



Allometry of tree biomass and carbon partitioning in ponderosa pine plantations grown under diverse conditions

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ABSTRACT

Forests not only provide forest products to meet people's demands, but also sequester enough carbon to offset more than 11% of anthropogenic CO₂ release in the United States. An accurate estimate of forest carbon sequestration over different forest and forest product combinations requires the species-specific and site-specific allometric biomass equations for trees and understory vegetation at particular forest developmental stages. Here, we constructed the above- and below-ground allometric equations by harvesting 108 20-year-old ponderosa pine (*Pinus ponderosa*) trees grown under four different silvicultural treatments (four combinations of with and without competing vegetation control (H) and fertilization (F): C = control with no vegetation control and no fertilization, H, F, and HF) at three diverse site conditions in northern California. We found that the logarithmic regressions provided superior estimations of biomass for total, aboveground, bole, coarse roots, branches, and foliage compared to simple or scaled power-law fits. Treatment effect in allometric equations was generally lacking but site effect was significant, suggesting site specific allometric relations exist. With the best allometric equations, we estimated the biomass and carbon for each plot among treatments and sites. In addition, understory woody plant biomass was also measured with fixed area subplots. Results show significantly more total carbon sequestration at the high-quality sites with 113.1–162.5 Mg ha⁻¹ than the lower ones with 85.8–105.9 Mg ha⁻¹ at the intermediate site and 29.3–70.4 Mg ha⁻¹ at the poorest site, respectively. The range of carbon stocks indicates the treatment differences at each site, with the largest effect (240%) at the poorest site and similar at other two sites (~130%). If planted trees only were considered, a trend among sites exists with 93.4–149.3 Mg ha⁻¹ at the richest site, 26.2–88.1 Mg ha⁻¹ at the intermediate site, and 17.1–64.2 Mg ha⁻¹ at the poorest site, respectively. Therefore, if we manage forests for carbon or forest products, intensive management practices will substantially enhance plantation productivity and stand development while site quality cannot be changed.

1. Introduction

Global climate has been changing at an unprecedented rate. From 1850–1900 to 2006–2015 mean land surface air temperature has increased by 1.53 °C (IPPC, 2019). During the last six years, the world experienced the warmest climate on record since 1880 (Voosen, 2021). The warming trends are believed to be associated with the anthropogenic increase of greenhouse gases (GHGs). Worldwide, net emissions of GHGs from human activities increased by 35% from 1990 to 2010 (EPA, 2021). Carbon dioxide (CO₂), which is a major component of GHGs, increased by 42% over this period. Furthermore, not only has CO₂ and GHG concentration increased significantly, but also the rate of increase

has far exceeded pre-industrial values.

Forests play a significant role in offsetting CO₂ emissions by converting CO₂ into wood through photosynthesis. The products of photosynthesis are stored in the forest for decades or centuries. Despite uncertainties, annual carbon sequestration is about 188.5 million megagram (Mg) by forests in the United States (EPA 2020), which offsets about 11% of US CO₂ emissions. Additional 47 million Mg C could have sequestered if all understocked timberland were fully stocked in the conterminous United States (Domke et al., 2020).

Central to assessing forest carbon is the capacity to estimate individual and stand tree biomass because this is a baseline for assessing changes in net primary production and fuel loading. Yet, the choice of

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biomass estimation models is one of the most important sources of uncertainty (Sileshi, 2014; Temesgen et al., 2015; Vorster et al., 2020). Therefore, allometric biomass estimation and stand biomass partitioning play an important role in accurately estimating carbon sequestration in forest stands.

As one of the most widely distributed pine species in North America, ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) forests occupy over 9.3 million ha out of 76.9 million ha of western conifer forests (Oswalt et al., 2019). It is not only planted for timber production, wildlife habitat, recreational use, and esthetic values, but also for carbon sequestration (Oliver and Ryker, 1990; Zhang et al., 2010). Because of its drought tolerance and fire resistance, it is regarded as a favorable species for rapid reforestation after stand-replacing wildfires. These factors have led to extensive research with this species, with multiple allometric equations having been developed. Jenkins et al. (2004) compiled a set of diameter-based biomass estimations of ponderosa pine from four sources across the United States. Among them, Gholz et al. (1979) constructed some allometric equations with various above-ground components of biomass from 9 trees (DBH 15.5–79.5 cm) sampled from a natural stand at the Fort Valley Experimental Forest in Arizona, which was extensively used for ponderosa pine biomass estimation. Another source used in the compilation of Jenkins et al. (2004) was Means et al. (1994) who actually led to an unpublished source that was most likely the same as Gholz et al. (1979). The third one was Cochran et al. (1984), who used 23 natural trees (DBH 5.3–38.7 cm) from two different stands varying with stand density in southeastern Oregon. Lastly, Brown (1978) modelled only crown biomass for mature trees based on 44 destructively sampled ponderosa pine trees with DBH ranging from 25.0 to 86.4 cm from 8 natural forest stands across northern Idaho and western Montana. In addition, to the above-mentioned sources, other allometric equations either existed or have been recently established. Gower et al. (1993) fitted allometric regressions with 18 trees (DBH ca. 10–30 cm) from either fertilized plots or control plots in western Montana. Laclau (2003a; b) did similar work for aboveground and belowground biomass based on 48 trees (3–25 cm) from 10- and 20-year-old plantations in northwest Patagonia, Argentina. Zhang et al. (2010) established an aboveground biomass equation by compositing 146 harvested trees (DBH 4–152 cm) from both natural stands and plantations across the Sierra Nevada and southern Cascades of California. Tinker et al. (2010) harvested 32 trees (DBH 6–53.5 cm) for aboveground and 16 trees (DBH 6–24 cm) for belowground from natural forests in the Black Hills of Wyoming. Ritchie et al. (2013) established biomass equations based on 79 trees (DBH 12–52 cm) harvested from several thinning regimes and untreated stands at Blacks Mountain Experimental Forest in northeastern California. Vorster et al. (2020) sampled 10 natural trees (DBH 5–62 cm) in northern Colorado. Zhang et al. (2020) fitted 30 plantation trees (DBH 8–40 cm) grown at Challenge Experimental Forest, California. Besides these allometric equations for total aboveground biomass and some with belowground biomass, others still exist such as crown biomass developed from 21 trees (DBH 4.8–70.6 cm) in northern Idaho (Monserud and Marshall, 1999) and coarse roots for 42 trees (DBH 18–68 cm) in New Mexico (Omdal et al., 2001).

These previous works have revealed two aspects. First, there were more aboveground biomass equations than belowground equations as being summarized above. Second, allometric biomass estimation models not only changed with the analytical methods (Sileshi, 2014), but also varied with site, stand conditions, and silvicultural treatments in ponderosa pine (Cochran et al., 1984; Ritchie et al., 2013; Temesgen et al., 2015; Vorster et al., 2020; Zhang et al., 2020). Therefore, our first goal of this study was to develop new allometric equations for predicting biomass or carbon for ponderosa pine growing in different management regimes and sites.

The second goal of this study was to accurately estimate the stand-level biomass or carbon and to further determine the effects of silvicultural treatments on biomass accumulation or total carbon

sequestration among three diverse sites. A century of research and observations have recognized that site quality is a foundation of stand productivity (Powers et al., 2005a). Less understood is how silvicultural treatments such as fertilization and competing vegetation control influence stand production and whether the treatment effects interact with site quality under the current climates in northern California.

Ponderosa pine, as with all other plants, needs to lose water in the process of fixing carbon dioxide through photosynthesis. Worldwide, water is a limiting factor for plants, particularly in the Mediterranean climatic regions where there is a lack of any significant amount of rain during the growing seasons. Silviculturally, competing vegetation control (CVC) has been an effective practice in freeing soil water for the use by targeted trees rather than physiological needs of competing vegetation (McDonald and Fiddler, 2011; Zhang et al., 2019). We have found 40–105% increases in tree basal area with CVC compared with no CVC for ponderosa pine stands in California (Zhang et al., 2013). The earlier the CVC was applied, the larger the effect would be. In addition, CVC also increased the nutrient availability to the trees; studies have shown nutrient deficiencies in California (Powers and Jackson, 1978; Powers et al., 1988). Besides these direct benefits, soil moisture also helps trees take up nutrients (Powers and Ferrell, 1996).

Although silvicultural practices have long been used to increase stand productivity and wood biomass (Campioli et al., 2016; Noormets et al., 2015), their effects on carbon allocation and storage in understory, forest floor, and mineral soil may be neutral or negative due to an offset between planted trees and competing vegetation along stand developmental stages (Zhang et al., 2020). The third goal in this study is to better understand the interactions between silviculture practices and site biogeochemical processes that will aid in the development of management strategies that maximize carbon sequestration while also maintaining productive capacity.

The specific objectives for this study are to (1) compare different methods used for developing allometric equations of various tree components, and to determine the best ones based on a comprehensive examination of factors (Sileshi, 2014), (2) determine if these allometric equations differ among treatments and/or sites, (3) estimate the total overstory and understory biomass for these 20-year-old plantations, and (4) determine the total biomass and carbon partitioning among the ecosystem components.

2. Materials and methods

2.1. Study site

The study was conducted in northern California at three ponderosa pine research plantations installed in the late 1980s to study how plantation growth was constrained by natural limiting factors and what silvicultural treatments could be applied to mitigate these natural stresses (Powers and Ferrell, 1996). From 8 installations with a common design in the original study, we chose Elkhorn, Whitmore, and Feather Falls installations as representing low, intermediate, and high site quality, respectively (Table 1). These sites are in the typical Mediterranean climate with warm, dry summers and cool or mild, wet winters.

2.2. Treatments and experimental design

A completely randomized design was commonly used at each of all sites. When multiple sites were included in the analyses, we regarded the site as a block and therefore the overall design becomes a generalized randomized block design. At each site, each of eight factorial combinations between two levels of vegetation control, fertilizer, and insect control was replicated three times and randomly assigned to 24 plots. Plot size is about 22 m × 20 m. One-year-old seedlings raised from site-respective seed sources were planted at 2.5 m × 2.5 m spacing. A total of 72 trees were planted within each plot with the inner 20 trees composing the measurement plot and outside two rows of trees serving as the

Table 1

Geographic locations, site characteristics, and means (standard errors) when trees were harvested for allometric measurements of three plantations from poorest to highest site quality in northern California.

	Elkhorn	Whitmore	Feather Falls
Latitude (N)	40°04'57"	40°37'33"	39°37'11"
Longitude (W)	122°44'32"	121°53'56"	121°11'48"
Elevation (m)	1545	755	1246
Site index (m at age 50)	17	23	30
Annual mean T_{max} (°C)	16.4	21.4	18.3
Annual mean T_{min} (°C)	2.4	7.6	5.7
Annual precipitation (mm)	1015	1140	1780
Soil type	Sandy loam	Loam/Clay	Clay loam
Previous vegetation	Plantation	Brushfield	Natural stand
Year planted	1988	1986	1988
DBH (cm) when harvested			
Control	8.65 (0.42)	10.59 (0.42)	18.32 (0.87)
Fertilization	12.05 (0.71)	15.89 (0.54)	23.37 (0.73)
Herbicide	12.90 (0.34)	15.92 (0.45)	19.48 (1.05)
HF	14.46 (0.59)	18.24 (0.42)	22.00 (0.37)
Height (m) when harvested			
Control (C)	4.53 (0.18)	6.83 (0.25)	13.02 (0.69)
Fertilization (F)	6.18 (0.30)	9.54 (0.22)	14.56 (0.54)
Herbicide (H)	6.61 (0.14)	9.89 (0.19)	13.56 (0.81)
HF	7.30 (0.24)	11.54 (0.16)	14.11 (0.40)

buffers. The treatments consisted of applying or not applying herbicide, insecticide, and fertilizer. Both herbicide and insecticide were applied each year for the first six years. Fertilization, with granular commercial salts of full elements, was applied during the dormant season at years two, four, and six. Application was completed with a ramp schedule based on demand in the first six years (Powers and Ferrell, 1996). In this study, we used 12 plots with treatment combinations of herbicide and fertilization including control (C: do nothing after planting), herbicide (H: competing vegetation was controlled by herbicide), fertilization (F), and herbicide with fertilization (HF). Herbicides applied were either glyphosate, hexazinone, or triclopyr with the rate based on manufacturer's recommendations for the soil type and vegetation present.

2.3. Aboveground tree harvest

Tree height, diameter at 1.37 m height (DBH), height to live crown (HLC), and crown width (CW) were measured for all trees at various ages during the study. Prior to selecting trees for the biomass harvest, all trees were measured, and from these data one tree each was randomly selected from three size categories (small, medium, large) based on tree height and DBH at each plot. At each site, 36 trees were harvested.

The crown of a selected tree was removed from the bole above breast height so that remaining bole could be used to facilitate future root excavation (Fig. 1). Disks were removed from the bole just above the cut, immediately below the live crown, and from the middle of the live crown from each felled tree. The dimensions (diameter of two axes inside and outside bark and disk thickness at the end of each axis) of each sampled disk and length of each bole section were recorded in the field. The live crown was divided into five equal sections and all living branches were measured for diameter at a standard distance (6 cm) from the bole of the tree. Branch diameters were then squared, summed, and averaged in the field. The top of the main stem, as well as the branch of average squared diameter from each sector, were collected for later weighing of wood and foliage separately. Below the live crown, the dead branches were sampled in a similar way. Some of the operations are shown in Fig. 2A–D.

The samples for bole wood, branches and foliage brought back from the field were all weighed separately after drying to constant weight at 80° C, usually 48–72 h. Total bole biomass was estimated for each section as the product of the average of wood density of the ends of each section and the volume of that section. Separate biomass equations were established for the different treatments from the branch and foliage measurements; these equations were used to estimate all branches and

associated foliage on the tree stem. Total aboveground biomass (AGB) for an individual tree was the sum of all components (foliage, branch, and bole).

2.4. Coarse root excavation and measurement

Around each stump, 1-m deep holes were diagonally dug under the root wad for dynamite placement using a 4.5 cm auger either mounted on a hand-held gas engine or mounted on a small excavator and powered by the excavator's hydrologic system. Four to six holes were dug under each stump depending on the size of the stump. The charge put into each hole ranged from one half to a full stick of dynamite, intended to loosen the soil without destroying the root wad. Once the holes were dug, all the charges were wired and fuses were set so that all 36 root wads in a study area were blown at once. The entire blasting operation was conducted by a United States Forest Service certified blaster.

Once the blasting was done, all the spent blasting wire was picked up and disposed of leaving the site ready for the extraction of the root wads. A large excavator (John Deere Series 600, Moline, IL, USA) equipped with a bucket with an attached thumb was used to delicately lift the root wads. Using the thumb, the operator would grasp the aboveground tree stem with the bucket and gently tilt the root wad in several directions to loosen it. Then the operator would slowly begin to lift the stem/root wad straight up. As soon as the lateral roots were exposed (they are still below ground line) the lifting was stopped and the lateral root of average diameter was determined by measuring the diameter of each lateral root where it was attached to the tap root; summing the diameters and dividing by the number of laterals. This average lateral was then severed at the point where it was attached to the root wad and left intact in the ground. This selected root was excavated later by hand, measured, and collected. Once the selected average lateral was severed from the root wad, the lifting of the root wad continued until all remaining laterals were exposed above ground line. These roots were then severed from the root wad leaving a 30–60 cm length attached to the root wad. At this point the lifting was continued until the entire root wad was clear of the ground. It was then placed in the access trail by the excavator. A front-end loader with a four-in-one bucket then transported the root wad to the staging area. After all non-selected lateral roots were trimmed off flush to the tap root, the root wads were transported back to our laboratory (Fig. 2E) for further processing.

The processing of the root wads followed this procedure: (1) mark all root wads at 5 cm above topmost lateral root, (2) clean any remaining soil from root wads, (3) measure diameter of any broken taproots greater than 2 cm, (4) take photos that capture varying character of the root systems, (5) cut bole at 5 cm line and save the cut piece, and (6) promptly weigh the stump.

A disk at least 5 cm thick was cut and weighed immediately, labeled, bagged, and placed in the oven for drying. The drying procedure is the same as described for the field disks previously. From drying the disk, we were able to calculate the wood moisture content, from which the stump weight measured earlier was extrapolated to obtain the dry taproot biomass.

The selected lateral roots were excavated by hand. Workers doing the excavation followed the multiple orders of roots until root tips reached 2 mm in diameter. Roots smaller than this were regarded as fine roots (Fig. 2F). If a sinker root was present, it was excavated to a depth of 1 m regardless of its diameter. The lateral roots were dried in the oven and weighed. With the regression between dry weight and root diameter, we estimated the entire lateral root biomass. Total root biomass was calculated by summing root wad with tap roots and lateral roots.

2.5. Allometric equations

We used the power-law relationship or its logarithmic form as our blueprints to fit the allometric parameters with either nonlinear regression

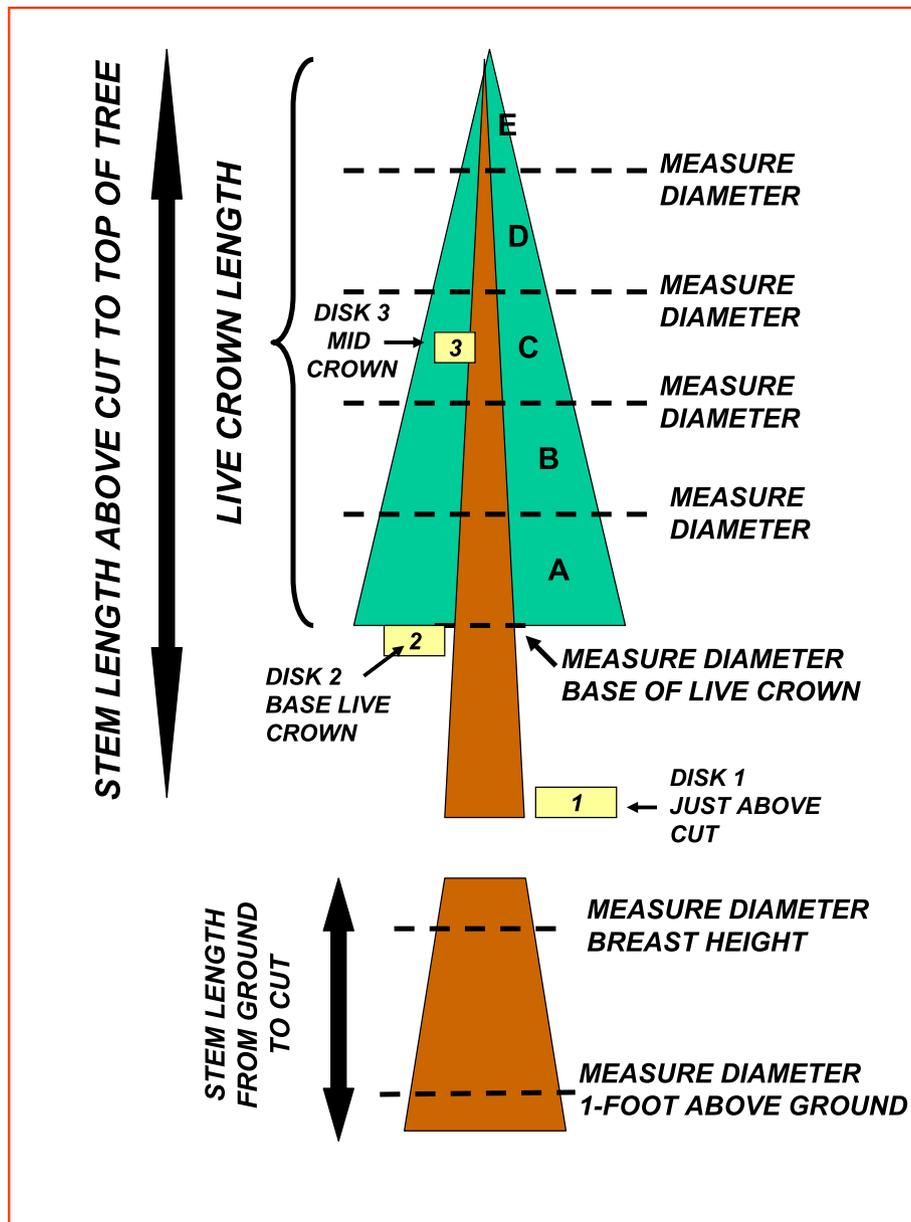


Fig. 1. A sketch of sampling sections and field measurements of the above ground components after a tree was felled.

$$\text{Biomass} = aDBH^b \quad (1)$$

or linear logarithmic regression

$$\ln \text{Biomass} = \ln(a) + b(\ln DBH) \quad (2)$$

where a and b are regression coefficients.

Because of structure of the experimental design that includes site and silvicultural treatments, we were able to test whether effects of both fixed terms were significant. Therefore, a modified logarithmic linear model from (2) was used to fit the allometric equations with PROC MIXED in SAS (SAS Institute Inc, 2012).

$$\ln \text{Biomass}_{ijklm} = \mu_{ijk} + \beta_{ijk} \ln DBH_{ijklm} + \delta_{ijkl} + \epsilon_{ijklm} \quad (3)$$

where Biomass_{ijklm} is the biomass for site i , fertilization level j , herbicide level k , plot l , and tree m and μ_{ijk} and β_{ijk} are the respective intercept and slope for site i , fertilization level j , and herbicide level k with

$$\mu_{ijk} = \mu + \mu_i^S + \mu_j^F + \mu_k^H + \mu_{ij}^{SF} + \mu_{ik}^{SH} + \mu_{jk}^{FH} + \mu_{ijk}^{SFH}$$

and

$$\beta_{ijk} = \beta + \beta_i^S + \beta_j^F + \beta_k^H + \beta_{ij}^{SF} + \beta_{ik}^{SH} + \beta_{jk}^{FH} + \beta_{ijk}^{SFH}$$

where the symbols represent the overall mean, main effects and 2- and 3-way interactions. δ_{ijkl} is the random effect of plot l associated with site i , fertilization level j , and herbicide level k with zero mean and variance σ_p^2 , and ϵ_{ijklm} is the residual error for tree m with zero mean and variance σ^2 .

We also fitted the nonlinear allometric equations with the non-transformed data using PROC NL MIXED. The two models use a similar notation as model (1):

$$\text{Biomass}_{ijklm} = a_{ijk} DBH_{ijklm}^{b_{ijk}} + \delta_{ijkl} + \epsilon_{ijklm} \quad (4)$$

$$\text{Biomass}_{ijklm} = a_{ijk} DBH_{ijklm}^{b_{ijk}} + \delta_{ijkl} + DBH_{ijklm} \times \epsilon_{ijklm} \quad (5)$$

with a_{ijk} and b_{ijk} being the respective multiplicative and exponent constants:

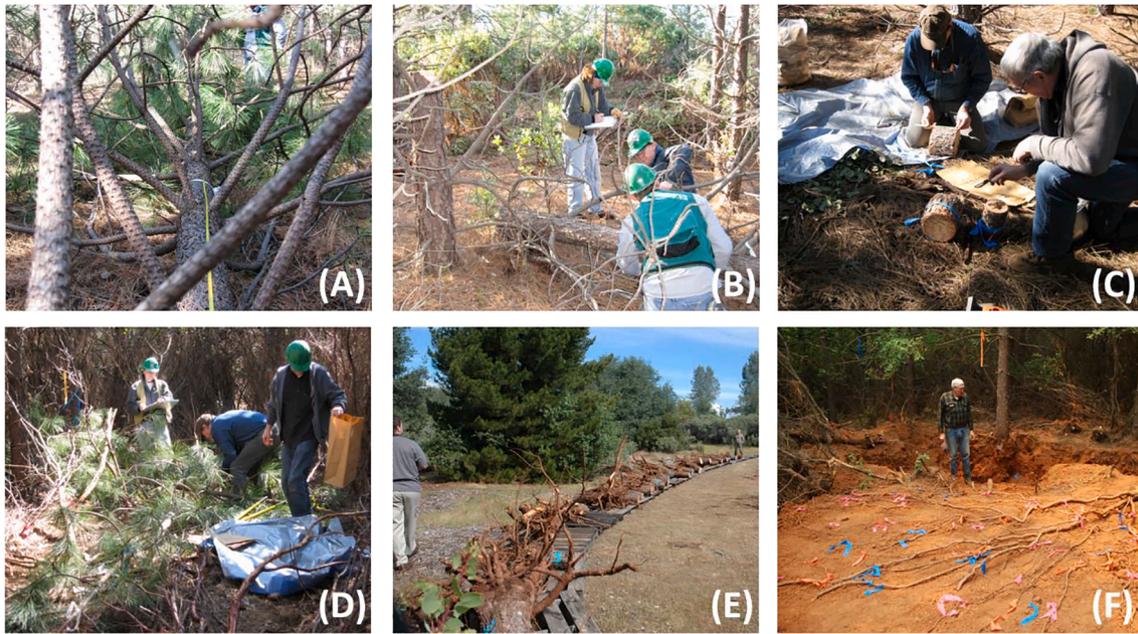


Fig. 2. Tree harvesting operations: (A) measuring tree height and crown length to decide where the disks were cut and to separate the sections, (B) inventorying all branches with base diameter and selecting a sampling branch within each section (In the picture from right to left: Robert Carson, Robert Powers, and Carol Shestak), (C) measuring dimensions of each disk (Gary Fiddler and R. Powers), (D) collecting foliage for each sampling branches (Donald Jones, R. Powers, and C. Shestak), (E) excavated roots (R. Powers and David Young), and (F) excavated selected lateral root (G. Fiddler).

$$a_{ijk} = a + a_i^S + a_j^F + a_k^H + a_{ij}^{SF} + a_{ik}^{SH} + a_{jk}^{FH} + a_{ijk}^{SFH}$$

and

$$b_{ijk} = b + b_i^S + b_j^F + b_k^H + b_{ij}^{SF} + b_{ik}^{SH} + b_{jk}^{FH} + b_{ijk}^{SFH}$$

where just as in the previous notation, the symbols represent the overall effect, the main effects, and the 2- and 3-way interactions.

The error terms were defined as in Eq. (3). However, the model (4) was dropped from consideration during the stage of data exploration because the observed increase in variance across values of DBH was not constant as implied by the model (Fig. 3).

Each linearly logarithmic model was then back-transformed to a power function of the form with a correction factor (CF) computed as Baskerville (1972):

$$CF = e^{\frac{MSE1 + MSE2}{2}} \quad (6)$$

MSE is the mean square error of the site by plot (MSE₁) and the regression (MSE₂).

To select the best allometric models during model fitting, we used some criteria recommended comprehensively by Sileshi (2014).

2.6. Stand vegetation biomass

Stand vegetation biomass was calculated as both planted tree biomass and understory woody plant biomass. Because there were no woody plants present in the H and HF plots, understory biomass, dominated mainly by *Arctostaphylos* spp. L. and *Ceanothus* spp. L., was only measured in the control and fertilizer plots. The planted tree biomass was individually estimated from the best model that we selected from the allometric equation fits described in the last section, and then summed up for all trees. Understory biomass was determined by collecting aboveground live and standing dead woody plant components in the randomly selected sampling areas on the C and F treatment plots, including roots; the roots for the standing dead plants were only those still attached to the main tap roots. There were three 6-m² square subplot at Elkhorn, three 1-m² circular subplots per treatment plot at Whitmore, and three 2-m² circular subplots per plot at Feather Falls,

respectively. The reason for using the different sampling sizes and shapes was due to the vegetation uniformity of species composition and distribution. Aboveground portion of plants was harvested before the roots were excavated by a small excavator or by hand. Aboveground and belowground samples were separately brought back to the laboratory for determining the biomass with the same methods used for the planted trees. The final carbon pools for all plant components were converted from biomass by assuming 50% of biomass being carbon.

Canopy cover was estimated from individual tree measurements of crown widths (CW). By assuming a ponderosa pine tree crown as a cone, we estimated crown volume as:

$$\text{CrownVolume} = \sum_{i=1}^n \frac{1}{3} (HT - HLC) \pi \left(\frac{CW}{2}\right)^2 \quad (7)$$

where (HT - HLC) is live crown length and $i = 1, 2, \dots, n$ referring all trees in each plot.

Leaf area index (LAI) was calculated from total leaf area (one-sided) divided by plot area. The total leaf area was estimated from total foliage biomass and specific leaf area measured on these sites.

2.7. Statistical analysis

We analyzed stand level biomass variables and overstory stand structure variables to test if the effects of site, treatments (fertilizer and herbicide), and their interactions were significant using SAS PROC MIXED (SAS Institute Inc, 2012), with site and treatment as fixed effects and plot as a random effect. The statistical model was:

$$y_{ijk\ell} = \mu + \alpha_i + \beta_j + \gamma_k + \alpha\beta_{ij} + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk} + \varepsilon_{ijk\ell} \quad (8)$$

where $y_{ijk\ell}$ is the dependent variable summarized for the i^{th} site, j^{th} level of fertilizer ($j = 0$ for no fertilizer and $j = 1$ for fertilizer applied), k^{th} level of herbicide ($k = 0$ for no herbicide and $k = 1$ for herbicide applied), and the ℓ^{th} plot, μ is the overall mean, α_i , β_j , and γ_k are the respective fixed effects of the i^{th} site ($i = 1, 2, \text{ and } 3$), j^{th} level of fertilizer ($j = 0, 1$), and k^{th} level of herbicide ($k = 0, 1$). The terms $\alpha\beta_i$, $\alpha\gamma_{ik}$, $\beta\gamma_{jk}$,

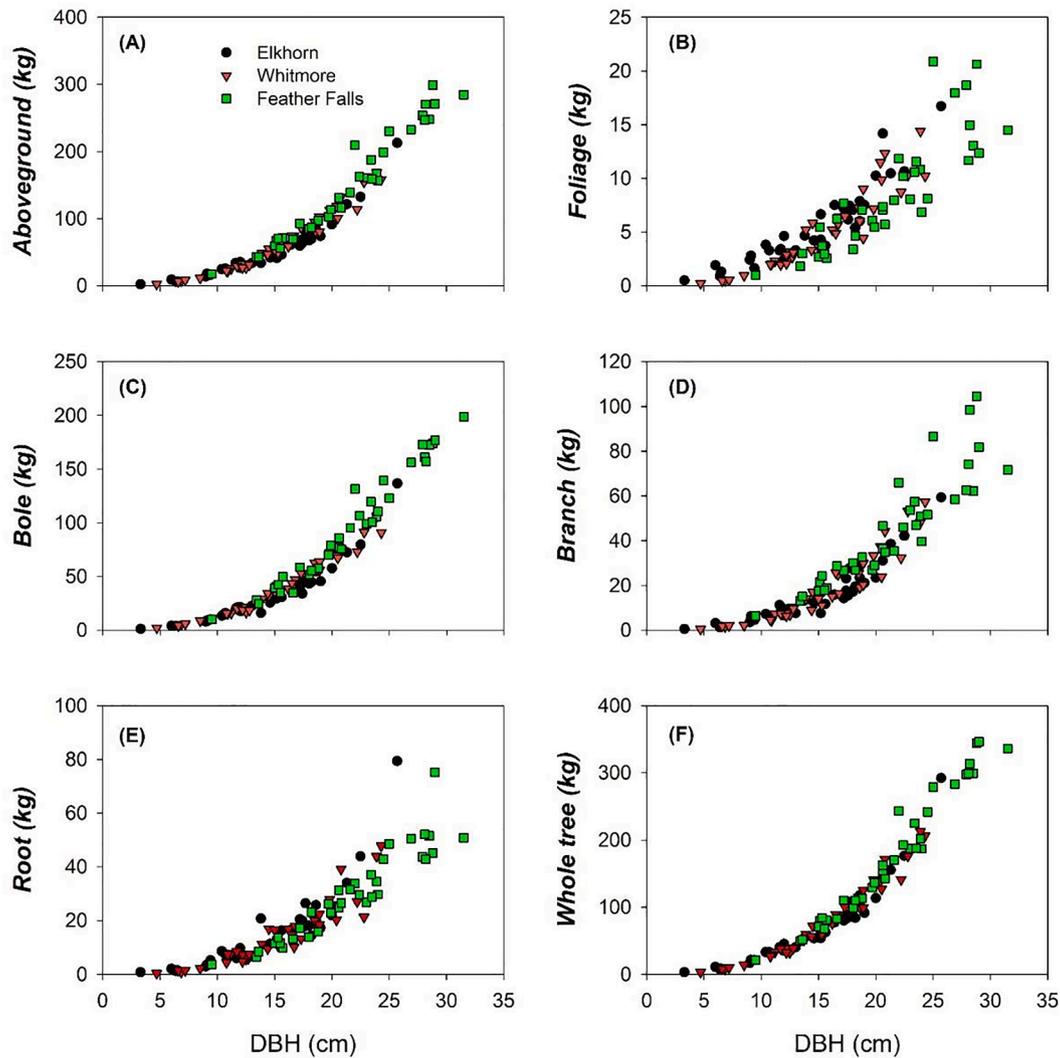


Fig. 3. Biomass (kg) for various tree components and tree DBH (cm) for 36 trees from 12 treatment plots at each of three sites in northern California. Nine trees were harvested from each of 4 treatments (C, F, H, and HF). Plantation age was 21 years at Elkhorn and 20 years at both Feather Falls and Whitmore.

and $\alpha\beta\gamma_{ijk}$ are the respective two-way and three-way interaction terms. Finally, ε_{ijk} is the experimental error, $\varepsilon_{ijk} \sim iidN(0, \sigma_e^2)$.

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. Multiple comparisons among sites or/and treatments were conducted for least squares means by the Tukey-Kramer test by controlling for the overall $\alpha = 0.05$.

3. Results

3.1. Allometric biomass equations

Biomass of each component and/or total tree spanned the tree sizes we selected on each plot at each site (Fig. 3). The figure also shows the general relationships between biomass and DBH. Apparently, non-consistent variance for the biomass occurred across values of DBH. Therefore, we eliminated model (4) as indicated previously.

After running the logarithmic model (3) and the DBH scaled power-law model (5), we found that the former was clearly superior to the later (Table S1). The smaller AICC, PRSE, and MAPE were found with results from model (3) versus model (5) for all biomass variables. Therefore, we present the logarithmic model (3) in detail here and used these parameters to estimate stand AGB and coarse root biomass for planted trees.

All biomass components except for the bole showed a significant site effect ($P < 0.03$, Table 2). However, the treatment and its associating interactions were in general non-significant ($P > 0.05$) with a few exceptions such as site*herb for foliage, site*herb*logDBH for branches, and site*fert*logDBH for bole, respectively ($P < 0.04$). Therefore, allometric equations by site and treatment shall appropriately estimate individual tree biomass.

To preserve the experimental design structure, we provided all parameter estimates for AGB and coarse root biomass in Table 3. These estimates and their associated correction factors were used to estimate stand AGB and coarse root biomass for planted ponderosa pine trees. We calculated that the average intercept $\ln(a)$ and exponent (b) for $\ln(AGB)$ were -2.306 and 2.284 at Elkhorn, -2.908 and 2.532 at Whitmore, and -2.305 and 2.360 at Feather Falls, respectively (Fig. 4A–C). More variation of these parameter estimates was found for coarse root biomass than for AGB (Table 3). Means of intercept $\ln(a)$ and exponent (b) for $\ln(\text{Roots})$ were -2.349 and 2.241 at Elkhorn, -4.932 and 2.732 at Whitmore, and -4.176 and 2.435 at Feather Falls, respectively (Fig. 4D–F). The apparent differences in the HF at Elkhorn were caused by a few trees with relatively massive root systems and outstanding growth at this rather low quality site (Fig. 3A–F; Fig. 4A, D).

The parameter estimates for other components shows that more variation was seen in the model fits for foliage and branches than in the bole only and total tree (Table S1, Fig. S1). For any biomass variables,

Table 2

An analysis of variance results (Pr > F and covariance parameter estimates for site*plot and residual) for testing the effects of various components in the model [3], which was regarded as a superior model comparing to its power-law model.

Source of Variation	Num df	Den df	ln (AGB)	ln (Foliage)	ln (Bole)	ln (Branch)	ln (Root)	ln (Tree)
Site	2	24	0.044	<0.001	0.943	<0.001	0.019	0.001
Fertilizer (F)	1	60	0.611	0.898	0.689	0.448	0.952	0.632
Site × F	2	60	0.110	0.611	0.026	0.762	0.459	0.130
Herbicide (H)	1	60	0.119	0.761	0.051	0.987	0.241	0.387
Site × H	2	60	0.090	0.032	0.557	0.134	0.340	0.119
F × H	1	60	0.061	0.888	0.281	0.027	0.958	0.170
Site × F × H	2	60	0.164	0.221	0.339	0.269	0.421	0.240
ln (DBH)	1	60	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
ln (DBH) × Site	2	60	0.027	<0.001	0.827	<0.001	0.019	0.005
ln (DBH) × F	1	60	0.625	0.707	0.533	0.635	0.982	0.640
ln (DBH) × Site × F	2	60	0.109	0.522	0.026	0.765	0.319	0.108
ln (DBH) × H	1	60	0.118	0.947	0.051	0.935	0.306	0.349
ln (DBH) × Site × H	2	60	0.097	0.059	0.588	0.132	0.297	0.105
ln (DBH) × F × H	1	60	0.050	0.696	0.302	0.017	0.879	0.130
ln (DBH) × Site × F × H	2	60	0.162	0.251	0.352	0.259	0.444	0.218
Site*plot			0.000	0.008	0.000	0.000	0.011	0.000
Residual			0.013	0.044	0.014	0.043	0.043	0.013

Notes: The parameter estimate of the 0.000 is too small to show with 3 decimal places.

Table 3

Parameter estimates of intercept (ln a) and exponent (b) with standard errors, the percent relative standard errors (PRSE), back-transformed of intercepts (a) with the correction factors (CF), and the mean absolute percentage error (MAPE) for ponderosa pine trees grown under different levels of silviculture treatments at three diverse sites in northern California.

Biomass component	Site	Treatment	ln (a)	ln (a) (SE)	b	b (SE)	PRSE % (ln a)	PRSE % (b)	a	CF	MAPE %
AGB	Elkhorn	C	-1.916	0.175	2.151	0.077	9.1	3.6	0.147	1.007	13.0
		F	-1.614	0.259	2.039	0.098	16.1	4.8	0.199	1.007	11.4
		H	-1.940	0.481	2.147	0.177	24.8	8.2	0.144	1.007	8.1
		HF	-3.753	0.481	2.797	0.166	12.8	5.9	0.023	1.007	7.6
		C	-2.871	0.242	2.528	0.100	8.4	4.0	0.057	1.007	7.8
	Whitmore	F	-2.804	0.362	2.480	0.133	12.9	5.4	0.061	1.007	5.6
		H	-2.795	0.235	2.514	0.088	8.4	3.5	0.061	1.007	5.1
		HF	-3.163	0.465	2.607	0.161	14.7	6.2	0.042	1.007	8.3
		C	-2.667	0.369	2.488	0.127	13.8	5.1	0.069	1.007	8.1
		F	-2.058	0.585	2.280	0.186	28.4	8.2	0.128	1.007	6.8
	Feather Falls	H	-2.490	0.485	2.406	0.162	19.5	6.7	0.083	1.007	3.1
		HF	-2.004	0.479	2.267	0.154	23.9	6.8	0.135	1.007	11.9
		C	-3.172	0.342	2.107	0.148	10.8	7.0	0.042	1.028	29.2
		F	-3.568	0.492	2.234	0.185	13.8	8.3	0.028	1.028	15.3
		H	-3.054	0.903	2.061	0.332	29.6	16.1	0.047	1.028	12.9
Roots	Elkhorn	HF	-4.179	0.885	2.561	0.306	21.2	11.9	0.015	1.028	19.3
		C	-5.493	0.461	2.965	0.189	8.4	6.4	0.004	1.028	32.4
		F	-4.717	0.671	2.634	0.246	14.2	9.3	0.009	1.028	12.4
		H	-4.673	0.438	2.680	0.161	9.4	6.0	0.009	1.028	17.4
		HF	-4.843	0.852	2.647	0.294	17.6	11.1	0.008	1.028	15.6
	Whitmore	C	-4.630	0.686	2.597	0.236	14.8	9.1	0.010	1.028	12.8
		F	-5.157	1.080	2.741	0.343	20.9	12.5	0.006	1.028	16.9
		H	-4.102	0.888	2.394	0.296	21.6	12.4	0.017	1.028	9.3
		HF	-2.817	0.877	2.006	0.282	31.1	14.1	0.060	1.028	12.9
		C	-4.630	0.686	2.597	0.236	14.8	9.1	0.010	1.028	12.8
	Feather Falls	F	-5.157	1.080	2.741	0.343	20.9	12.5	0.006	1.028	16.9
		H	-4.102	0.888	2.394	0.296	21.6	12.4	0.017	1.028	9.3
		HF	-2.817	0.877	2.006	0.282	31.1	14.1	0.060	1.028	12.9
		C	-4.630	0.686	2.597	0.236	14.8	9.1	0.010	1.028	12.8
		F	-5.157	1.080	2.741	0.343	20.9	12.5	0.006	1.028	16.9

Notes: C = control; F = fertilization; H = herbicide application for controlling competing vegetation; HF = herbicide and fertilization.

the logarithmic model showed a higher prediction power and less uncertainties than the power-law model, with which the percent relative standard errors (PRSE) for intercepts, 71 of 72 of them, were greater than 30%, which was the most liberal cutoff number suggested by Sileschi (2014). In contrast, there were 3 PRSEs for the branch and 1 for the root logarithmic models that were beyond 30%. There was none (PRSE > 30%) for the exponent (b) from the logarithmic model, compared with 3 from the power-law model. In addition, the mean absolute percentage errors were larger from the power-law model than from the logarithmic model.

With our selected logarithmic model, the intercept (a) was plotted against the exponent (b) in Fig. 5, which showed considerably more exponent (b) variation for foliage (mean = 2.5; range 1.9–3.0), branch (2.4; 1.5–2.8), and root (2.5; 2.0–3.0) than for AGB (2.4; 2.0–2.8), bole (2.4; 2.2–2.8), and whole tree (2.4; 2.1–2.7), respectively. For intercept (a), the inverse trends seem true with AGB and whole tree showing

larger variation (0.11; 0.02–0.22 range) than others (0.03; 0.00–0.11). As we expected, both a and b of the allometric relationship for bole showed the least variation (Table 2).

3.2. Individual tree biomass partitioning

The slope of regression between coarse roots and AGB differed among sites with 0.32 at Elkhorn, 0.23 at Whitmore, and 0.19 at Feather Falls, respectively (Fig. 6A). Neither treatment nor site effect was found to be significant (P > 0.11). Yet, the variation among sites increases with an increase of tree size. Also, from Fig. 6A, we can see that one tree at Elkhorn and one at Feather Falls have large coarse root biomass relative to their aboveground biomass, which had a considerable effect on the regression lines. Because these regression lines did not go through the origin, the R:S ratio (root to shoot) varied slightly from the slopes with 0.28 at Elkhorn, 0.23 at Whitmore, and 0.21 at Feather Falls,

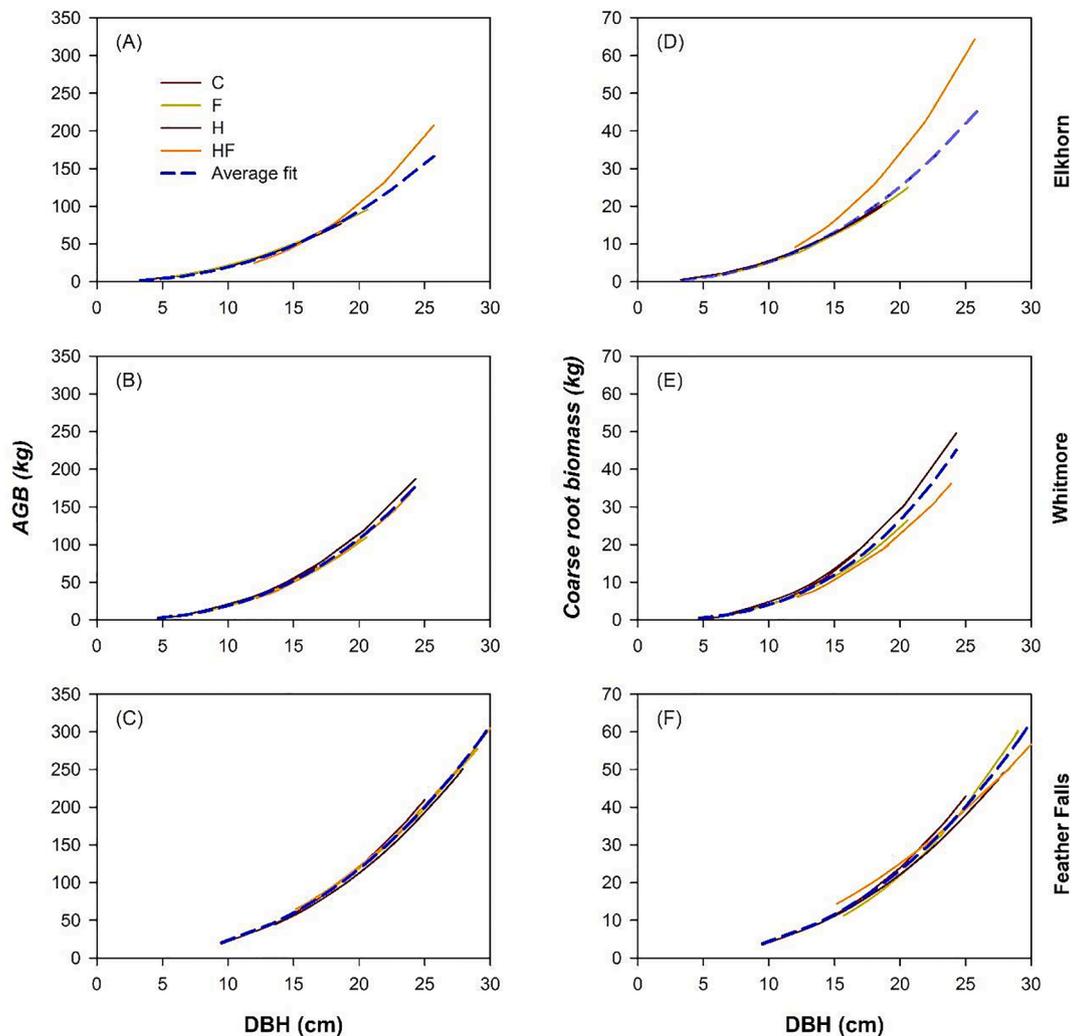


Fig. 4. Biomass predictions from the logarithmic model (3) for the AGB (A–C) and coarse root (D–F); the numbers were back-transformed with correction factors (CF). The average curves (blue and dash lines) were obtained using average a and b across the treatments with the CF. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

respectively.

Similarly, foliage biomass was about 5–9% of the total tree biomass including coarse roots (Fig. 6B). For a given amount of net primary production, i.e. biomass accumulation, trees at Feather Falls showed the least foliage allocation (0.05) while trees at Elkhorn required the most foliage (0.09) and Whitmore trees with 0.07.

3.3. Stand vegetation biomass and carbon pools

Aboveground biomass for planted trees significantly differed among sites (Table 4) with about 3.5 times more AGB at the highest site than at the lowest site being 58.7 (27.2–96.2) Mg ha^{-1} at Elkhorn, 97.9 (42.7–145.1) Mg ha^{-1} at Whitmore, and 203.9 (155.9–248.8) Mg ha^{-1} at Feather Falls, respectively. Except for root biomass, Site*F*H effect was non-significant for other variables. So were the F*H interactions. In general, the site by treatment (F and H) interactions were highly significant for all variables; the trends of AGB from the highest to the lowest were HF > H > F > C at both Elkhorn and Whitmore. Yet, at Feather Falls, the trend was F > HF > H > C. Similar trends were also found in coarse root biomass, foliage, bole, and total tree biomass. Interestingly, a proportion of bole biomass over total tree biomass was about 48% at Elkhorn, 52% at Whitmore, and 53% at Feather Falls.

Understory woody biomass varied significantly among sites and between treatments C and F, the only two treatments where understory

woody plants grew (Table 5). Live woody biomass was greater in the C than in the F plots across sites. Aboveground understory biomass in study year was highest at Whitmore, intermediate at Elkhorn, and the least at Feather Falls, respectively, with no significant difference between Elkhorn and Whitmore. The dead plant biomass did not differ between Elkhorn and Feather Falls, with the highest dead plant biomass at Whitmore. Therefore, understory across F plots had died earlier, which was also supported by the disproportionately smaller dead root biomass, presumably due to decomposition.

Ecosystem carbon or biomass was calculated with all vegetation components estimated in this study, along with forest floor and fine root data from previous work on these same sites by McFarlane et al. (2009); fine roots were not distinguished as tree or understory plant source. We did not include carbon in the mineral soil because McFarlane et al. (2009) estimated soil carbon without measuring bulk density. Because of the strong correlations between vegetation biomass and fine roots/forest floor, total carbon or biomass accumulation varied even more substantially than the vegetation biomass among combinations between treatment and site (Fig. 7). Stand carbon at Feather Falls was 2.3–3.9 times (depending on the treatment) more than at Elkhorn and 1.3–1.7 times more than at Whitmore, respectively. Whitmore plots stored 1.5–2.9 times more carbon than Elkhorn plots. Similarly, treatment variation in carbon storage was huge, with 29.3–70.4 Mg ha^{-1} at Elkhorn, 85.8–105.9 Mg ha^{-1} at Whitmore, and 113.1–162.5 Mg ha^{-1} at

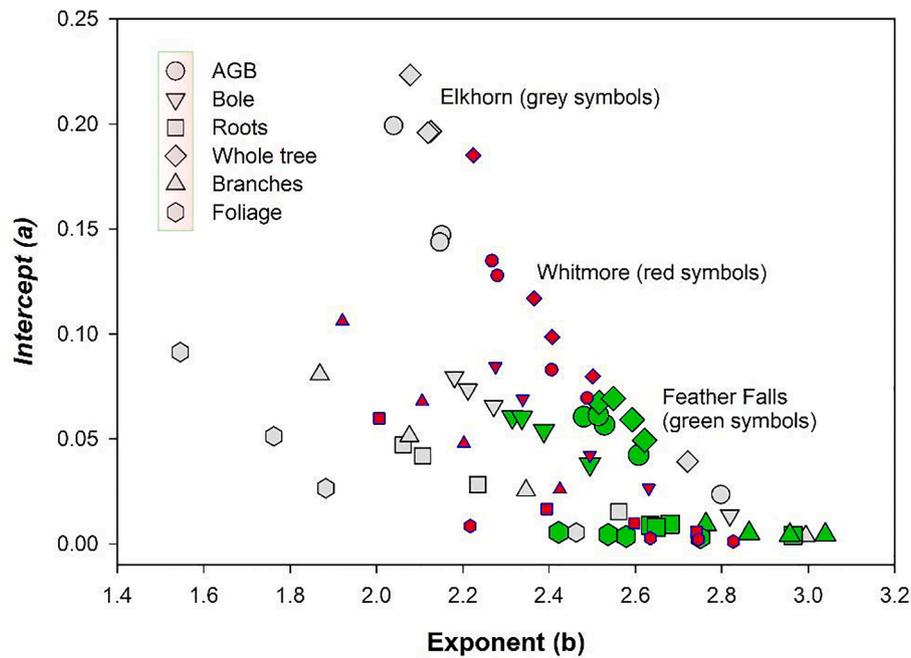


Fig. 5. Relationship between intercept (a) and exponent (b) from 72 allometric equations for 6 biomass components over 108 ponderosa pine trees grown at Elkhorn (with the medium-size gray symbols), Whitmore (the small-size pink symbols), and Feather Falls (the large-size green symbols). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Feather Falls, respectively.

3.4. Canopy cover and leaf area index

Canopy cover, crown volume, and LAI showed significant site and treatment effects, with the highest values at Feather Falls and the lowest at Elkhorn for their respective treatment comparisons in general (Table 6). Because of the different specific leaf area among sites, there was a slightly different LAI trend between Elkhorn and Whitmore. The relationships between total tree biomass and LAI (Fig. 8) showed that not only was the trend of growth efficiency (biomass accumulation per LAI) Feather Falls > Whitmore > Elkhorn, but also the trend among treatments varied between Feather Falls (F and HF vs C and H) and the other two sites (H and HF vs C and F).

4. Discussion

The purposes of this study were to find reliable allometric equations for accurately estimating the stand biomass for ponderosa pine forests, and to compare the differences in biomass accumulation and potential carbon sequestration among the silvicultural regimes and site qualities. The results indicate that we have achieved these goals. In the following discussion, we will compare our allometric equations with other existing equations worldwide for ponderosa pine. Then, we will discuss the biomass and carbon sequestration potentials for ponderosa pine plantations, and the capability of silvicultural treatments to enhance these potentials. Finally, we will provide our perspectives concerning what roles ponderosa pine plantations can play in offsetting CO₂ and mitigating climate change.

4.1. Allometric biomass models

The results show that the logarithmic models provided the best allometric equations compared with either the power-law or the scaled power-law equations, as determined from 108 destructively sampled ponderosa pine trees grown in 3 northern California plantations (Table S1). Silesi (2014) criteria guided our examination and

selections. Surprisingly, allometric equations for all biomass components were consistently superior to logarithmic models, which indicates that theoretical allometry is the same within this species. Comparing the extensive data in Silesi's (2014) meta-analysis, a narrower range of both intercepts and exponents was found in this study, especially for intercepts (Fig. 5), which would be expected because a single species was measured. If it is true that the intercept is determined by trees' physiological and allocation traits (Silesi, 2014), the differences in intercepts among sites and treatments within each component reflect plant adjustment of these traits to the site variation and silvicultural treatments. Pretzsch and Dieler (2012) regarded the exponent as a distribution coefficient for the growth resources which should have varied less. If these assumptions are right, we would expect that foliage, branches, and roots would respond more actively to the treatments and sites than the bole. Certainly, results from this study support these hypotheses.

Significant differences in allometric equations among sites indicate that site-specific biomass models are required if an accurate measure of biomass or carbon needs to be estimated. Although fewer treatment effects were statistically significant, a single treatment may still cause a large difference such as the HF at Elkhorn (Fig. 4A, D). There are about a dozen allometric biomass equations that have been developed for ponderosa pine during the last 45 years. Even though we are unable to assess their PRSE and MAPE as we did in the current study, we can derive them to match the current DBH ranges. As a result, substantial differences in AGB were estimated among these equations (Fig. 9A). The fitting curves from this study were among those in the middle group with the lowest at Elkhorn, the highest at Feather Falls, and intermediate at Whitmore, respectively. Yet, three curves from other studies were higher than our Feather Falls (Gower et al., 1993; Ritchie et al., 2013; Vorster et al., 2020) and two others were lower than our Elkhorn (Gholz et al., 1979; Laclau, 2003a). Apparently, the discrepancy was caused by different sites or environments and stand ages and origin. Ritchie et al. (2013) sampled 100-year-old trees at Blacks Mountain Experimental Forest, where an old 30-cm DBH tree would carry a lot of branches. Although Gholz et al. (1979) allometric equations for this species were extensively used, data were not traceable with 9 trees; but these could have been the

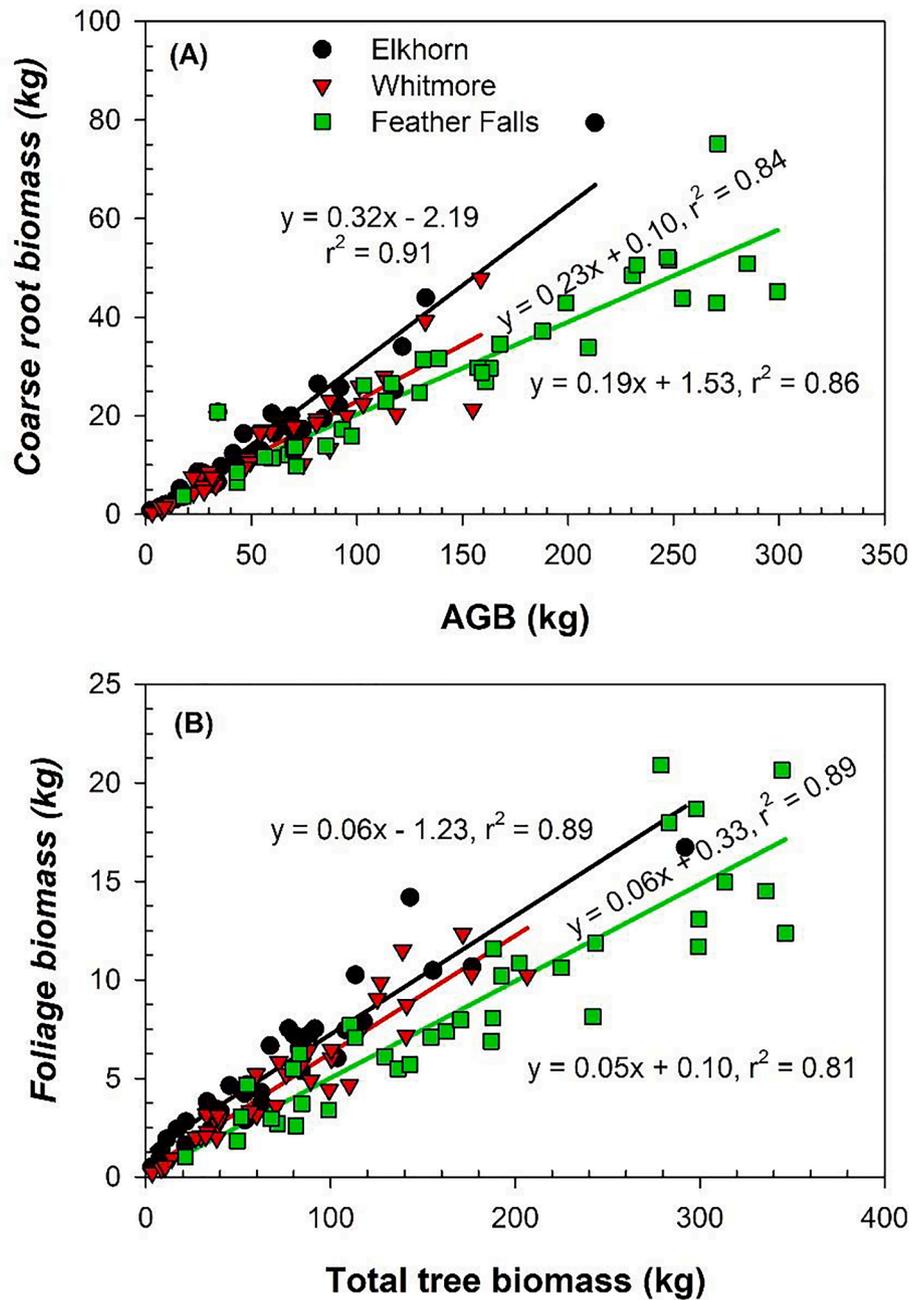


Fig. 6. The relationships between (A) coarse root biomass and AGB as root/shoot ratio and (B) foliage biomass and total tree biomass for 108 20-year-old ponderosa pine trees grown at three sites in Northern California.

“old” trees at Fort Valley in Arizona. The lowest one in the group are young trees grown in 10- and 20-year-old plantations in Argentina, outside the natural range of this species. In addition, trees < 15 cm DBH from the Black Hills of Wyoming looked unusual because Tinker et al. (2010) used a different biomass estimation approach. The curve of Cochran et al. (1984) is very similar to our Elkhorn, and the site quality is similarly low in that southeastern Oregon site. The remaining two, developed in our lab from plantations or plantation and natural trees in northern California, are between Feather Falls and Whitmore in this study (Zhang et al., 2010; 2020).

Belowground coarse root biomass has not been measured often in ponderosa pine. The most citations for belowground live tree biomass have been by Birdsey (1992), who estimated root biomass based on an unpublished consulting report that regarded belowground root weight as a percentage of total oven-dry tree weight (Koch, 1989), which has

never been vigorously tested and cannot be compared. Three datasets were compared here (Fig. 9B). Despite having the lowest AGB when this species was grown in Argentina, the root growth changed most along DBH (Laclau, 2003b). This drastic change might be due to the changes from trees with mixed DBH ranges from age 10 to age 20 or could be due to an allocation shift with age. The root biomass patterns with DBH in our study were similar to the trees at Black Hills (Tinker et al., 2010), especially at Elkhorn and Feather Falls. However, the tree roots sampled in New Mexico were much lower because the study only sampled roots with ≥ 0.6 cm diameter (Omdal et al., 2001).

As for individual tree biomass allocation among roots, shoot, and foliage, results from this study are consistent with the common analogy that plants grown on the poorest soils allocate more biomass to roots in order to access more nutrients and water (Poorter et al., 2012). The trees at Elkhorn followed this pattern with R/S being 0.32 (Fig. 6A). At

Table 4

Means and common standard errors for a stand-level tree aboveground biomass (AGB), coarse root biomass, foliage biomass, bole biomass, and total tree biomass as well as analysis of variance with type 3 for testing site, treatments, and site by treatment interactions for ponderosa pine trees grown at three diverse sites.

Site	Treatment	AGB (Mg ha ⁻¹)	Root (Mg ha ⁻¹)	Foliage (Mg ha ⁻¹)	Bole (Mg ha ⁻¹)	Total tree (Mg ha ⁻¹)					
Elkhorn	C	27.15	g	7.09	e	3.78	e	15.75	f	34.06	h
	F	49.35	fg	12.22	de	6.04	de	30.93	ef	61.54	gh
	H	62.20	efg	16.51	de	5.72	de	37.94	ef	78.54	fgh
	HF	96.18	de	32.27	b	8.63	bcd	59.22	de	128.54	f
Whitmore	C	42.71	fg	9.61	e	4.04	e	26.06	f	52.49	gh
	F	85.90	e	20.12	cd	7.54	cd	56.76	de	105.95	f
	H	118.00	cd	29.55	bc	8.41	bcd	72.69	cd	147.53	cde
	HF	145.05	bc	31.07	b	11.10	ab	93.30	bc	176.13	c
Feather Falls	C	155.93	bc	30.91	b	10.23	b	96.47	bc	186.20	bc
	F	248.81	a	49.86	a	12.70	a	162.17	a	298.59	a
	H	172.49	b	33.88	b	11.53	ab	109.00	b	205.78	b
	HF	238.51	a	47.66	a	13.02	a	152.96	a	285.95	a
	SE	8.66		1.89		0.66		5.65		10.53	

Analyses of variance with type 3 tests of fixed effects

Source of variation	Num/Den DF	F	P	F	P	F	P	F	P	F	P
Site	2/24	300.54	<0.001	168.73	<0.001	82.87	<0.001	295.84	<0.001	274.80	<0.001
Fertilizer (F)	1/24	90.31	<0.001	100.01	<0.001	45.29	<0.001	101.20	<0.001	93.26	<0.001
Herbicide (H)	1/24	54.97	<0.001	86.66	<0.001	38.18	<0.001	48.59	<0.001	60.51	<0.001
F × H	1/24	1.08	0.309	0.31	0.595	0.25	0.623	1.66	0.210	0.90	0.353
Site × F	2/24	10.32	<0.001	7.52	0.003	0.72	0.496	11.79	<0.001	9.58	<0.001
Site × H	2/24	13.82	<0.001	20.10	<0.001	5.76	0.009	12.47	<0.001	14.62	<0.001
Site × F × H	2/24	1.32	0.285	7.53	0.003	0.46	0.644	1.54	0.238	1.99	0.158

Notes: C = control; F = fertilization; H = herbicide application for controlling competing vegetation; HF = herbicide and fertilization. For each variable, treatment by site combination with different letters indicates P < 0.05 in the multiple comparisons.

Table 5

Means and common standard errors for live and dead stand-level understory woody aboveground biomass (AGB) and coarse root biomass as well as analysis of variance with type 3 for testing site, treatment, and site by treatment interactions with overstory ponderosa pine trees at three diverse sites.

Site	Treatment	Live AGB (Mg ha ⁻¹)	Live root (Mg ha ⁻¹)	Dead AGB (Mg ha ⁻¹)	Dead root (Mg ha ⁻¹)				
Elkhorn	C	12.51	a	5.75	a	0.00	b	0.00	a
	F	10.71	a	4.13	a	1.72	b	0.01	a
Whitmore	C	46.92	a	14.92	a	35.44	a	2.27	a
	F	18.43	a	5.18	a	33.62	a	3.21	a
Feather Falls	C	6.74	a	1.88	b	4.68	b	1.13	a
	F	0.33	b	0.24	b	1.49	b	0.13	a
	SE	1.86		1.82		1.46		1.34	

Analyses of variance with type 3 tests of fixed effects

Source of variation	Num/Den DF	F	P	F	P	F	P	F	P
Site	2/8	17.43	0.001	15.09	0.002	30.87	0.001	7.98	0.012
Fertilizer (F)	1/8	8.58	0.019	9.11	0.017	0.07	0.792	0.00	0.972
Site × F	2/8	4.11	0.059	2.48	0.146	3.44	0.084	1.02	0.403

Notes: C = control; F = fertilization. For each variable, the site with different letters indicates P < 0.05 in the multiple comparisons.

Feather Falls with the richest soils and highest site index (Table 1), tree R/S ratio was 0.19 while the intermediate site quality at Whitmore, R/S was 0.23. Similarly, allocation to foliage per given total biomass including roots was also the highest at Elkhorn, the lowest at Feather Falls, and intermediate at Whitmore, respectively (Fig. 6B), again following a trend with site quality. The results suggest that trees at higher quality sites have a higher growth efficiency than trees at lower quality sites (Oren et al., 1987; Zhang et al., 2017).

4.2. Biomass and carbon sequestration potential

Total stand biomass was very much consistent with traditional forest growth yield along site quality (Meyer, 1938), although plantations often grow faster than natural stands (Oliver and Powers, 1978). General

results of the previous findings have been extensively tested, and growth potential of plantations has been significantly enhanced with intensive management practices during the last half of the century (Powers, 1999; Mead, 2005; Vance et al., 2010). Results from this study not only proved the previous findings to be true for the planted trees, but also demonstrated varying trends of entire vegetation or carbon pools among treatments and sites (Fig. 7; Tables 4 and 5). Current results also indicated that treatment variability was greater at the poor and intermediate quality sites such as Elkhorn and Whitmore than at the fertile site Feather Falls. Biomass response for the CVC declined when fertilization was applied, with the HF treatment increasing biomass 109% over the F treatment at Elkhorn and 66% at Whitmore, albeit still impressive increases. In contrast, at the highest quality site Feather Falls, the H treatment increased total tree biomass 10% over the Control, and yet the

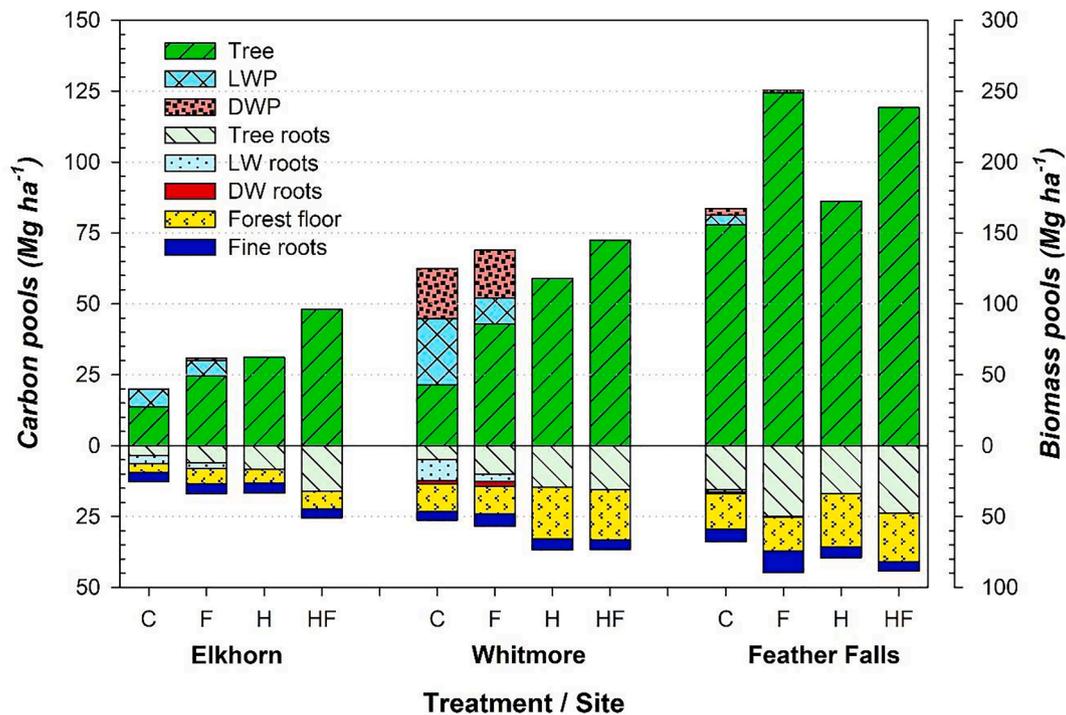


Fig. 7. Carbon or biomass pools for plantations grown under four treatments at three study sites in northern California. Tree: aboveground tree; LWP: live woody understory plants; DWP: dead woody understory plants. Both forest floor and fine root data were from McFarlane et al. (2009).

Table 6

Means and common standard errors for a stand-level overstory tree canopy cover, crown volume, and leaf area index (LAI) as well as analysis of variance with type 3 for testing site, treatment, and site by treatment interactions for ponderosa pine trees grown at three diverse sites.

Site	Treatment	Canopy cover (m ² m ⁻²)		Crown volume (m ³ m ⁻²)		LAI (m ² m ⁻²)	
Elkhorn	C	0.50	d	1.82	f	1.43	de
	F	0.69	cd	3.69	ef	2.28	bcd
	H	0.82	c	4.29	f	2.16	e
	HF	1.10	b	6.43	cd	3.26	ab
Whitmore	C	0.55	cd	2.50	f	1.19	e
	F	0.82	c	5.28	cde	2.22	cd
	H	1.11	b	6.90	bc	2.47	bc
	HF	1.15	b	7.81	bc	3.26	ab
Feather Falls	C	1.18	b	9.09	b	2.94	b
	F	1.66	a	12.61	a	3.64	a
	H	1.26	b	9.17	b	3.31	ab
	HF	1.56	a	12.00	a	3.74	a
	SE	0.06		0.50		0.20	

Analyses of variance with type 3 tests of fixed effects

Source of variation	Num/Den DF	F	P	F	P	F	P
Site	2/24	150.46	<0.001	193.53	<0.001	41.10	<0.001
Fertilizer (F)	1/24	68.28	<0.001	65.80	<0.001	49.17	<0.001
Herbicide (H)	1/24	70.62	<0.001	44.69	0.001	41.60	<0.001
F × H	1/24	2.66	0.116	1.77	0.197	0.16	0.692
Site × F	2/24	4.79	0.018	2.10	0.144	1.18	0.326
Site × H	2/24	19.19	<0.001	15.21	<0.001	5.54	0.011
Site × F × H	2/24	2.40	0.112	1.16	0.329	0.54	0.592

Notes: C = control; F = fertilization; H = herbicide application for controlling competing vegetation; HF = herbicide and fertilization.

For each variable, treatment by site combination with different letters indicates P < 0.05 in the multiple comparisons.

HF treatment was 4% reduced compared to the F treatment at age 20; these results differed substantially from the results at age 6 (Powers and Ferrell, 1996). These differences are clearly related to the speed of stand development with lesser CVC effects at high site quality and fertilizer treatment (Zhang et al., 2013). All these factors could significantly influence the interactions between overstory planted trees and understory vegetation and therefore speed up stand development (Oliver and

Larson, 1996).

The responses of plantations to the treatments and interactions with plantation ages can be explicitly demonstrated by including understory changes (Fig. 7; Table 5). There was a significant variation in woody shrub communities among sites (Zhang et al., 2016), although understory biomass at each site was dominated by two major shrub species. Across the sites, understory biomass (live and dead) was higher in the

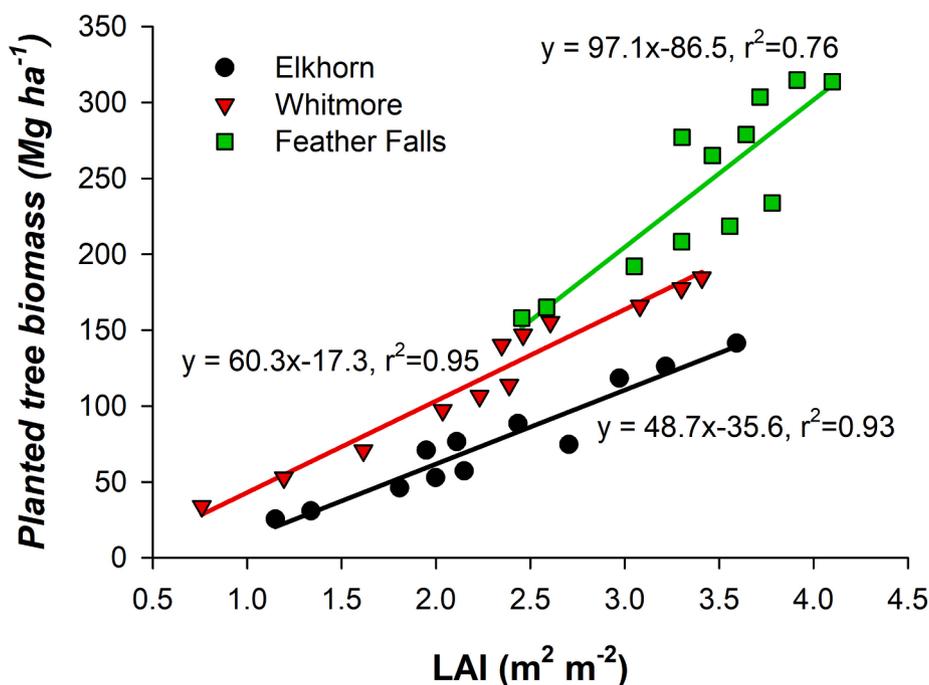


Fig. 8. Relationships between total tree biomass and leaf area index (LAI) for stand-level ponderosa pine grown at three sites at age 20. At Feather Falls, lower six data points were from control and herbicide (H) plots and other six were from fertilizer (F) and HF plots. At both Elkhorn and Whitmore, the lower six points were from the control and F plots while the upper six points were from H and HF plots.

Control than in the F treatment by 1.1, 1.6, and 6.6 times at Elkhorn, Whitmore, Feather Falls, respectively. Conversely, there was more dead plant biomass in the F treatment than in the Control, suggesting that the F treatment enhanced stand development resulting in earlier crown closure and understory mortality. There was no statistical difference in dead plant biomass between the poorest site Elkhorn and the highest Feather Falls (Table 5), for different reasons: no woody plants were dead in the control plots and only a few in the F treatment plots at Elkhorn, whereas at Feather Falls most dead plants had laid on the ground and had decomposed by age 20. At Whitmore, live plant biomass was higher than dead plant biomass in the control but was inverse in the F treatment. Therefore, the factors that increased tree growth and enhanced stand development also increased understory mortality in fixed-time (e. g. at 20 years) where competing vegetation was not controlled (Powers et al., 2005b).

Collectively, although total vegetation biomass or carbon would have been expected to be different among sites due to their respective site quality, treatment differences in total vegetation associated biomass or carbon pools were only expressed in the planted trees (Fig. 7). The trends indicated the superior effect of HF treatment. The similar carbon pool shifts from understory-dominated stand biomass to tree-dominated biomass in no-CVC plots were found in previous studies in California (Zhang et al., 2017; Zhang et al., 2020). Here, an age-related partitioning of plantation biomass was not estimated.

Comparing carbon sequestration or net primary productivity (NPP) in the current study with others is difficult (Clark et al., 2001), especially because we did not measure fine root biomass and fine root turnover, although we used the fine root data from McFarlane et al. (2009). Nonetheless, our total carbon sequestration for vegetation was in general higher than what was measured ($58.9 \text{ Mg C ha}^{-1}$) for this species grown in plantations in Argentina (Laclau, 2003b), with the exception of the control plots at Elkhorn. Just using current total biomass or carbon accumulation divided by stand age, we obtained a NPP of $1.5\text{--}3.5 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at Elkhorn, $4.3\text{--}5.3 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at Whitmore, and $5.7\text{--}8.1 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at Feather Falls, respectively. Lieth (1975) reported NPP in closed-canopy temperate forests of $2\text{--}25 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. Whittaker and Niering (1975) found that NPP of 150-year-old ponderosa pine

forests in Arizona was $4.9\text{--}5.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. Studying a 40-year-old ponderosa pine plantation in the Sierra Nevada of California, Campbell et al. (2009) found that NPP of a plantation without thinning was about $6.02 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$. Our Feather Falls site is close to their site. However, without considering fine root turnover but including soil carbon, Zhang et al. (2020) obtained $2.7\text{--}3.7 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at age 28 and $1.1\text{--}1.9 \text{ Mg C ha}^{-1} \text{ yr}^{-1}$ at age 52 for research plots with varying stand density with and without CVC. Therefore, to meaningfully compare the reported NPP among studies, we must carefully consider if studies used the same components or methods, natural or plantation ages, other silvicultural treatments including CVC, and possibly site disturbance history and plantation site preparation practices, with these latter factors often not being considered by most studies.

4.3. Potential mechanisms for growth efficiency and fertilizer effect

As data indicated (Fig. 8), growth efficiency was higher at Feather Falls than at Whitmore which was higher than at Elkhorn, following decreasing site quality respectively. Among treatments, the HF and H treatments were more productive than the F treatment and Control at the poor and intermediate sites, while at Feather Falls the F and HF treatments were more productive than the H treatment and Control. One possible explanation is that the higher site quality produced a lot more foliage, i.e. high LAI. Had its LAI been reduced to the same LAI as the poor site, biomass production would have presumably been the same, which was apparent between treatments (C and H) at Feather Falls and the H treatment at Whitmore (Fig. 8). Another possibility is a longer growing season at both Feather Falls and Whitmore than at Elkhorn. In California's Mediterranean climate growing season, onset is controlled by temperature while the end of growing season depends on soil water availability. The two more productive sites are located at lower elevations with warmer temperatures, more precipitation, and have deeper and finer-textured soils with much higher soil water holding capacity than the Elkhorn site (Table 1).

Not only does soil water availability have a direct effect on tree growth, it also positively interacts with nutrient uptake. Bracho et al. (2018) reported that fertilization effects on carbon accumulation

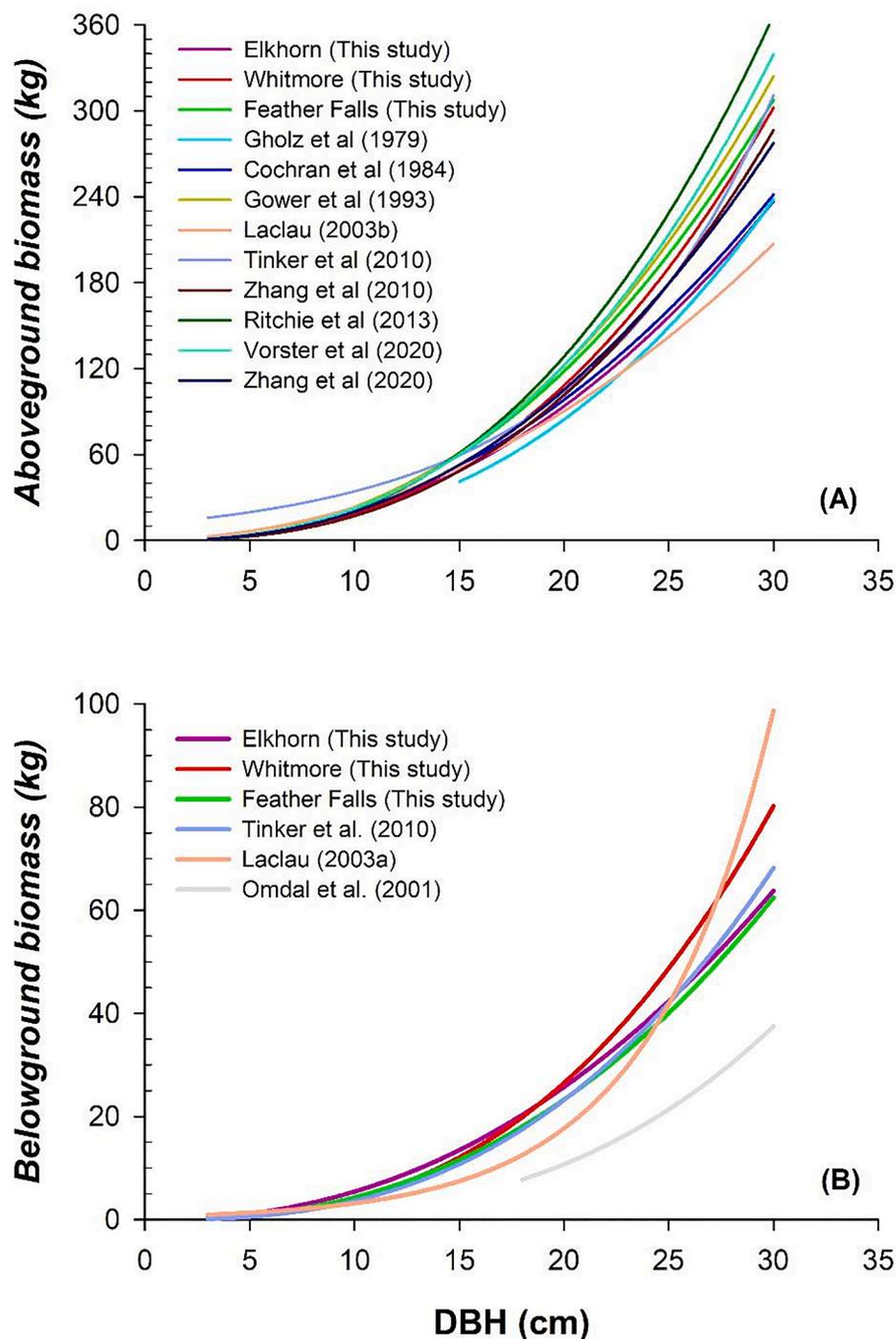


Fig. 9. Aboveground (A) and belowground coarse root (B) biomass with DBH at three sites in this study, compared to existing published functions for ponderosa pine allometric equations established across the world.

followed a gradient of water availability in loblolly pine (*Pinus taeda* L.) plantations. Results from this study provide a perfect example of fertilizer effect being increased by more soil water by comparing the F treatment effect at Feather Falls with results at other sites. In a Mediterranean climate especially, CVC provides tree-benefits by reducing competition for water more than nutrients. With these installations, Reynolds and Powers (2000) showed that moisture stress develops quickly on droughty sites. Although stomatal conductance, transpiration, and net assimilation rates were similar on all sites in the spring when soil moisture was high, rates on droughty sites fell well-below those on better sites by mid-summer. Powers and Ferrell (1996) found that trees growing in brush on a droughty site were not affected by fertilization, but that manzanita leaf mass and area were doubled by

fertilization, which through transpiration created water stress in trees and blocked N uptake.

The last unanswered question may explain more total biomass accumulation or carbon sequestration observed in the F versus HF treatment at Feather Falls. Because the forest stand at this high-quality site developed so quickly, especially with fertilization, it is possible that competing vegetation posed a marginal impact to tree growth in the F treatment plots. In addition, the contribution of understory litter on soil quality was absent in the HF treatment plots (Busse et al., 1996; Winsome et al., 2014). Studying a similar setting close to Feather Falls, Winsome et al. (2014) found that CVC caused a decline in litter-derived carbon and nitrogen in the soil, although the soil microbial community was resilient and functionally unaffected.

4.4. Management implications

Although some mechanisms need to be further clarified and tested, controlling competing vegetation enhances stand biomass accumulation and carbon sequestration for the planted trees in our study, because CVC not only reallocates available soil water and nutrients to planted trees, but also improves their nutrient uptake. Since both water and nutrients are very often the limiting factors for world plants, especially water during the growing season in Mediterranean climates, any silvicultural practices that ameliorate their availability will increase stand productivity and carbon sequestration.

Direct fertilization can also improve nutrient availability. Yet, as shown here and in other studies, vegetation nutrient uptake requires certain levels of soil water availability. In addition, fertilization may be a mitigation tool for a potential soil quality degradation from a CVC treatment or other management practices (Busse et al., 2021) or could be used to boost stand growth and development on certain nutrient deficient soils (Powers et al., 2005b).

Of course, in an operational setting these plots would have been pre-commercially thinned to increase growth of the targeted trees for use as saw timber as a final product, or to make forest stands more resilient to wildfire and other abiotic disturbances. The actual planting density reflected the contemporary regeneration practice which expected significantly lower survival rate in this region of California. Unexpectedly, none of these plots showed onset of self-thinning, even after crown closure at 8–12 years at the more productive Whitmore and Feather Falls sites. Therefore, results from this study may not reflect carbon sequestration on real operational plantations at age 20 years, but demonstrates the productivity potential of 20-year-old plantations with different treatments at different site qualities. High plantation density also “stresses” the maximum exploitation of site resources earlier in time for studies involving fundamental soil/site productivity and sustainability research questions. The maximum net primary production as influenced by further management and silvicultural practices can be explored by thinning effect with some sites in the future.

Finally, in fire-prone ecosystems, we must consider wildfire as a driving ecological factor in managing our forests for carbon sequestration. As Powers (2012) indicated, keeping closed forests intact with their increased carbon storage capacity was not an option because wildfires can release these carbon stocks rather quickly, especially in a crown-fire scenario. Many management recommendations and policies have been proposed for wildfire resilience, which are beyond the objectives of this study. However, our results demonstrate clearly that if one of the objectives of reforestation is carbon sequestration, both CVC and fertilization will enhance tree growth significantly. If an objective is to grow large trees rapidly to achieve fire resistance more quickly, the same silvicultural treatments may be employed although we would thin the plantation to a lower density. Thus, we can silviculturally manipulate stand composition, density, and structure for the purpose of tending to individual trees, and in turn accelerate stand development and promote forest resilience to drought and fire, given time for stand development to occur.

5. Conclusions

Despite diverse treatments applied to ponderosa pine plantations at each site, allometric biomass equations were substantially similar, suggesting that fundamental allometry between biomass and tree DBH is largely genetic and consistent. Significant site variation in allometric equations indicates geographic variation within the same species. The logarithmic models were statistically superior to the simple or DBH scaled power-law models in estimating tree biomass. Although it is not surprising that significantly more biomass or carbon was accumulated at the high-quality sites than the lower quality sites, the silvicultural treatments such as fertilizer and competing vegetation control produced similar magnitudes of more tree biomass than controls, especially

significant at lower quality sites. Therefore, intensive management practices will substantially enhance plantation productivity and stand development.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.foreco.2021.119526>.

References

- Baskerville, G.L., 1972. Use of logarithmic regression in the estimation of plant biomass. *Can. J. For. Res.* 2 (1), 49–53.
- Birdsey, R.A. 1992. Carbon storage and accumulation in United States forest ecosystems. USDA For. Serv. Gen. Tech. Rep. WO-59. 51 p.
- Bracho, R., Vogel, J.G., Will, R.E., et al., 2018. Carbon accumulation in loblolly pine plantations is increased by fertilization across a soil moisture availability gradient. *For. Ecol. Manage.* 424, 39–52.
- Brown, J. 1978. Weight and density of crowns of Rocky Mountain conifers. Res. Pap. INT-197. Ogden, UT. USDA For. Serv. Intermountain For. and Range Exp. Stn. 56 p.
- Busse, M.D., Cochran, P.H., Barrett, and J.W., 1996. Changes in ponderosa pine site productivity following removal of understorey vegetation. *Soil Sci. Soc. Am. J.* 60, 1614–1621.
- Busse, M.D., Zhang, J.W., Fiddler, G.O., Young, D.H., 2021. Compaction and organic matter retention in mixed-conifer forests of California: 20-year effects on soil physical and chemical health. *For. Ecol. Manage.* <https://doi.org/10.1016/j.foreco.2020.118851>.
- Campbell, J., Alberti, G., Martin, J., Law, B., 2009. Carbon dynamics of a ponderosa pine plantation following a thinning treatment in the northern Sierra Nevada. *For. Ecol. Manage.* 257, 453–463.
- Campoli, M., Malhi, Y., Vicca, S., Luysaert, S., Papale, D., Peñuelas, J., Reichstein, M., Migliavacca, M., Arain, M.A., Janssens, I.A., 2016. Evaluating the convergence between eddy-covariance and biometric methods for assessing carbon budgets of forests. *Nature Commun.* 7, 13717.
- Clark, D.A., Brown, S., Kicklighter, D.W., Chambers, J.Q., Thomlinson, J.R., Ni, J., 2001. Measuring net primary production in forests: Concepts and field methods. *Eco. Appl.* 11(2), 356–370.
- Cochran, P., Jennings, J., Youngberg, C., 1984. Biomass estimator for thinned second-growth ponderosa pine trees. Res. Note PNW-415. Portland, OR. USDA For. Serv. Pacific Northwest For. and Range Exp. Stn. 6 p.
- Domke, G.M., Oswalt, S.N., Walters, B.F., Morin, R.S., 2020. Tree planting has the potential to increase carbon sequestration capacity of forests in the United States. *PNAS* 117, 24649–24651.
- EPA, 2021. U.S. Environmental Protection Agency, Climate Change Indicators: Global Greenhouse Gas Emissions, Available online at <https://www.epa.gov/climate-indicators/climate-change-indicators-global-greenhouse-gas-emissions>, Accessed [5/4/2021].
- EPA, 2020. Inventory of U. S. Greenhouse Gas Emissions and Sinks: 1990 – 2018. U.S. Environmental Protection Agency, EPA 43-R-20-002, 733 p.
- Gholz, H.L., Grier, C.C., Campbell, A.G., Brown, A.T. 1979. Equations for estimating biomass and leaf area of plants in the Pacific Northwest. Res. Pap. 41. Corvallis, OR: Oregon State University. 39 p.

- Gower, S.T., Haynes, B.E., Fassnacht, K.S., Running, S.W., Hunt, E.R., 1993. Influence of fertilization on the allometric relations for two pines in contrasting environments. *Can. J. For. Res.* 23, 1704–1711.
- IPCC., 2019. *Climate Change and Land: an IPCC special report on climate change, desertification, land degradation, sustainable land management, food security, and greenhouse gas fluxes in terrestrial ecosystems*. 864 p.
- Jenkins, J. C., Chojnacky, D.C., Heath, L.S., Birdsey, R. A., 2004. Comprehensive database of diameter-based biomass regressions for North American tree species. Gen. Tech. Rep. NE-319. Newtown Square, PA: USDA, For. Serv., N.E. Res. Station. 45 p.
- Koch, P., 1989. Estimates by species group and region in the USA of: I. below-ground root weight as a percentage of overstory complete-tree weight; and II. Carbon content of tree portions. Consulting Report. 23 p. (cited from Birdsey 1992).
- Laclau, P., 2003a. Root biomass and carbon storage of ponderosa pine in a northwest Patagonia plantation. *For. Ecol. Manage.* 173, 353–360.
- Laclau, P., 2003b. Biomass and carbon sequestration of ponderosa pine plantations and native cypress forests in northwest Patagonia. *For. Ecol. Manage.* 180, 317–333.
- Lieth, H., 1975. Primary production of the major vegetation units of the world. In: Lieth, H., Whittaker, R.H. (Eds.), *Primary Productivity of the Biosphere*. Springer-Verlag, New York, pp. 203–215.
- Mead, D.J., 2005. Opportunities for improving plantation productivity. How much? How quickly? How realistic? *Biomass Bioenergy* 28, 249–266.
- Means, J. E., Hansen, H.A., Koerber, G.P., Alaback, P.B., Klopsch, M.W., 1994. Software for computing plant biomass—BIOPAK users guide. Gen. Tech. Rep. PNW-GTR-340. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 180 p.
- Meyer, W.H., 1938. Yield of even-aged stands of ponderosa pine. In: Washington, D.C. (Ed.), *Technical Bulletin 630*. United States Department of Agriculture, pp. 1–59.
- McDonald, P.M., Fiddler, G.O., 2011. Twenty-five years of managing vegetation in conifer plantations in northern and central California: results, application, principles, and challenges. Gen. Tech. Rep. PSW-GTR-231. Albany, CA: USDA For. Serv., Pacific Southwest Research Station. 87 p.
- McFarlane, K.J., Schoenholtz, S.H., Powers, R.F., 2009. Plantation management intensity affects belowground carbon and nitrogen storage in Northern California. *Soil Sci. Soc. America J.* 73, 1020–1032.
- Monserud, R.A., Marshall, J.D., 1999. Allometric crown relations in three northern Idaho conifer species. *Can. J. For. Res.* 29, 521–535.
- Noormets, A., Epron, D., Domec, J.C., McNulty, S.G., Fox, T., Sun, G., King, J.S., 2015. Effects of forest management on productivity and carbon sequestration: A review and hypothesis. *For. Ecol. Manage.* 355, 124–140.
- Oliver, C.D., Larson, B.C., 1996. *Forest stand dynamics*. McGraw-Hill Inc., New York.
- Oliver, W.W., Powers, R.F., 1978. Growth models for ponderosa pine: I. yield of unthinned plantations in northern California. Res. Pap. PSW-RN-133. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 21 p.
- Oliver, W.W., Ryker, R.A., 1990. Ponderosa pine. Burns, R.M. and B.H. Honkala, *Silvics of North America*. Agriculture Handbook 654. pp. 413–424. USDA Forest Service, Washington, D.C.
- Omdal, D.W., Jacobi, W.R., Shaw III, C.G., 2001. Estimating large-root biomass from breast-height diameters for ponderosa pine in northern New Mexico. *West. J. Appl. For.* 16, 18–21.
- Oren, R., Waring, R.H., Stafford, S.G., Barrett, J.W., 1987. Twenty-four years of ponderosa pine growth in relation to canopy leaf area and understory competition. *For. Sci.* 33, 538–547.
- Oswalt, S.N., Smith, W. B., Miles, P.D., Pugh, S. A., 2019. Forest Resources of the United States, 2017: a technical document supporting the Forest Service 2020 RPA Assessment. Gen. Tech. Rep. WO-97. Washington, DC: U.S. Department of Agriculture, Forest Service, Washington Office. 223 p. <https://doi.org/10.2737/WO-GTR-97>.
- Poorter, H., Niklas, K.J., Reich, P.B., Oleksyn, J., Poot, P., Mommer, L., 2012. Biomass allocation to leaves, stems and roots: meta-analyses of interspecific variation and environmental control. *New Phytol.* 193, 30–50.
- Powers, R.F., 1999. On the sustainable productivity of planted forests. *New Forests* 17, 263–306.
- Powers, R.F., 2012. Forests for energy: Can productivity be sustained? An overview and personal perspective. *Int. J. For. Eng.* 23, 7–14.
- Powers, R.F., Ferrell, G.T., 1996. Moisture, nutrient, and insect constraints on plantation growth: the “Garden of Eden” experiment. *NZ J. For. Sci.* 26, 126–144.
- Powers, R.F., Jackson, G.D., 1978. Ponderosa pine response to fertilization: influence of brush removal and soil type. USDA Forest Service. Pacific Southwest Forest and Range Experiment Station. Research Paper PSW-132.
- Powers, R.F., Scott, D.A., Sanchez, F.G., Voldseth, R.A., Page-Dumroese, D., Elioiff, J.D., Stone, D.M., 2005a. The North American long-term soil productivity experiment: findings from the first decade of research. *For. Ecol. Manage.* 220 (1–3), 31–50.
- Powers, R.F., Webster, S.R., Cochran, P.H., 1988. Estimating the response of ponderosa pine forests to fertilization. pp. 219–25 in Proceedings, “Future Forests of the Mountain West: A Stand Culture Symposium”, 29 September–3 October 1985. USDA Forest Service, Logan, UT, Intermountain Research Station. General Technical Report INT-243.
- Powers, R.F., Young, D.H., Fiddler, G.O., Spear, T.H., 2005b. Balderston plantation revisited: A tale of two sites 25 years after early treatments. In: Cooper, S.L., compiler. *Where we’ve been, where we are, and where we’re going*. Proceedings 25th Forest Vegetation Management Conference; 2004 January 20–22; Redding, CA. Redding, CA: University of California, Shasta County Cooperative Extension; 61–72.
- Pretzsch, H., Dieler, J., 2012. Evidence of variant intra- and interspecific scaling of tree crown structure and relevance for allometric theory. *Oecologia* 169, 637–649.
- Reynolds, P.E., Powers, R.F., 2000. Gas exchange for managed ponderosa pine stands positioned along a climatic gradient. *J. Sustain. Forestry* 3/4, 257–265.
- Ritchie, M.W., Zhang, J.W., Hamilton, T.A., 2013. Aboveground tree biomass for *Pinus ponderosa* in Northeastern California. *Forests* 4, 179–196.
- SAS Institute Inc., 2012. *SAS User’s guide*. SAS Institute Inc., Cary, NC, USA.
- Sileshi, G.W., 2014. A critical review of forest biomass estimation models, common mistakes and corrective measures. *For. Ecol. Manage.* 329, 237–254.
- Temegen, H., Affleck, D., Poudel, K., Gray, A., Sessions, J., 2015. A review of the challenges and opportunities in estimating above ground forest biomass using tree-level models. *Scandinav. J. For.* 30 (4), 326–335.
- Tinker, D., Stakes, G.K., Arcano, R.M., 2010. Allometric equation development, biomass, and aboveground productivity in ponderosa pine forests, Black Hills. Wyoming. *West. J. Appl. For.* 25 (3), 112–119.
- Vance, E.D., Maguire, D.A., Zalesny Jr., R.S., 2010. Research strategies for increasing productivity of intensively managed forest plantations. *J. Forestry* 108 (6), 183–192.
- Voosen, P., 2021. Global temperatures in 2020 tied record highs. *Science* 371, 334–335.
- Vorster, A.G., Evangelista, P.H., Stovall, A.E.L., Ex, S., 2020. Variability and uncertainty in forest biomass estimates from the tree to landscape scale: the role of allometric equations. *Carbon Balance Manage.* 15, 8. <https://doi.org/10.1186/s13021-020-00143-6>.
- Whittaker, A.H., Niering, W.A., 1975. Vegetation of the Santa Catalina Mountains, Arizona: V. Biomass, production and diversity along the elevation gradient. *Ecology* 56, 771–790.
- Winsome, T., Silva, L.C.R., Scow, K.M., Doane, T.A., Powers, R.F., Horwath, W.R., 2014. Plant-microbe interactions regulate carbon and nitrogen accumulation in forest soils. *For. Ecol. Manage.* 384, 415–423.
- Zhang, J.W., Busse, M.D., Fiddler, G.O., Fredrickson, E., 2019. Thirteen-year response of ponderosa pine plantations to dominant shrubs (*Arctostaphylos* and *Ceanothus*). *J. Forestry Res.* 31, 1445–1451.
- Zhang, J.W., Busse, M.D., Young, D.H., Fiddler, G.O., Sherlock, J.W., Tenpas, J.D., 2017. Aboveground biomass responses to organic matter removal, soil compaction, and competing vegetation control on 20-year mixed conifer plantations in California. *For. Ecol. Manage.* 401, 341–353.
- Zhang, J.W., Powers, R.F., Oliver, W.W., Young, D.H., 2013. Response of ponderosa pine plantations to competing vegetation control in Northern California, USA: A meta-analysis. *Forestry* 86, 3–11.
- Zhang, J.W., Powers, R.F., Skinner, C.N., 2010. To manage or not to manage: the role of silviculture in sequestering carbon in the specter of climate change. In: Jain, T.B., Graham, R.T. & Sandquist, J. (tech. eds.) *Integrated Management of Carbon Sequestration and Biomass Utilization Opportunities in a Changing Climate*. Proceedings, 2009 National Silviculture Workshop. RMRS-P-61. Fort Collins, CO: USDA Forest Service, Rocky Mountain Research Station. pp. 95–110.
- Zhang, J.W., Young, D.H., Oliver, W.W., Fiddler, G., 2016. Effect of overstorey trees on understorey vegetation in California (USA) ponderosa pine plantations. *Forestry* 89, 91–99.
- Zhang, J., Zhang, J.W., Mattson, K., Finley, K.A., 2020. Effect of silviculture on carbon pools during development of a ponderosa pine plantation. *Forests* 11, 997. <https://doi.org/10.3390/f11090997>.