations, but are included in 'All trees' summary

DBH within site locations using analysis of variance with seed source as the main factor. Tukey's-adjusted multiple comparisons were used to distinguish among effects of factor levels where warranted.

In 2018, the Morris and Lamberton sites were revisited and increment cores were collected from existing ponderosa pine trees. In total, 114 trees were cored (one from each tree) from 23 seed sources at a height of 30 cm above the ground from trees originating from three regions: two regions identified by Radsliff et al. (1981) as promising seed sources measured by their survival and height growth (Eastern High Plains [$n=20$] and South and East Montana [$n=49$]), and a third region (Black Hills [$n=45$]) that was planted on the aforementioned ASCC study. In the laboratory, extracted cores were mounted, sanded, and measured using a Velmex micrometer for their annual ring width using standard dendrochronological practices (Stokes and Smiley 1968) and crossdated using COFECHA (Grissino-Mayer 2001; Holmes 1983) to ensure dating accuracy.

Individual tree models

Modeling height-diameter relationship

For modeling the static HT-DBH relationship with the 2016 ponderosa pine data, we used a mixed models framework. The seed source of ponderosa pine was selected as the random effect as past studies have highlighted the advantages of incorporating seed sources or genetic varieties as random effects (Leites et al. 2012b; Sabatia and Burkhart 2013). The random effect was specified on the intercept term and the Robinson and Wykoff (2004) mixed model form was evaluated as:

$$\text{HT} = 1.37 + \exp\left[\alpha_0 + a_i + \alpha_1 \text{DBH}^{\alpha_2}\right] \tag{1}$$

where HT is the predicted total tree height (m), DBH is outside-bark diameter at breast height (cm), α_i's are fixed-effects parameters, and a_i is a random intercept parameter for the ith seed source in the study. A variance power function on DBH was used to represent the non-homogeneous variance observed in the response variable. This function took the form $\text{Var}\left(\varepsilon_{\text{ijk}}\right) = \sigma^2 \text{DBH}_{\text{ijk}}^{\delta}$, where σ^2 was the residual sums of squares and δ was the variance function coefficient.

Modeling diameter increment

We used tree cores collected in 2018 to reconstruct individual tree DBH for the three primary regional seed sources. For each annual ring width measurement, we first calculated outside-bark stump diameter at 30 cm using the equations of Larsen and Hann (1985) for ponderosa pine. This corresponded with the height where cores were extracted. We then estimated DBH from stump diameters using the equations of Demaerschalk and Omule (1982) for ponderosa pine (labeled 'western yellow pine' in their study). This allowed us to reconstruct annual DBH for trees at the Morris and Lamberton sites. To minimize issues with within-tree correlation from diameter-age pairs collected from the tree cores, we followed an approach outlined by Sánchez-González et al. (2005) through selecting every fifth diameter-age pair within a tree. In total, 768 growth observations were used from the 114 trees resulting in a minimum and maximum DBH of 1 and 39 cm, respectively.

We also used a mixed models framework to model the annual diameter increment. Using the Hann et al. (2003) model as a baseline, we ultimately chose a model form that included a random effect on the slope parameter on the DBH^2 term:

$$\Delta DBH = \exp\left[\beta_0 + \beta_1 \log(DBH + 1) + (\beta_2 + b_i)DBH^2\right] \tag{2}$$

where ΔDBH is the predicted annual diameter increment (cm) obtained through the annualization approach of Weiskittel et al. (2007), β_i's are fixed-effects parameters, and b_i is a random intercept parameter for the ith seed source in the study. A variance power function on DBH was used to represent the non-homogeneous variance and a first-order continuous autoregressive correlation structure (CAR1) related consecutive measurements of DBH and allowed the fitting of unbalanced data (Gregoire et al. 1995).

Intra- and inter-species model comparisons

We compared results from our fitted models to those existing in the literature. We made predictions of HT using three equations developed for ponderosa pine in the western US, including Eastern Montana (Keyser and Dixon 2008b) and the central Rockies (Keyser and Dixon 2008a). For ΔDBH we compared to an equation developed in southwest Oregon (Hann and Larsen 1991), with the anticipation that this region could present a near-maximum greatest growth potential for the species. Because ponderosa pine is considered a species that could have the potential to replace the ecological niche of red pine across Minnesota's landscape, we also compared our developed models to commonly used ones for red pine. This included two equations for HT (Dixon and Keyser 2008; VanderSchaaf 2012) and ΔDBH (Dixon and Keyser 2008; Lessard et al. 2001) that have been developed for red pine in the region. A complete presentation of these equations can be found in Supplemental Material 1.

The mean predictions and mean and standard deviation of bias were calculated for each model on the Minnesota ponderosa pine dataset. We also used the 'equivalence' package in R (Robinson 2016) to conduct two one-sided tests of equivalence. We analyzed the difference in diameter increment from the observed HT or ΔDBH and predicted values from the developed equations in addition to those compiled from the literature (i.e., Supplemental Material 1). The magnitude of the region of similarity was specified as 25% of the standard deviation of the difference in observed and predicted values. We also calculated the minimum percentage of standard deviation that would have resulted in a successful validation, termed the minimum detectable negligible difference (Parkhurst 2001), where higher values for MDND indicate more dissimilarity between observations and predicted values.

Results

Ponderosa pine tree data

Survival at the Grand Rapids, Lamberton, and Morris sites was 49, 38, and 39%, respectively, for a total of 1903 surviving trees (Table 1). Individuals at the Lamberton and Morris sites displayed similar tree HT and DBH characteristics after 48 years, with some differences after analyzing by regional seed source group (Table 1). Eastern High Plains seed sources displayed the tallest (13.9 ± 1.6 [mean $\pm$ SD] and 13.7 ± 0.9 m) and largest diameter trees (26.5 ± 4.6 and 26.1 ± 5.5 cm) when compared to all regional groups at Lamberton

Table 2 Summary of tree measurements collected from 50-year-old ponderosa pine grown in Minnesota, USA used for diameter growth modeling

Variable[a]	n	Mean	SD	Min	Max
DBH (cm)	114	19.5	8.6	6.1	40.6
HT (m)	114	13.4	7.7	1.8	16.5
CR (%)	114	50.0	16.1	9.3	91.3
ΔDBH (cm year^{-1})	768	0.53	0.38	0.02	2.16

[a]Variables are: number of trees (n); diameter at breast height (DBH); total tree height (HT); uncompacted live crown ratio (CR); annual diameter increment (ΔDBH)
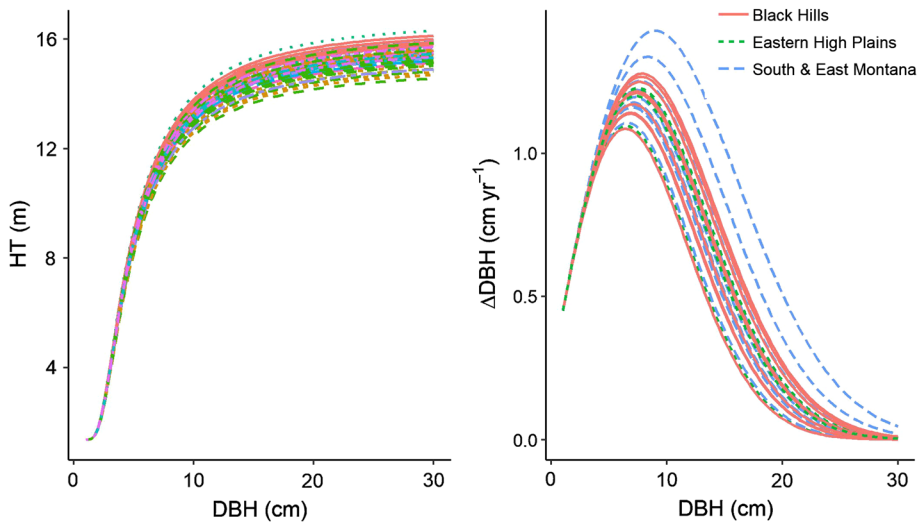
Fig. 2 Predictions of total tree height (HT) and annual diameter increment (ΔDBH) for ponderosa pine grown in Minnesota, USA from three different regions representing 70 and 23 different seed sources for HT and ΔDBH, respectively

and Morris, respectively. The Black Hills and South and East Montana seed sources were the second and third next tallest seed sources on average at these sites. When measured in 2018, the mean HT for the top 50% tallest trees at Morris and Lamberton was 14.7 m at 50 years old, which may serve as an approximation for site index that is commonly collected across the region. After 12 years at the Grand Rapids site, the South and East Montana and North Central Montana seed sources displayed the greatest HT (3.7 ± 0.7 m) and DBH (7.6 ± 2.0 cm), respectively (Table 1; Figure S1).

For the trees in which cores were extracted for diameter increment modeling, mean DBH was 19.5 ± 8.6 and ranged from 6.1 to 40.6 cm. Mean ΔDBH of these data was 0.53 ± 0.38 cm year^{-1} (Table 2).

Height-diameter

Models indicated an increasing HT for larger-diameter trees, reaching an asymptote around 12 cm DBH (Fig. 2). Models of HT improved marginally when incorporating seed source as a random effect (fit index of 0.89 with fixed effects, only compared to a

Table 3 Parameters (standard errors in parentheses) for estimating total tree height (HT; Eq. 1) and annual diameter increment (ΔDBH; Eq. 2) for ponderosa pine grown in Minnesota, USA

Parameter	Value	Parameter	Value
HT (m)		ΔDBH (cm year^{-1})	
α_1	2.6737 (0.0165)	β_0	-1.4735 (0.1167)
α_2	-65.3377 (8.1588)	β_1	0.9893 (0.0630)
α_3	-1.7897 (0.0600)	β_2	-0.0083 (0.0005)
SD (α_1)	0.0325	SD (β_2)	0.0014
Residual standard error (m)	1.10	Residual standard error (cm)	2.16
Fit index (fixed effects, only)	0.89	Fit index (fixed effects, only)	0.45
Fit index (fixed + random effects)	0.90	Fit index (fixed + random effects)	0.51

[a]Models are: $HT = 1.37 + \exp\left[\alpha_0 + a_i + \alpha_1 DBH^{\alpha_2}\right]$, and $\Delta DBH = \exp\left[\beta_0 + \beta_1 DBH + (\beta_2 + b_i)DBH^2\right]$

[b]Variables are: total tree height (HT; m); diameter at breast height (DBH; cm)

fit index of 0.90 with fixed and random effects; Table 3). The mean HT prediction of the fixed and fixed plus random effect models (10.4 and 10.5 m, respectively) was similar to the mean observed HT in the data (10.5 m), mean bias for both models was within 0.11 m, and equivalence tests with a null hypothesis of dissimilarity were rejected (Table 4; Figure S2).

When compared to all other static HT models available in the literature, equivalence tests with a null hypothesis of dissimilarity were not rejected, indicating large disagreement between observed and predicted values. The best-performing HT model examined was the Black Hills ponderosa pine submodel available in the Central Rockies variant of FVS (Keyser and Dixon 2008a), but led to overprediction of HT when compared to observed values (mean bias of -0.58 m). The two models of red pine available in the US Lake States resulted in a much greater overprediction of HT (mean bias of -2.63 and -3.32 m; Fig. 3; Table 4).

Diameter increment

Models indicated a maximum ΔDBH between 8 and 10 cm (Fig. 2). The random effects of seed source had a greater influence on ΔDBH compared to HT: fit index was 0.45 for a fixed effects only model compared to 0.51 for a model that employed both fixed and random effects (Table 3). The mean ΔDBH prediction of the fixed and fixed plus random effect models (0.54 cm year^{-1}) was similar than the mean observed ΔDBH in the data (0.53 cm year^{-1}). However, mean bias for both models was relatively minor and equivalence tests with a null hypothesis of dissimilarity were rejected (Table 4; Figure S3).

When compared to all other ΔDBH models available in the literature, equivalence tests with a null hypothesis of dissimilarity were not rejected, indicating large disagreement between observed and predicted values. The best-performing ΔDBH model examined was the ponderosa pine model developed in southwest Oregon by Hann and Larsen (1991), but led to overprediction of ΔDBH when compared to observed values (mean bias of -0.08 cm year^{-1}). The two models of red pine available in the US Lake States resulted in underprediction of ΔDBH (mean bias of -0.24 and 0.31 cm year^{-1}; Fig. 3; Table 4).

Table 4 Mean predictions, mean bias, and equivalence test results of total tree height (HT) and annual diameter increment (ΔDBH) for ponderosa pine grown in Minnesota using various models compiled from the literature

Species and region	Citation	HT (m)			Result[a]	MDND (%)[b]
		Mean prediction	Mean bias	SD bias		
Ponderosa pine; fixed effects	This study	10.4	0.11	1.41	E	23
Ponderosa pine; fixed + random effects	This study	10.5	0.08	1.37	E	21
Ponderosa pine; Black Hills	Keyser and Dixon (2008a)	11.1	−0.58	1.73	NE	47
Ponderosa pine; Central Rockies	Keyser and Dixon (2008a)	9.2	1.38	1.77	NE	90
Ponderosa pine; Eastern Montana	Keyser and Dixon (2008b)	9.8	0.73	1.61	NE	58
Red pine; Minnesota	VanderSchaaf (2012)	13.2	−2.63	1.75	NE	164
Red pine; Lake States	Dixon and Keyser (2008)	13.9	−3.32	1.81	NE	198
		ΔDBH (cm year⁻¹)				
		Mean prediction	Mean bias	SD bias		
Ponderosa pine; fixed effects	This study	0.54	−0.01	0.29	E	22
Ponderosa pine; fixed + random effects	This study	0.54	−0.01	0.26	E	22
Ponderosa pine; Southwest Oregon	Hann and Larsen (1991)	0.61	−0.08	0.46	NE	26
Red pine; Minnesota	Lessard et al. (2001)	0.29	0.24	0.40	NE	69
Red pine; Lake States	Dixon and Keyser (2008)	0.22	0.31	0.36	NE	96

Mean observed HT and ΔDBH ponderosa pine grown in Minnesota were 10.5 m and 0.53 cm year⁻¹, respectively

[a]Equivalent (E) or not equivalent (NE)

[b]Minimum detectable negligible difference (MDND) required to reject dissimilarity, expressed in percent of standard deviation
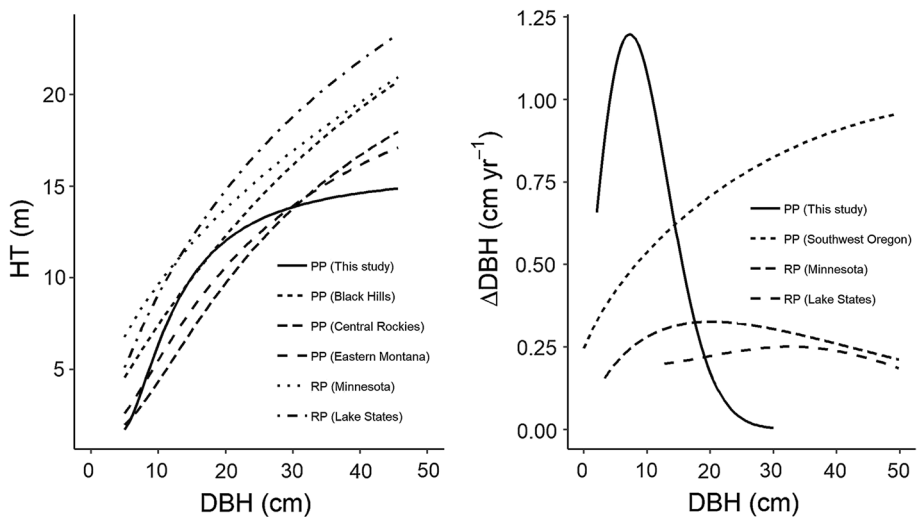
Fig. 3 Predictions of total tree height (HT) and annual diameter increment (ΔDBH) for ponderosa (PP) and red pine (RP). Solid lines show the performance of ponderosa pine grown in Minnesota using Eqs. 1 and 2 for HT and ΔDBH, respectively. For reference, additional models are shown for PP and RP using equations from the Black Hills and Central Rockies (Keyser and Dixon 2008a), Eastern Montana (Keyser and Dixon 2008b), and Lake States regions (Dixon and Keyser 2008). Predictions of ΔDBH for Southwest Oregon derives from Hann and Larsen (1991). For Minnesota RP models, HT and ΔDBH predictions are from VanderSchaaf (2012) and Lessard et al. (2001), respectively

Discussion

Assessments of ponderosa pine growth and yield on 50-year-old trees planted in Minnesota indicate that models applied to the species that were developed in the western US provided greater accuracy and less bias compared to models developed for a similar species in the same region (i.e., red pine in Minnesota). These results imply that if forest resource managers choose to plant non-native species in new areas, utilizing HT and ΔDBH equations developed from their native region may be a suitable first choice to quantify growth and yield relationships. This indicates that regardless of specific site conditions, attributes such as tree diameter may explain a large portion of the variability in HT and ΔDBH, and caution should be used if implementing equations within the same genus but not the same species. Lam et al. (2016) specified a taxonomic hierarchy and concluded that accounting for both genus and species led to an improvement in describing HT in Malaysian tropical forests. Chojnacky et al. (2013) observed substantial differences in the estimation of biomass of western pines in North America when comparing a genus-specific model from Jenkins et al. (2003) to a more generalized equation, suggesting that models developed at the species rather than the genus level may be required for accurate estimates of forest yield. In particular for trees planted in new regions, understanding species-specific functional traits, such as their shade and drought tolerance, will provide insights into their influence on growth and yield.

Incorporating seed source as a random effect in a mixed modeling framework allowed us to capture the dynamics of ponderosa pine HT and ΔDBH in Minnesota. Compared to the developed HT equation in which a large portion of variability was explained by DBH,

the inclusion of random effects in the ΔDBH equation relied more on seed source (i.e., fit index of 0.51 with random effects compared to 0.41 with fixed effects, only; Table 3). Incorporating seed sources avoided the common issues associated with representing tree attributes from multiple seed sources in provenance experiments, such as limited observations from a large number of seed sources. While our equation forms are driven primarily by tree DBH, it accounts for most of the variation explained by HT and ΔDBH (Weiskittel et al. 2011) and is flexible to be used in other tree attributes such as volume and biomass. The developed HT curves reach an asymptote earlier than other equations for the same species and for red pine, which may reflect relatively few observations of large diameter trees. The peak in ΔDBH may represent the rapid utilization of site resources available at the Lamberton and Morris sites whereas other developed equations are simultaneously used to describe growth in natural (i.e., not planted) and mixed-species stands (i.e., Dixon and Keyser 2008). Although both sites are similar in terms of their temperature and precipitation, specification of seed sources as random effects may also capture variability in tree growth related to climate (Leites et al. 2012b). The peak in ΔDBH occurred earlier for the developed models compared to existing ones (Fig. 3) also reflecting the rapid utilization of site resources. Future modeling efforts may quantify additional stand attributes such as spatial structure to account for the "genetic neighborhoods" that ponderosa pine may show, particularly in natural stands (DeWald and Kolanoski 2017).

While ponderosa pine may be selected for planting in Minnesota due to its improved tolerance to drought (Nagel et al. 2017), relative to red pine it displays a lower wood specific gravity (Miles and Smith 2009) and shade tolerance (Niinemets and Valladares 2006). While a lower specific gravity results in less tree biomass (Chojnacky et al. 2013; e.g., Woodall et al. 2011) and impacts stand stocking assessments (Woodall et al. 2005), lower shade tolerance may result in diameter increment to peak earlier compared to more shade tolerant species (Castle et al. 2018). These factors may have contributed to the differences in model comparisons for both ponderosa and red pine (i.e., Fig. 3). Soils at the Lamberton and Morris sites are very fertile with high organic matter content and greater water holding capacity. These soils likely differ from typical ponderosa pine growing conditions in the western US and may explain the differences when comparing the model results.

Two of the ponderosa pine regional groups that were tallest in 2016 were the same ones identified by Radsliff et al. (1981) as being tallest in the 1977 measurement, namely the Eastern High Plains and South and East Montana regions (Table 1; Figure S1). Seed sources of ponderosa pine from these regional groups has been demonstrated to have the greatest height and survival in comparison to other regional groups in plantings throughout the Great Plains (Read 1983; Van Deusen 1980). This finding highlights the importance of early survival and growth on future growth and yield. Our survival rates of the different seed sources of ponderosa pine were similar to the 3-year survival rates (46%) observed by Muller et al. (2019) in a forested region in Minnesota. The success in growth of the Black Hills seed source is somewhat surprising given the high elevation in which it originates (up to 1920 m; Radsliff et al. 1981) but is geographically the closest to the planted areas in Minnesota. Given that the tallest 50% of trees averaged 14.7 m at 50 years, in comparison this would equate to a low or moderate-low site index for red pine in the region (Gilmore and Palik 2005) and ponderosa pine in western Montana (Milner 1992). The suggested site index from this study would rank as a moderate to high-quality site compared to the Black Hills region, where base ages of 100 years are still commonly used for ponderosa pine (Hann 1975; e.g., Myers and Van Deusen 1960). The number of sites in this study was limited ($n = 3$) which largely precluded the analysis of site index as a predictor of HT and

ΔDBH. However, future modeling efforts could integrate site quality in growth and yield equations for non-native species provided data are collected from an adequate number of sites.

There continues to be a need to assess the growth potential of non-native trees planted in new regions. While adaptive management strategies in forestry are being implemented to address future conditions related to climate change (Millar et al. 2007; Nagel et al. 2017) and climate-based seed zones are modified to match seed procurement regions with planting areas under anticipated climate changes (e.g., Castellanos-Acuña et al. 2018), there have been few efforts that forecast the growth and yield potential under such novel conditions. Historical data from provenance trials such as those planted with ponderosa pine in Minnesota can provide a long-term record to investigate the growth potential of species planted outside of their natural range and/or in anticipation of future climate scenarios (Leites et al. 2012a). In the case of the US Lake States, both red and ponderosa pine also serve as hosts to the mountain pine beetle (*Dendroctonus ponderosae* Hopkins), providing additional stressors to the growth and survival of pines in the region (Rosenberger et al. 2017; Windmuller-Campione 2018). To better represent these forest health threats in modeling scenarios, modifications of growth and mortality could be developed for insects such as the mountain pine beetle. An accurate assessment of the survival and growth of species planted in areas outside of their natural range is essential for forest managers to weigh alternative decisions in the context of adaptive forest management.

Conclusions

In anticipation of future climate conditions, forest managers are seeking to plant novel tree species in areas outside of their natural range due to their improved tolerance to changing environmental conditions (e.g., drought). However, few quantitative tools are available to determine the growth potential of these species planted in new areas. This study showed that in the absence of the availability of models for a species in the new region, employing existing growth and yield equations from the species' native range (i.e., ponderosa pine in the western US) provides a more accurate representation of total tree height and diameter increment compared to models from a similar species in its native range (i.e., red pine in Minnesota). Analysis after 50 years of ponderosa pine growth in Minnesota indicates a peak in diameter growth in small-diameter trees (approximately 10 cm DBH) and height that reaches an asymptote much earlier compared to ponderosa pine outside the region and red pine within the region. In summary, the quantification of ponderosa pine growth as analyzed here provides forest managers with better tools for their consideration under a variety of adaptive management scenarios.

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