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Research Article

Silviculture

Growth Response of Ponderosa Pine to Intensive Cultural Treatments Varies with Site Quality and Plantation Age

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Abstract

Long-term forest experiments provide valuable knowledge in managing forests for productivity and other ecosystem services. California's "Garden of Eden" experiment was established to determine growth potential of *Pinus ponderosa* plantations in response to intensive cultural treatments. We examined the 20-year growth-response of tree volume to intensive cultural treatments consisting of combinations of herbicide on competing vegetation (H), fertilization (F), and insecticide (I). We found that both H and F treatments synergistically increased tree growth at intermediate and lower-quality sites. Growth increased by 1.5–2.1 times with F, 2.1–2.5 times with H, and 2.3–3.8 times with HF treatments versus control (range = 39.3–109.2 m^3 ha^{-1}). Across the highest productive site, H and F effects on volume seemed additive at younger ages, but largely dissipated by age 20, with volume increasing by 1.6, 1.2, and 1.6 times relative to control in F, H, and HF treatments, respectively. However, 20-year mean annual increment was 21.7 m^3 ha^{-1} yr^{-1} for the F treatment, the highest volume reported for ponderosa pine in California. The results underscore how site-specific cultural treatments, especially H and F, may widely enhance plantation productivity and boost stand development.

Study Implications: In Mediterranean climates, competing vegetation control is essential for ponderosa pine planation establishment and early growth, especially at intermediate and poor-quality sites. At higher-productivity sites, fertilization enhances stand growth and development, although fertilization's beneficial effects on growth do not appear until canopy closure. Precommercial thinning in herbicide and fertilization treatments will not reduce overall stand growth 10 years postthinning. Intensively managed plantations appear to have a higher maximum stand density index compared to natural stands or unmanaged plantations. Therefore, these cultural treatments can be used to rapidly reforest areas after disturbances and subsequently promote larger trees on reforested landscapes.

Keywords: Garden of Eden study, multi-level interactions, intensive cultural treatments, stand development, volume growth potential

Foresters require long-term research data to guide their management decisions, particularly for long-lived species such as ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson). Due to a lack of information on growth potential of intensively managed plantations for this species, Robert F. Powers conceived and established the "Garden of Eden" experiment in the 1980s. The Garden of Eden was designed to study the long-term effects of fertilization, competing vegetation control through the use of herbicide, and insecticide application on ponderosa pine plantation productivity across a range of site quality and climatic conditions in northern California. Since then, this study has served as a springboard to address many scientific and management questions using various types of data collected on individual sites. Yet the tree growth summary for all installations was limited to a report with 6-year data by Powers and Ferrell (1996), although later growth data for certain sets of installations have been included in other publications (Powers and Reynolds 1999, McFarlane et al. 2010). Of the eight original installations, two were abandoned after they were accidentally thinned by their original landowners before reaching 10 years of age. For the remaining sites (Table 1, Figure 1), we have at least 20 years of data, including data for three installations (Elkhorn, Feather Falls, and Whitmore) that were harvested and replanted to study the carryover effects of first rotation treatments on growth in second rotation plantations, and a fourth (Jaws) that was lost to a backfiring operation during the 2016 Gap Fire. These data provide an important opportunity to determine the effects of intensive cultural treatments on plantation growth after canopy closure.

Across western North America, ponderosa pine is the most widely distributed pine species and has been extensively planted due to its value for timber production (Oliver and Ryker 1990). It is also the most widely used species for successful postfire reforestation (Powers and Ferrell 1996). In California alone, there are currently 162,000 ha of ponderosa pine plantations on National Forest lands and 128,000 ha on forest industry lands (Zhang et al. 2019b). Overwhelming evidence across this region demonstrates that ponderosa pine seedling survival and growth are primarily influenced by soil water availability on all sites as well as nutrient deficiency

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Table 1. Geographic locations and site characteristics of six installations for Garden of Eden study in northern California. Weather data are summarized for each test site from the year planted to the year when trees were last measured. Annual precipitation is calculated from October of the previous year to September of the current year.

	Chester	Elkhorn	Feather Falls	Jaws	Pondosa	Whitmore
Latitude (N)	40.3077	40.0824	39.6198	41.8867	41.2083	40.6259
Longitude (W)	121.0998	122.7424	121.1966	123.0552	121.6252	121.8990
Elevation (m)	1533	1539	1250	1018	1181	747
Geomorphic province	Cascade	Klamath	Sierra	Klamath	Cascade	Cascade
Site index (m at age 50)	20	17	30	23	18	23
Annual mean T_{max} (°C)	16.1	16.8	18.1	18.0	17.4	22.3
Annual mean T_{min} (°C)	0.4	6.7	7.0	4.5	2.1	8.4
Annual precipitation (mm)	859	1010	2035	736	755	1030
Parent material	Volcanic	Metasediment	Volcanic	Metasediment	Volcanic	Volcanic
Soil group	Palexereralfs	Xerochrepts	Haploxeralfs	Haploxeralfs	Palereralfs	Haplohumults
Previous vegetation	Brushfield	Plantation	Natural stand	Natural stand	Brushfield	Brushfield
Year planted	1987	1988	1988	1988	1988	1986
Tree measurement ages	4, 6, 8, 10, 12, 24, 30	2, 4, 6, 8, 10, 15, 20	2, 4, 6, 8, 10, 15, 20	4, 6, 8, 10, 13, 23	2, 4, 6, 8, 10, 23, 29	5, 6, 9, 10, 12, 15, 21

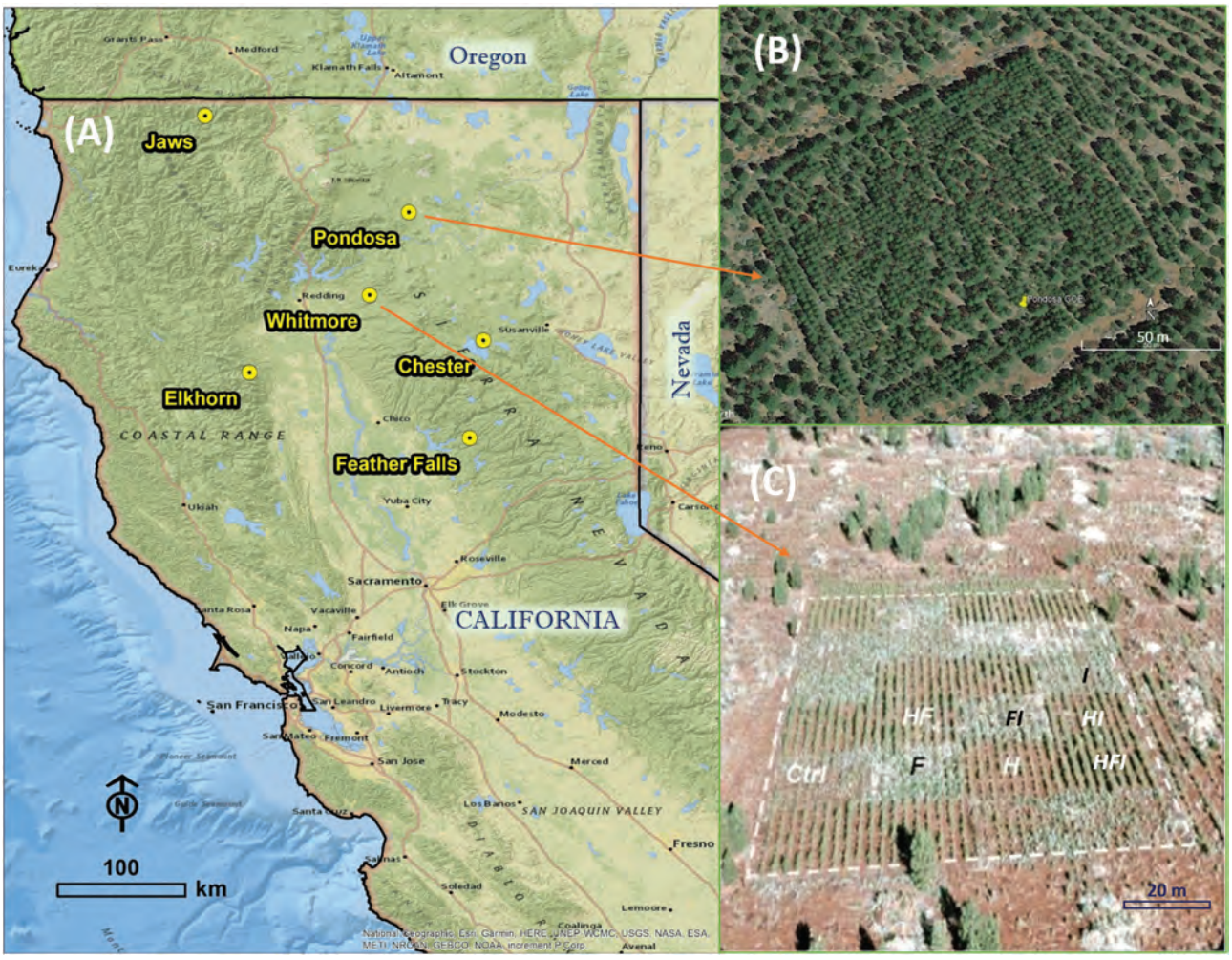

Figure 1. Locations of the Garden of Eden experiment in northern California (A), the Pondosa installation with thinned plots shown in 2007 google earth image (B), and the 1990 aerial photo at Whitmore (C), from which competing vegetation control by herbicide plots were clearly separated from the nonherbicide plots.

on some sites (Powers et al. 1988, Powers and Ferrell 1996). As a mitigating tool, competing vegetation control becomes a key factor in successful forest regeneration and early growth (McDonald and Fiddler 1990, 2011, Zhang et al. 2013c). It not only redistributes the limited soil water and nutrients to the planted trees, but also increases trees' nutrient uptake with water serving as a transporting media. This is particularly important in temperate regions with Mediterranean climates because growing seasons are usually dry.

Two companion woody shrubs in ponderosa pine forests are manzanita (*Arctostaphylos* spp. L.), an evergreen genus, and ceanothus (*Ceanothus* spp. L.), a genus that includes both evergreen and deciduous species. These two genera are capable of regenerating from their massive seed banks (Quick 1956, Knapp et al. 2012), and some species will resprout following disturbance, such as timber harvesting and wildfire. Without control, they quickly colonize a site and aggressively compete for soil nutrients and water with the planted trees. For example, shrub cover can reach 40% in a 4-year-old plantation (Zhang et al. 2016), which is double the 20% shrub cover threshold previously established as a benchmark to avoid reducing growth of young pine plantations (Oliver 1984, Shainsky and Radosevich 1986, White & Newton 1989). The negative effects of shrub competition on ponderosa pine plantations can delay crown closure and extend rotation lengths (Zhang et al. 2006, 2016).

Soil water availability depends on precipitation and soil water holding capacity, and plants will compete for water using species-specific strategies (Kramer 1983, Klein 2014). For example, ponderosa pine closes its stomata when leaf water potential falls below −1.5 MPa (Lopushinsky 1969), whereas manzanita conducts photosynthesis under much lower water potential, thus depleting soil moisture more rapidly and ultimately extracting a greater fraction of the available water (Royce and Barbour 2001). This suggests that manzanita has a competitive advantage over ponderosa pine under low soil water availability, particularly during establishment. Plantations often fail when tree seedlings, which are usually planted in numbers <750 trees ha^{-1}, die or are not growing at the rate of their site potential after being overwhelmed by competition from naturally regenerated or resprouted shrubs, which can number up to 250,000 seedlings ha^{-1} (McDonald and Fiddler 2011). During the first few years of ponderosa pine seedling development, higher stem diameter growth can be correlated to reduced competition and can be used as an indicator of initial establishment success (McDonald and Fiddler 2011).

Although ponderosa pine plantation establishment is often most successful on nutrient-rich soils, plantations can respond well to fertilization regardless of site quality (Powers et al. 1988). A single application of nitrogen at 200 kg ha^{-1} increased 5-year volume growth by an average of about 25% when shrubs were not controlled, but the response doubled when shrub competition was low. However, on poor, droughty sites in California, shrub competition precluded fertilizer response entirely, even when trees were severely deficient in nitrogen (Powers and Jackson 1978). When the treatments were combined, the herbicide and fertilization effects seemed to interact synergistically on poor sites and additively on better sites (Powers 1983, Nambiar and Sands 1993).

The objectives of the current study were to extend previous Garden of Eden research by examining the implications of the ≥20-year measurements (1) to determine the long-term growth potential of planted ponderosa pine in California, (2) to find whether the growth trends reported at age 6 (Powers and Ferrell 1996) persist at age 20, (3) to evaluate how differences in site quality combine with treatment to affect tree performance, and (4) to explore how relationships between silvicultural effects of herbicides and fertilizer treatments on stand growth change over time across a broad geographical array of ponderosa pine forests. With more than two decades of forest science advances and more than 14 years of additional data, these questions may be rigorously addressed, providing the longer-term perspectives that are the most valuable for managing plantations (Pretzsch et al. 2019, Zhang et al. 2020).

Materials and Methods

Study Site

Six sites with a common experimental design were installed across northern California from 1986 to 1988 (Figure 1). Site characteristics are shown in Table 1. The sites were originally occupied by forests or shrubs, but all sites were within ponderosa pine zones and cleared with contemporary site preparation practices before study installation. The six sites represent three geomorphic provinces with varying site indices and soil characteristics (Powers and Ferrell 1996). Temperature and precipitation are summarized by site (Table 1) from the PRISM climate group at Oregon State University (https://prism.oregonstate.edu/). Due to different establishment years among sites, we provide mean monthly maximum and minimum temperature and annual precipitation from the year the first site was established through the year the most recent measurement was taken in Figure S1.

Trees were planted at ca. 2.4 × 2.4 m spacing. Each treatment plot is ca. 22 × 20 m. Seedlings were raised by the Forest Service Placerville Nursery using local seed zone seeds for each respective site. Installation years varied because of lack of resources to handle all sites within the same year.

Experimental Design and Measurement

A completely randomized plot design assigned eight factorial treatment combinations to twenty-four plots, producing three replications of each treatment combination for each installation. Each study site had identical designs. The treatments are as follows: control (C), herbicide to control competing vegetation(H), fertilization (F), and insecticide (I). Combinations of the three treatment types were also included in the study: herbicide and fertilization (HF); herbicide and insecticide (HI); fertilization and insecticide (FI); and herbicide, fertilization, and insecticide (HFI). Pulse treatments of herbicide, fertilizer, and insecticide were applied for the first 6 years. The treatments and the detailed methods of application can be seen in Powers and Ferrell (1996). Briefly, the insecticide treatment consisted of acephate or dimethoate applied directly to trees each spring when new needles had broken their bundle sheaths. Formulations were based on manufacturer's recommendations for the insects likely to be present and were applied by backpack sprayer to the crowns for the first 6 years. Vegetation control using herbicides consisted of annual spring applications of glyphosate, hexazinone, or triclopyr based on manufacturer's recommendations for the soil type and vegetation present. Herbicides were applied by backpack sprayer directly to all vegetation other than planted trees for the first 6 years. Nutrient control using fertil-

izers involved application of dry commercial salts of nitrogen, phosphorus, potassium, calcium, magnesium, sulfur, boron, copper, and zinc during the dormant season. Application followed a ramp schedule in which nutrient supply increases with demand, in the spring of years 1, 3, 5, and 7. Final cumulative amounts of . kg (N), 530 kg (P), 540 kg (K), 416 kg (Ca), 221 kg (Mg), 112 kg (S), 73 kg (Zn), 36 kg (Cu), and 36 kg (B) were applied per hectare.

Treatment plots with HI and HFI were thinned following crown closure at all sites except Elkhorn, where trees remained small due to poor site quality. Thinning was performed at plantation age 8 for Feather Falls, 10 for Jaws, Pondosa, and Whitmore and 12 for Chester. HI and HFI treatment plots were chosen for lack of insect outbreaks or visible damage, an observation that continues for existing plots even today. Trees were thinned by hand with a chainsaw at a thinning intensity of 50%; that is, leaving half the original number by prioritizing retention of better quality trees, and otherwise thinning uniformly.

Measurement plots were consistent across treatments, with the innermost twenty trees serving as the measurement trees and two rows of trees serving as a buffer around each measurement plot. Tree height, diameter at 20 cm above ground level when trees were small, diameter at breast height (DBH at 1.37 m) when they grew larger, and height to the live crown were measured in various years (six to seven times) and varied by site (Table 1). All sites were measured at age 6 and age 10. Tree measurements at certain sites prior to age 6 are not included here (but see Powers and Ferrell 1996) nor are the competing vegetation data measured at various years, which were previously reported (Zhang et al. 2016).

Tree stem volumes were estimated from a conic formula when DBH was not reached. Otherwise, volume was estimated from allometric equations, established from thirty-six trees per site at Elkhorn, Feather Falls, and Whitmore, developed in the course of constructing biomass equations through destructive sampling (Zhang et al. 2021). Volume equations encompassed the range of height and DBH observed in this study. The equations of total volume including bark from the ground with tree DBH and height or DBH only are shown in Figure 2. Because neither treatment effect nor the interactions between site and treatment were significant in the model fittings, but site effect was, we present here only site-specific volume models. If trees were measured for both height and DBH, we used the equations in Figure 2A. If height was not measured, we used the equations in Figure 2B. We applied the equations from Whitmore for Chester, Jaws, and Pondosa installations because these sites showed a similar site index (Table 1).

Periodic annual increment (PAI) for volume was calculated for each period between two measurement years, although the first period was calculated with 6-year volume divided by 6. Thinning volume was considered when we calculated the PAI volume for HI and HFI treatment plots. Mean annual increment (MAI) was estimated around 20–24 years depending on how old a site was when measured. Similarly, leaf mass was estimated with allometric equations established at the three sites mentioned above (Zhang et al. 2021).

Individual tree height and diameter variability among sites, treatments, and plantation ages was analyzed with coefficients of variation. In addition, the site-specific stand density index (SDI) for ponderosa pine was calculated for each treatment plot at each site following Zhang et al. (2013a).

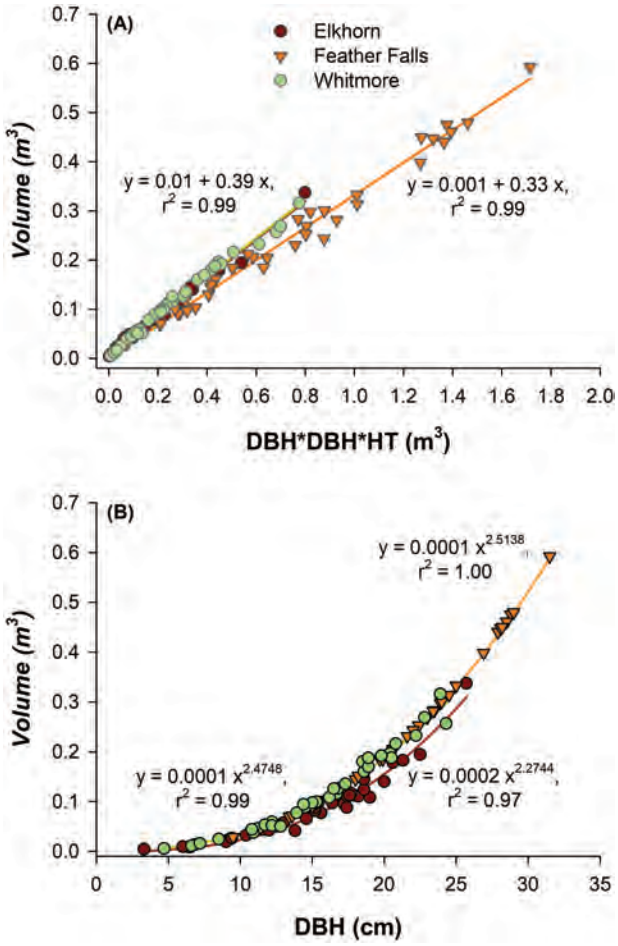

Figure 2. Volume estimation equations established from thirty-six constructively sampled trees at Elkhorn, Feather Falls, and Whitmore Garden of Eden installations. (A), the equations for trees with both height and DBH measured and the same equation for Elkhorn and Whitmore. (B), the equations for trees with only DBH measured. Because neither treatment effect nor the interactions between site and treatment were significant in the model fittings but site effect was, we presented here only site-specific volume models. Please see Zhang et al. (2021) for the detailed analyses.

Statistical Analysis

We analyzed all variables with doubly repeated measures in space (site effect) and in time (age effect) as a complete randomized design with plot as our experimental unit using SAS PROC MIXED (Gbur et al., 2012, SAS Institute Inc., 2012). Treatment, site, and stand age were fixed effects and plot was a random effect. The following full model was used

$$y_{ijkl} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \gamma_k + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk} + \varepsilon_{ijkl} \quad (1)$$

where y_{ijkl} was the dependent variable measured for the i^{th} treatment and the j^{th} site, k^{th} age, and l^{th} plot; μ was the overall mean; α_i was the fixed effect of the i^{th} treatment (i = 1, 2, 3, 4); β_j was the fixed effect of the j^{th} site (j = 1, 2, …, 6); γ_k was measured year or plantation age; and ε_{ijkl} was an experimental error, $\varepsilon_{ijkl} \sim iid\ N(0, \sigma_e^2)$.

For each variable analysis, residuals were examined to ensure that statistical assumptions of normality and homoscedasticity were met. If not, a natural log transformation was applied. During the model selection process, we selected the model with not only the minimum Akaike information criterion but

also the most appropriate Pearson's residual panels. Multiple comparisons among treatments were conducted for least square means by the Tukey-Kramer test by controlling for the overall $\alpha = 0.05$.

Results

Individual Tree Growth and Variation

Average tree height and DBH showed significant effects for all terms tested except for site*treatment and age*site*treatment (Table 2). The results were expected because these trees grew on a diverse range of site quality (Table 1), treatments (Figure 1C), and plantation ages. Because the latest measurements were not collected at the same ages among the six sites, we calculated least square means (Figure 3) showing that 20-year-old heights were 3.9–15.9 m and DBHs were 7.6–24.0 cm over the range of treatment plots and sites. Not surprisingly, trees grew better in the treated plots than in the controls and at higher quality sites than at poorer sites. Yet the magnitude of within-site variation in treatment effects on growth was comparable to the across-site variation in effect size. Among the six sites at age 20, the average within-site ratio of height in treated versus control plots ranged from 1.1 to 1.6 (calculated from Figure 3). By comparison, the average across-site ratio of treated versus control tree height ranged from 1.0 to 1.6. Similar trends were apparent for average DBH at age 20, with within-site variation in treated plot DBH ranging from 1.2 to 1.7 times relative to controls, whereas across-site variation in the ratio of treated versus control plot DBH ranged from 1.0 to 1.7. In addition, we found a lower coefficient of variation for DBH in treatments with high- versus low resource availability (especially H treatments) and on higher- versus lower-quality sites across all measurement years (Figure 4). Similar trends were found for height (Figure S2).

Stand Growth and Dynamics

Stem volume varied among sites, treatments, ages, and their two-way interactions (Table 2). The mixed model resulted in a better fit if a quadratic term for plantation age was included. Plantation growth at 20 years showed a maximum potential of about 420 m^3 ha^{-1}, corresponding with fertilization at Feather Falls, the highest-quality site (Figure 5). Significantly more volume accumulated at Feather Falls across all treatments and measurement years. In addition to the exceptional growth at Feather Falls, we also found that higher volume accumulated at higher-quality sites than at poorer sites, although there were exceptions due to interactions among sites, treatments, and plantation ages (Figure 5). There were no detectable effects of insecticide on volume growth. Other trends are as follows: (1) When plantations were naturally grown without fertilization and H (i.e., in C and I treatments), stand volume was the lowest among the treatments, whereas volume trends were closely associated with the site quality (Figure 5C and I). (2) When plots received fertilizer but not H, volume accumulations were similar among the three intermediate quality sites (Chester, Jaws, and Whitmore) as were volume accumulations between two poorer sites (Elkhorn and Pondosa) (Figure 5F and FI). (3) When trees were grown under H treatment and without fertilization, the trends followed the site quality gradient more closely than in C and I treatments. (4) When trees grew under both HF and HFI treatments, trees at Whitmore had volume growth either second only to Feather Falls or equivalent to Jaws (Figure 5HF and HFI). (5) Lower volume in HI and HFI treatments than in H and HF treatments, respectively, reflected thinning effects at all sites except for the unthinned Elkhorn. In addition, Jaws showed a different trend because volume was significantly higher in HFI than in HF at the final measurement (Figure 5HF and HFI). (6) These trends were also indicated by calculating relative volume to control (treatment/control) for each combination of treatment and site (Figure S3). Heatmaps (Figure S3) showed that treatment effects on volume changed among plantation ages. For example, the H-associated treatment (H, HI, HF, and HFI) effects changed from an average of 4.0 (4 times more volume produced relative to the control) at age 6 to 2.0 at age 10 and later. The H-associated effect was the smallest at Feather Falls. At 20 years and older, the biggest H effects occurred either at the poorest quality Elkhorn and Pondosa sites or at Whitmore, where shrubs were very dense if left untreated.

Because overall comparisons were complicated by 50% thinning of trees on the HI and HFI plots between 8 and 12 years, we present PAI for volume in Figure 6. Results show significant PAI volume differences (0.2–32.5 m^3 ha^{-1} yr^{-1}) among not only sites and treatments but also plantation ages. The PAI volume was low during plantation establishment stage, which lasted 6 or more years depending on site and treatment. Growth then increased rapidly to peak first at higher quality sites or in higher resource-available treatments between 10 and 20 years. Relative to the control or insecticide

Table 2. Probabilities for type 3 tests of fixed effects from the mixed model procedures in the Garden of Eden study. The results were from the best model selected for each variable.

Source of variation	Num df	Den df*	*ln*(height)	DBH	*ln* (volume)	PAI volume	*sqrt* (SDI)
Site	7	16	<0.001	<0.001	<0.001	0.040	<0.001
Treatment	5	637	<0.001	<0.001	<0.001	0.030	<0.001
Site*Treatment	35	637	0.089	<0.001	0.017	0.999	0.468
Age	1	637	<0.001	<0.001	<0.001	<0.001	<0.001
Age*Age	1	637			<0.001	<0.001	<0.001
Age*Site	7	637	0.006	<0.001	<0.001	<0.001	<0.001
Age*Treatment	5	637	<0.001	<0.001	<0.001	<0.001	0.001
Age*Site*Treatment	35	637	0.842	<0.001	0.793	0.181	0.151

* Denominator degree of freedom (Den df) has changed (except for Site) with 637 for height and diameter at breast height (DBH), 636 for volume, 624 for periodic annual increment (PAI) volume, and 474 for stand density index (SDI). Num df refers numerator degree of freedom.

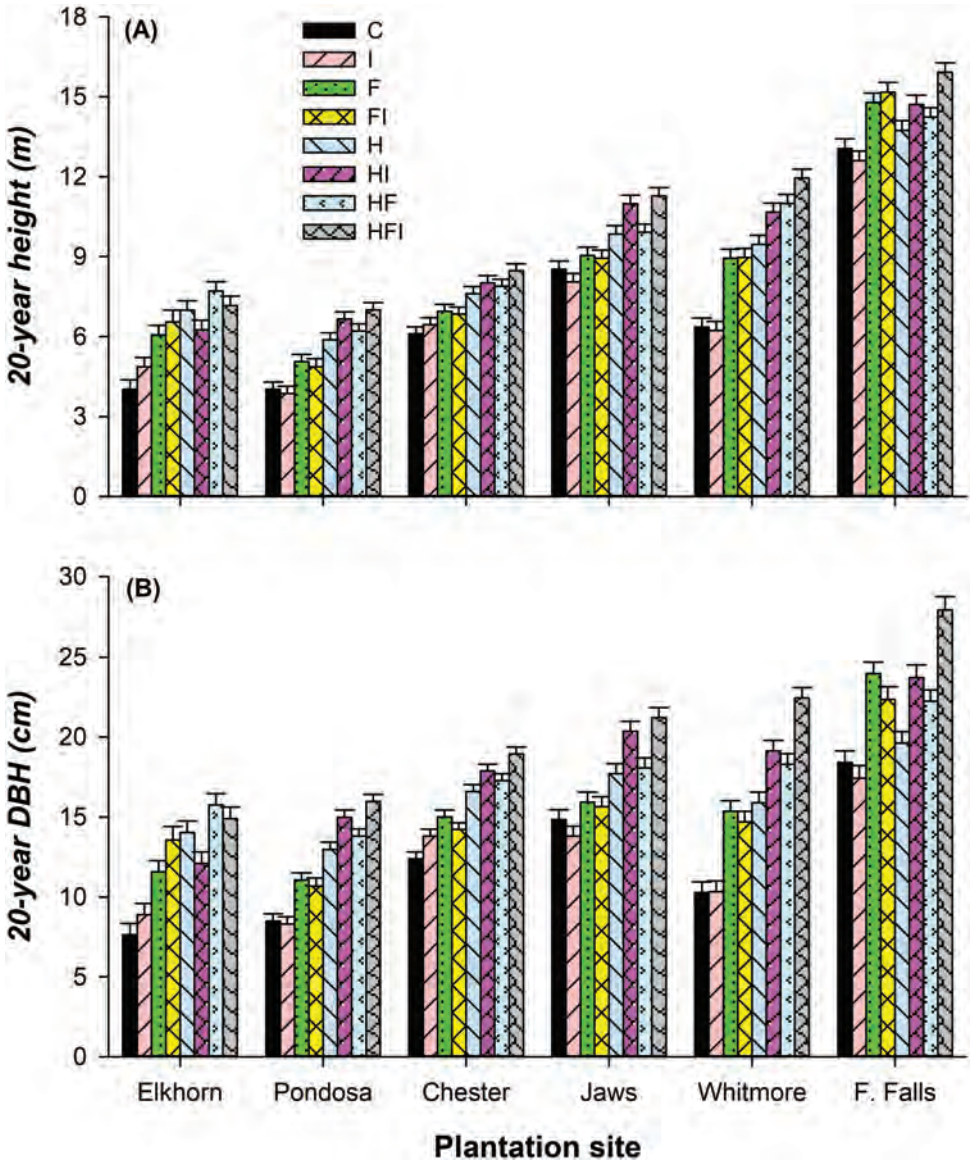

Figure 3. Least square means and standard errors from analysis of variance models for 20-year-old height (m) and diameter at breast height (DBH) (cm) for ponderosa pine trees grown in eight treatments at six sites from low to high site quality. C: control, I: insecticide application, F: fertilization, H: herbicide application. At all sites except Elkhorn, HI and HFI treatment plots were thinned with 50% intensity between ages 8 and 12.

treatment, PAI volume in the other treatments was at least 10% and as much as 200% higher for the last measurement period (Figure S3), with the exception of F and FI treatments at Elkhorn and Jaws that had greater mortality during the first 2 years of installations due to an interaction between fertilizers and soil parent materials (Powers and Ferrell 1996).

SDI differed among sites and treatments and was similar to PAI volume (Table 2; Figure 7). As expected, SDI was higher and reached earlier at the more resource-rich sites or treatments. As of age 20 at Elkhorn, the lowest quality site, no plots except for a few HF plots had reached the imminent mortality zone equivalent for the region described by Oliver and Uzoh (1997). In contrast, at the highest quality site, Feather Falls, SDI reached the imminent mortality zone in most treatments at age 15. Surprisingly, apparent self-thinning mortality had not occurred at any sites by age 20, even at present for Chester and Pondosa, the two sites where original plantation plots have continued to be measured every 5 years, despite all plots being over the imminent mortality zone at Chester during the last inventory year (2016) and some over the maximum SDI in 2012 (Figure 7C).

Relationships between leaf mass and MAI for volume were strong and significant (Figure 8). Slopes were steeper at higher-quality sites than at lower ones. It appears that slopes were similar at Chester, Elkhorn, and Pondosa, the three lower-quality sites.

Discussion

As far as we are aware, this is the most comprehensive study with a common design replicated on sites of varying quality to examine the effects of multiple silvicultural treatments on productivity of ponderosa pine plantations over a 20-year period. Significant interactions among site, treatment, and plantation age in this study demonstrated that silvicultural prescriptions should ideally have been site specific, as plantation developmental stages varied with age among sites of different quality. Although both historical research and management practices have established

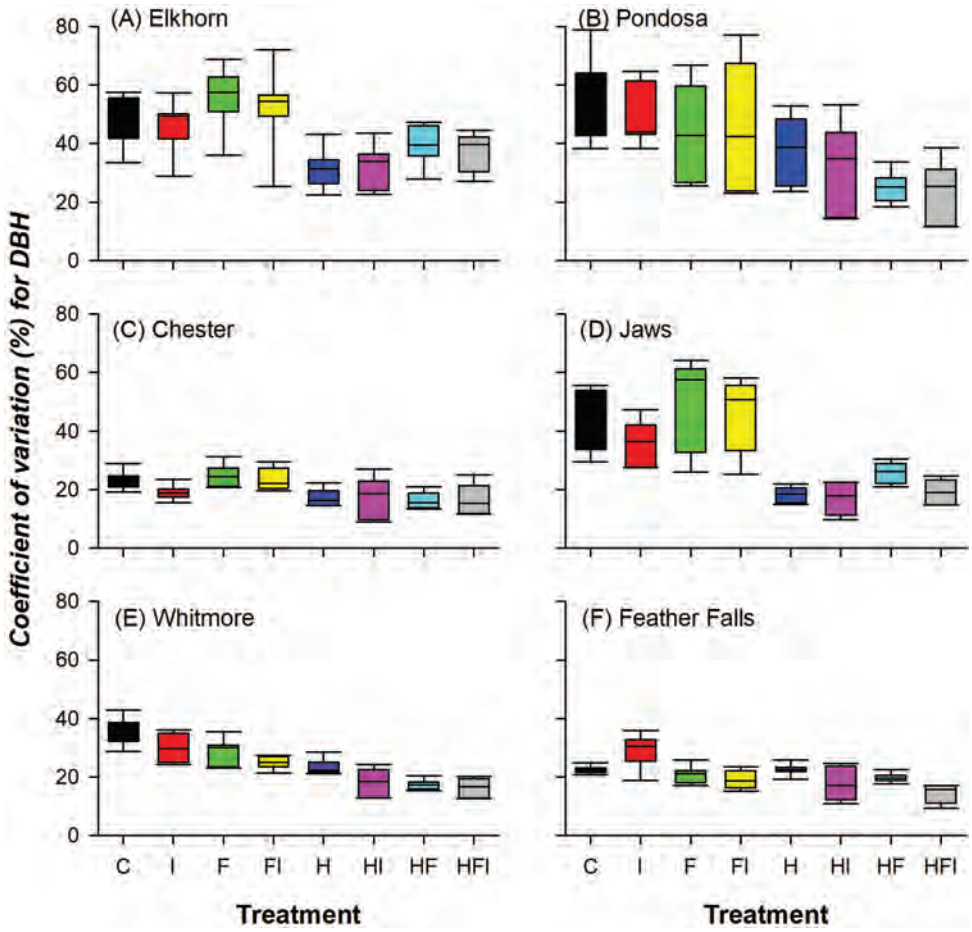

Figure 4. Coefficient of variation for diameter at breast height (DBH) calculated over three plots within each treatment at each site measured during varying years (five to seven times). Individual treatments included control (C), insecticide application (I), fertilization (F), herbicide application (H), and their combinations.

site-specific productivity in ponderosa pine (Meyer 1938, Oliver and Powers 1978) and other forest types (Skovsgaard and Vanclay 2008), our results provide clear evidence that intensive cultural treatments could enhance plantation production at lower-quality sites to a level of volume growth comparable to higher-quality sites without the same treatments (Figure 5). For example, at around age 20, the HF treatment at the poorest site, Elkhorn, had a volume of 150 m^3 ha^{-1} which was greater than both the C and I treatments' volume at all but the highest-quality site, Feather Falls (Figure 5C, I, & HF). In addition, the growth rate for stem volume (MAI) was significantly related to leaf biomass (Figure 8), which makes biological sense. Although soil moisture could not practically be manipulated through irrigation treatments, significant precipitation differences among sites (Table 1 and Figure S1) allowed us to relate our H and F treatments to water availability. Because of a lack of insect outbreaks anywhere (even within the plantations around these installations) for the first 6 years when insecticide was applied, there were no significant differences between C and I, F and FI, H and HI, and HF and HFI. Therefore, insecticide-associated treatment effects will not be discussed further.

Plantation Growth

A wide range of volume production occurred across these research plots, treatment combinations, and sites (Figure 5). At age 20, we saw as little as 50 m^3 ha^{-1} in the control at the poorest site and as high as 420 m^3 ha^{-1} in the FI treatment at the richest site. The very large differences seen among these plantation plots across the northern California region present a significant challenge to accurately estimating forest productivity and carbon sequestration potentials at a regional scale, let alone worldwide (Skovsgaard and Vanclay 2008). By pointing to higher plantation growth rates, many people have advocated for and demonstrated the use of forest plantations as a substitute for natural forests in supplying forest products (Sedjo and Botkin 1997, Powers 1999, Fox 2000). Our results provide direct evidence for that possibility. Across natural forests in California, growth rates of 1.4–13.1 m^3 ha^{-1} yr^{-1} were found at various site indices for 20-year-old ponderosa pine stands (Meyer 1938). Without treatments, our plantation sites would have reached that growth level (Figure 8).

MAI, a measure of growth rate, can be influenced by factors such as plantation age, treatment, and volume allometric equations, making it an imperfect but still useful means of summarizing general trends among studies. Based on previous studies, the FAO (2001) reported MAI of 6–25 m^3 ha^{-1} yr^{--1} for pine plantations in South America (Brazil, Chile, and Venezuela) and Africa (Malawi, Madagascar, and Mozambique) at rotation age 10–25. Using data from plantation studies of pine species including *Pinus taeda* and *P. radiata*, often planted for their high productivity, Fox (2000) summarized pine plantation MAI at 14.5–32.0 m^3

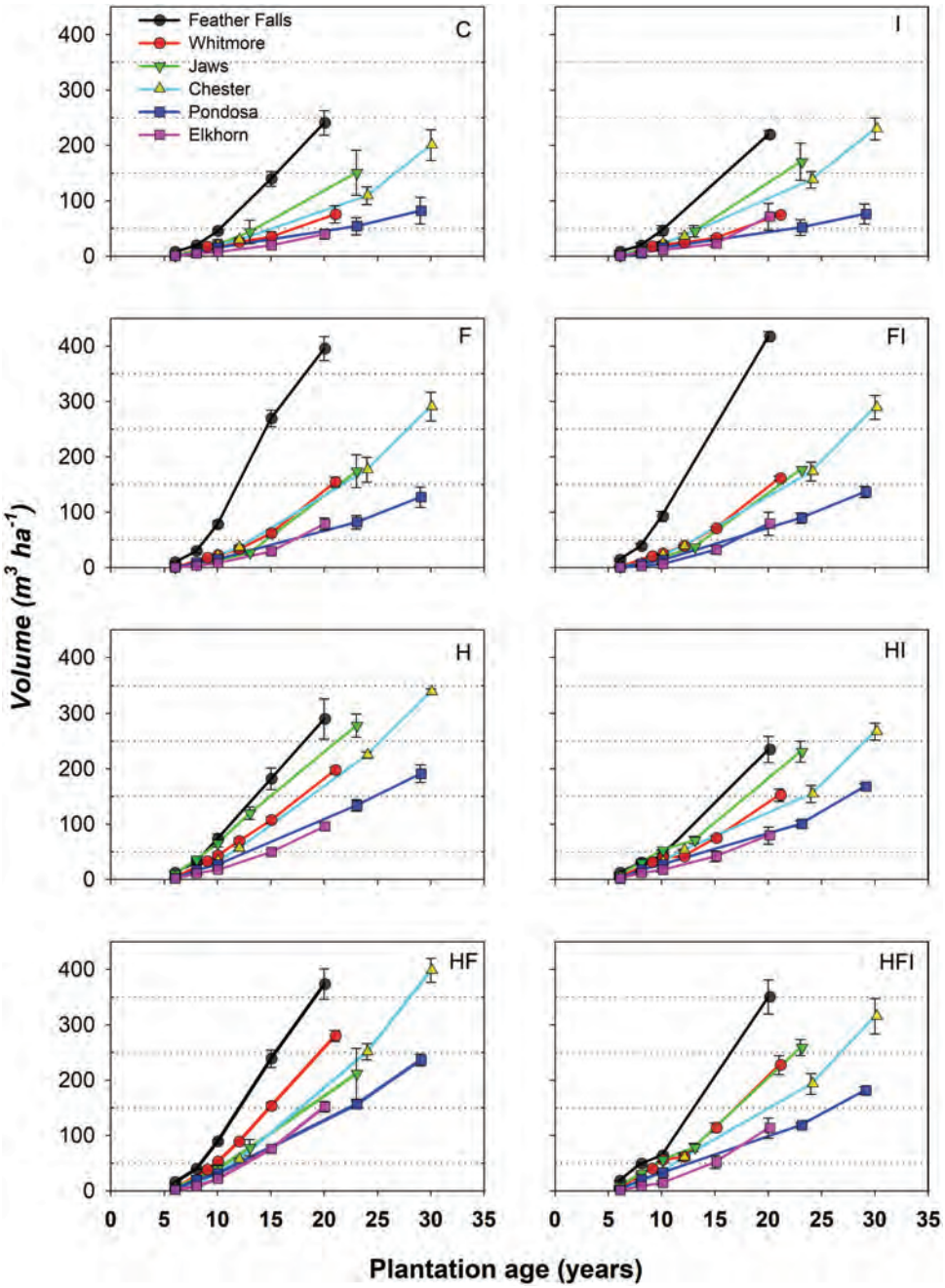

Figure 5. Average stem volume and standard error from 6 years to the last measurement at age 20–30 years for control (C), insecticide (I), fertilizer (F), herbicide (H), and their combinations in each plantation grown on Garden of Eden installations listed in order of site quality in northern California.

ha^{-1} yr^{-1} at age 8–25. The latest FAO report by Mead (2013) summarized large-scale pine plantation MAI at 2–34 m^3 ha^{-1} yr^{--1} at rotation ages 18–87 years. In California, MAI for natural ponderosa pine stands at age 90 was summarized as 4.1–6.1 m^3 ha^{-1} yr^{-1} at lower-quality sites and 8.3–9.6 m^3 ha^{-1} yr^{-1} at higher-quality sites (Show 1925, Dunning and Reineke 1933). Oliver and Powers' (1978) yield tables showed that MAI was 2.8–5.0 m^3 ha^{-1} yr^{-1} in 20-year plantations with similar site index and density as the Jaws and Whitmore sites in our study. By including similar treatments in other plantations ranging in age from 37 to 86 years, later studies summarized MAI at 5.7–17.0 m^3 ha^{-1} yr^{-1} across northern California (Powers et al. 2005, Zhang et al. 2006, 2013b). MAIs of 1.2–21.7 m^3 ha^{-1} yr^{-1} in our study are comparable to and in some cases exceed growth rates found in other studies.

Our results indicate that cultural practices are critical to achieving and surpassing growth expectations for ponderosa pine. At Elkhorn, our poorest-quality site, MAI rose from only 1.2 m^3 ha^{-1} yr^{-1} in the control plots to more than 8.5 m^3 ha^{-1} yr^{--1} in the HF plots at age 20. In contrast, MAI at Feather Falls ranged from 9.8 to 21.7 m^3 ha^{-1} yr^{-1}, a range comparable or superior to *Pinus taeda* (7.0–17.0 m^3 ha^{-1} yr^{-1}) and *P. palustris* (7–14 m^3 ha^{-1} yr^{-1}) grown both without cultural treatments and with fertilization and weed control treatments in Florida (Jokela et al. 2010). One caveat relating to our use of long-term study measurements is that individual tree volume was estimated from ground to tree

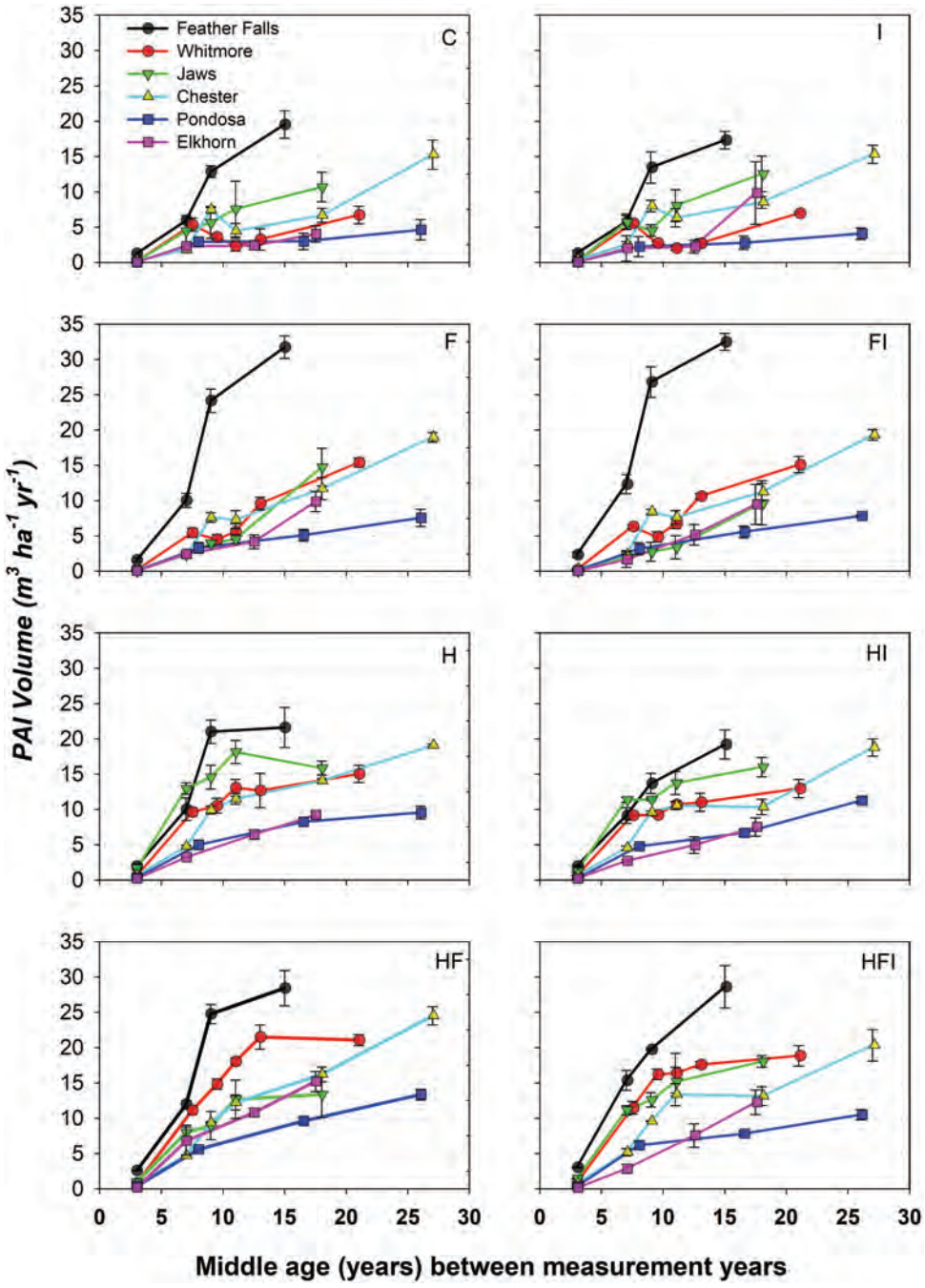

Figure 6. Periodic annual increment (PAI) for volume and standard error during each measurement period from 6 years to the last measurement at age 20–30 years for control (C), insecticide (I), fertilizer (F), herbicide (H), and their combinations in each plantation grown on Garden of Eden installations listed in the order of site quality in northern California.

tip and included the outside bark, whereas other California studies estimated volume from 0.3 m stump to tip of tree and excluded outside bark, making our volume estimates about 20% higher. However, when our estimates were reduced by 20%, all H- and F-associated treatments still accumulated more volume than predicted based on Oliver and Powers (1978), with volume-growth rates at Feather Falls exceeding all previous reports for ponderosa pine in California. Nonetheless, because we could not determine what volume estimation methods were used for pine plantations in FAO (2001), Fox (2000), and Mead (2013), comparisons remain uncertain.

Impressive ponderosa pine growth rates have also been observed within the Patagonian Andes of Argentina. Gonda et al. (2009) reported that after thinning 20-year-old plantations to reduce density, periodic annual volume increment (PAI) was 18–36 m^3 ha^{-1} yr^{-1} from age 20 to 29, which is greater than Oliver (1997) reported for ponderosa pine trees aged 20–30 grown on Elliot Ranch in California (9.0–17.7 m^3 ha^{-1} yr^{-1}). However, the two studies differed in density, plantation history, treatments, and understory plant communities. The volume achieved under the F-associated treatments at our Feather Falls site (Figure 6) at age 10–20 years was comparable to the 20-year numbers reported in Gonda et al. (2009). These

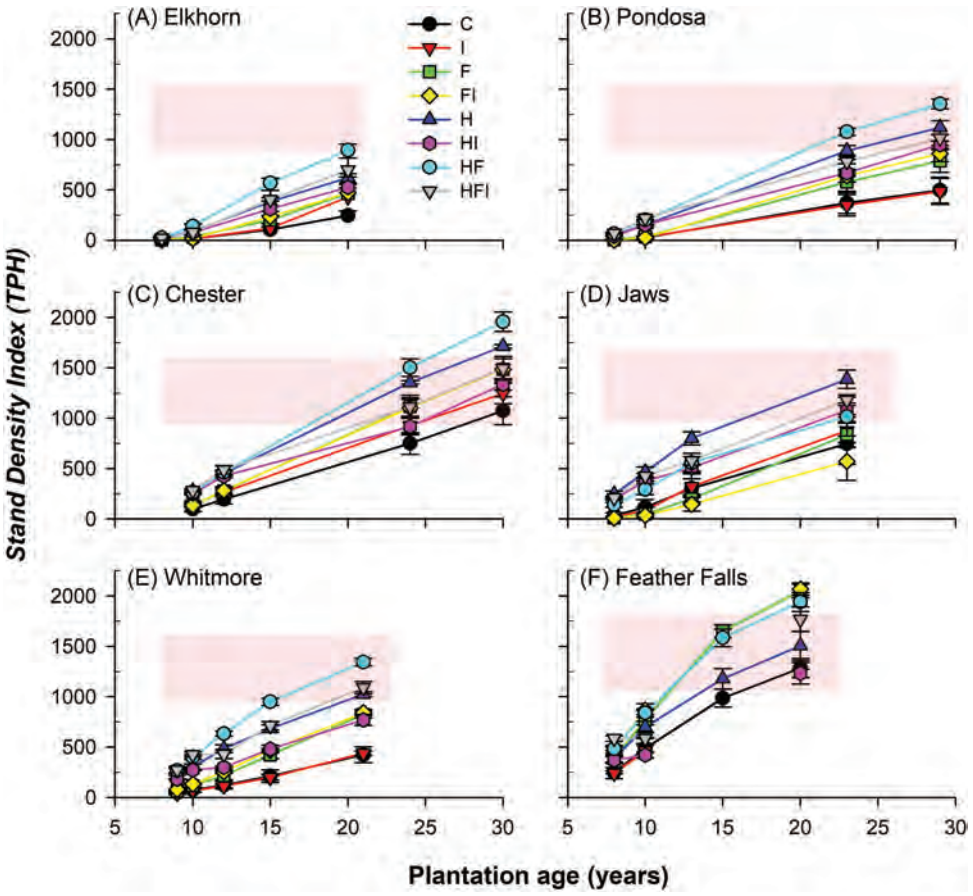

Figure 7. Average stand density index (SDI) and standard error for each treatment at six sites along plantation ages from 8–10 years to 20–30 years. SDI was calculated with the site-specific equations developed for ponderosa pine (Zhang et al. 2013a). Shaded red areas are the imminent mortality zones equivalent to what have been defined by Oliver and Uzoh (1997). The top edges of shaded areas were the maximum SDI.

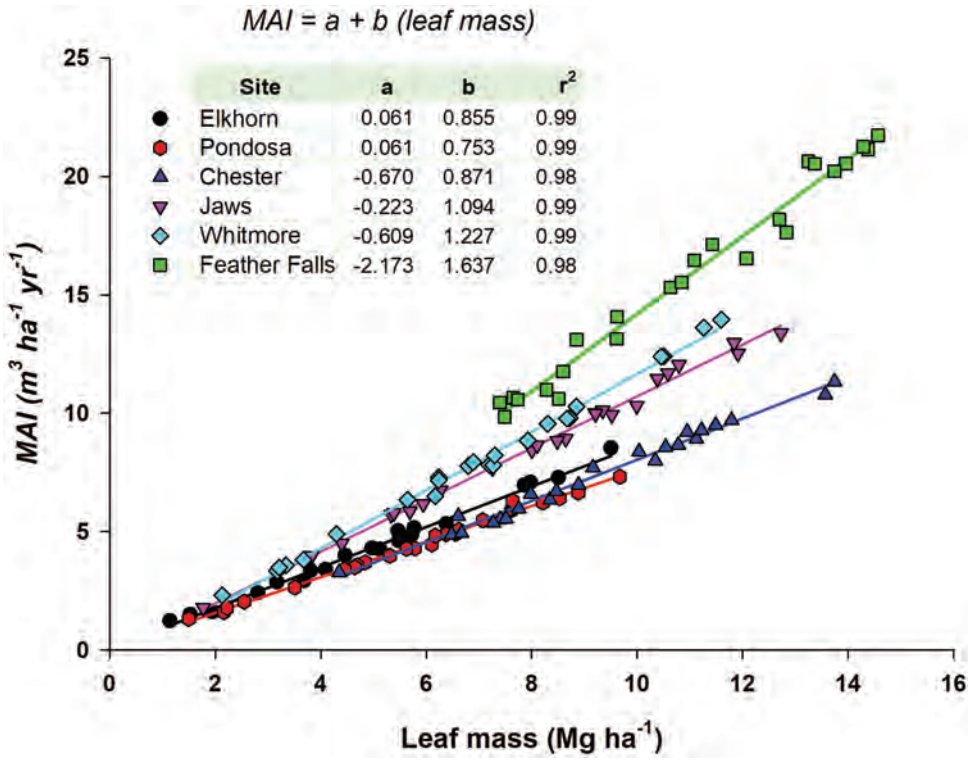

Figure 8. Relationships between mean annual increment (MAI) for volume and leaf mass estimated with site- and treatment-specific allometric biomass equations for ponderosa pines grown on various treatments at six sites in northern California.

results suggest that ponderosa pine not only is a favorable conifer species in its native habitat but also shows potential to be a highly productive species when planted in different regions of the world. Our findings are especially striking considering that ponderosa pine plantings in the current study used native rather than genetically improved stock, in contrast to exotic pine plantations (Mead 2013).

Achieving rapid growth through intensive ponderosa plantation management may open several possibilities for forest management. Ecological forestry practices on federal lands greatly reduce harvest yields compared with traditional even-aged management (Franklin and Johnson 2012). The ability of plantations to meet demands for wood products on a smaller land base and with lower-quality sites may permit western forests to balance wood production with less intensive ecosystem management or conservation objectives elsewhere on the landscape (Seymour and Hunter 1992, Binkley 1997). Another key application of highly productive plantation management would be in reforestation projects, which are considered to have the greatest potential among options for natural carbon capture and storage (Fargione et al. 2018). We will discuss the implications of faster tree growth for disturbance resilience below. Cultural practices permitting rapid rotations followed by replanting with climate-adapted stock could reduce the risk of project losses to climate change impacts (Puettman 2011). Incorporating intensive cultural practices would diversify approaches to climate change adaptation, which have focused on long-rotation ecological forestry in North America.

Site-Specific Treatment Effect on Growth

Although all our study sites have a Mediterranean climate, the significance of precipitation varied by site, ranging from an average of 736–2,035 mm (29.0–80.1 in) from October of the previous year to September of the current year (Table 1; Figure S1). Different soil types with varying water-holding capacity interacted with precipitation to further influence water availability. At Elkhorn, the poorest site in the study, the average 1,010 mm of precipitation appears favorable for growth, but the shallow and rocky soils suggest very low available water-holding capacity (USDA NRCS 2021). Because the majority of precipitation at all study sites occurs in winter, when plant photosynthetic gas exchange is limited, soil water storage capacity and possibly the weathered regolith become as important as precipitation during the growing season (Kelly and Gould 2016). By reducing shrub competition, the H treatment increased the amount of water available to and possibly nutrient uptake by planted trees, which in turn improved plantation productivity (Figures 5, 6, and S3). In contrast, fertilizer application (F and FI) without H showed a negative effect at the plantation initiation stage at Elkhorn and Jaws, with their metasedimentary soils, most likely due to competition from the drought-resistant shrub layer. With plantation development, however, trees that survived in these plots grew faster, likely by taking advantage of the now more available soil water and nutrients, until their volume accumulation ultimately caught up with trees in the control plots. By age 20, volume in F and FI treatments at Elkhorn doubled compared to the control, with a similarly increasing volume trend (ratios of F or FI and C) observed at Jaws (Figure S3).

At Feather Falls, the most productive site, which received twice as much precipitation as the other sites and has relatively deep and fertile Cohasset soil (Table 1, Figure S1), treatment effects appeared additive at age 6. Because this stand developed rather quickly, the effect of H-associated treatments achieved a higher positive effect on volume growth than F-associated treatments during stand development. The H-treatment effect gradually declined, but the size of the F-treatment effect increased. By age 20, F and FI treatments had accumulated more volume than HF treatments (Figure 5), which may relate to soil quality changes from understory litter (Busse et al. 1996, Winsome et al. 2014) in the absence of H treatment on a less-water-limited site. This hypothesis needs to be tested in future studies.

H-associated treatments had a higher positive effect than F-associated treatments on volume growth during stand development on three intermediate sites with volcanic soils, Chester, Pondosa, and Whitmore, but not on Jaws (Figures 5, S3). Growth in HF treatments was superior and appears synergetic. These results are consistent with previous reports (Powers and Ferrell 1996, Powers and Reynolds 1999). Interestingly, the H-treatment effect was very high relative to the control (2–10 times control volume) at age 6, less pronounced at age 10 (1.7–3.1 times control volume) and reached 1.4–3.7 times control volume at age 20–24, at which time volume in H and HF treatments at Chester, Pondosa, and Whitmore was still double that in the controls. In comparison, F-treatment effects varied with site and plantation age (Figure S3), with volume increases at Elkhorn, Chester, Jaws, and Whitmore peaking at the final measurement. There were no age trends at Pondosa and Feather Falls. Although we cannot generate a trend among site characteristics, presumably nutrient availability levels were as important as for coastal Douglas-fir plantations (Littke et al. 2017).

Whitmore was a unique site, with precipitation similar to Elkhorn and fine-textured Aiken clay soil as deep as at Feather Falls. Because it is located at the lowest elevation (Table 1), average temperatures were the warmest (Figure S1), suggesting that this site had the highest evapotranspiration. Trees should have experienced more water stress, especially later in the growing season (Powers and Reynolds 1999). In addition, aggressive *Arctostaphylos* formed a solid shrub layer in the control with aboveground biomass of 47 Mg ha^{-1} for live shrubs and 35 Mg ha^{-1} for dead shrubs at age 20 (Zhang et al. 2021). At Pondosa and Chester, although shrub density was the same, precipitation was lower. Therefore, water stress and the aggressive shrubs explain why tree growth responses to fertilizer were small unless shrubs were controlled until trees finally began to dominate the understory (Figure S3). The greater abundance of N-fixing *Ceanothus* species in shrub communities at Pondosa and Chester may also have elevated the importance of competition for soil moisture versus soil nutrients in limiting early pine growth.

In summary, without controlling competing vegetation on intermediate- and lower-quality sites, the effect of fertilization was small and did not appear to improve growth until planted trees dominated the canopy layer years later. However, on higher-productivity sites, both H and F effects immediately appeared and would be expected to dissipate later in stand development beyond the timeframe of this study. In another plantation study, Powers et al. (2005) similarly found that trees on the poor Mariposa soils did not respond to N fertilization unless fertilization was combined with brush removal. In contrast, trees planted on immediately adjacent sites with

more productive Cohasset soils responded positively to brush removal and fertilization applied independently and as combined treatments (Powers et al. 2005).

Thinning Effect

When the Garden of Eden study was installed, plant spacing was much narrower than spacings used today due to lower survival rates and anticipation of precommercial thinning. Results from the Challenge Initial Spacing study suggest the narrow spacing at Garden of Eden plots prior to thinning may have reduced herbicide treatment effects (Zhang et al. 2006). Due to a lack of insect outbreaks for the first 6 years, the insecticide treatments during that time showed no effects. Following thinning of 50% of the trees in the HI and HFI treatment plots, volume growth caught up with the C and I and other associated H and HF treatments within 10 years or less (Figures 5, 6, and S3). Numerous long-term ponderosa pine density studies in northern California and southeastern Oregon have demonstrated that thinning stands to a lower density does not sacrifice stand growth because it imitates potential tree mortality (Zhang et al. 2013d, 2019a). These results have important implications in California because of intensified wildfires in recent decades. Thinning a stand to a lower density would reduce fire risk, usually by removing smaller trees that contribute to ladder fuels, and further enhance the growth rates and health of remaining trees by promoting taller growth and thicker bark (Zhang et al. 2019a), characteristics that are more resistant to wildfire (Regelbrugge and Conard 1993). Thinning to specific densities can be done without sacrificing midterm stand productivity if a management goal is wood volume for timber production.

Individual Tree Growth Variation and Stand Resiliency

The purpose of presenting individual tree height and DBH growth is to illustrate how these measures varied among sites and treatments, both alone and in combination. Significantly more variation was found in the plots or sites with lower available resources (Figures 4 and S2). Purposely managing forests for variability has been suggested to improve resilience to disturbances (North et al. 2009). Low resource availability reduces large tree growth efficiency, which may ultimately promote greater structural complexity by reducing self-thinning among smaller trees (Pretzsch and Dieler 2010). Managing forests for variability also has advantages for timber production. From a plantation management standpoint, higher variability provides an easier selection of smaller trees during precommercial thinning in resource-limited sites, which may yield stands similar to postthinned stand on resource-rich sites.

Stand Density Index and Self-Thinning

Ponderosa pine stands in California reach the onset of self-thinning when SDI is over 568 trees per ha (TPH), and at an estimated maximum SDI of 900 TPH, assuming that SDI is calculated as independent of site quality (Oliver and Uzoh 1997). Although we calculated SDI as dependent on site quality (Zhang et al. 2013a), treatment plots at multiple sites had reached or surpassed both 568 TPH and 900 TPH by age 20 (Figure 7). Surprisingly, self-thinning mortality had not occurred as of the most recent inventory year, even at Chester and Pondosa, where original plots are intact. There is a possibility that these intensive cultural treatments promote fundamental site carrying capacity and therefore increase stand maximum SDI (Zhang et al. 2013a, Kimsey et al. 2019). We have observed that many ponderosa pine plantations with vegetation control reach an SDI of 900 TPH without the onset of mortality (Zhang et al. 2017). Jokela et al. (2010) reported that fertilization and weed removal increase site index at a base age of 25 years from 19.5 to 26.5 m in loblolly pine and from 22.9 to 26.8 m in slash pine, which indirectly suggests that treated stands will have a higher maximum SDI than untreated or natural stands. SDI is understood to be a proxy for leaf area, and cultural treatments such as fertilization may temporarily increase leaf area index beyond species-specific maximums under typical conditions (Long et al. 2004). Herbicide treatments might similarly be considered a means to redistribute stand leaf area from the shrub layer to trees. Another key factor that may help avoid mortality losses in these plantations is relatively small average tree size, as large-diameter trees are at higher risk of western bark beetle (*Dendroctonus brevicomis*) attack (Fettig et al. 2007).

Conclusions

This study demonstrated the importance of competing vegetation control for plantation establishment and development at lower- and intermediate-quality sites, where fertilization effect will not be significant unless competing vegetation is also controlled by herbicide or until trees grow over the shrubs. At higher-productivity sites, H and/or fertilization will be effective, although the H effect will dissipate quickly starting at the time of canopy closure. Across the site-quality gradient, higher resource treatments are capable of doubling ponderosa pine volume growth compared with the control plots during the developmental years. It appears that treatment effect will be higher at lower-quality sites than at higher-productivity sites. A growth rate of 21.7 m^3 ha^{-1} yr^{-1} was the highest volume MAI at age 20 reported for ponderosa pine stands in California, approaching growth seen in exotic ponderosa plantations with genetically improved stock. Regardless of treatments and site quality, leaf biomass determines stand volume growth. Intensively managed plantations appear to have a higher maximum SDI than either natural stands or nonmanaged plantations. Therefore, these treatments can be used to rapidly reforest disturbed lands and promote larger trees on postfire landscapes. The results from this and other studies underscore the site-specificity of appropriate cultural treatments, especially H and F treatments, that will enhance plantation productivity and boost stand development.

Supplementary Material

Supplementary material is available at *Forest Science* online.

Acknowledgments

This article is dedicated to the memory of our late colleague Dr Robert F. Powers, who initiated the Garden of Eden experiment and oversaw the early data collections. More importantly, he contributed significantly to the knowledge base of silvicultural practices influencing forest productivity and sustainability in California and across the world. Thanks to our former and current supporting staff in our Redding laboratory, Thomas Spear (deceased), Terrie Alves, Donald Jones, Carol Shestak, Bob Carlson, and many others for their

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