

Early treatment effects on plantation growth and biodiversity in mature ponderosa pine forest

Jianwei Zhang  and Kaelyn Finley

USDA Forest Service, Pacific Southwest Research Station, 3644 Avtech Parkway, Redding, CA 96002, USA

Corresponding author: Jianwei Zhang (email: Jianwei.zhang2@usda.gov)

Abstract

We address the concerns that managed forest plantations may cause reductions of diversity of understory vegetation. We performed inventories of two mature ponderosa pine plantations in which multiple treatments were applied during plantation establishment. At stand age 35, we measured tree heights and diameters, understory plant cover and diversity, soil nutrients and chemical properties, and soil microbial biomass and diversity with phospholipid fatty acid. We found a significant, positive effect from both herbicide (H) and fertilizer (F) applications on subsequent overstory tree growth and development ($P < 0.05$); insecticide (I) effect was minimal. We observed negative effects on understory plant diversity decades later when herbicide was applied during stand establishment. However, lower plant diversity and ground cover appeared to have been caused primarily from overstory canopy closure, supported by the increased understory cover and diversity observed in the HI and HFI plots that had been thinned at age 12. Similarly, while fertilizer increased tree growth at both sites, it only negatively affected understory plants at the higher quality site. We did not find significant influence of treatment effects on soil nutrients and microbial communities. Therefore, to mitigate the potential loss of understory biodiversity in plantations, foresters can manage overstory trees with traditional pre-commercial thinning techniques and early tending.

Key words: fertilization, herbicide application, thinning, ponderosa pine plantation, understory vegetation diversity

Introduction

Forest plantations are stands composed of trees established through planting or artificial seeding for afforestation or reforestation (Helms 1998). Plantations were originally used to enhance timber and wood biomass production, prevent soil erosion, conserve water, and to reduce reliance on wood supplies from natural forests (FAO 2001). Today, they are regarded as among the most effective strategies for carbon sequestration and climate change mitigation (Bastin et al. 2019; Domke et al. 2020). Therefore, planted forests now cover 294 million ha, equivalent to 7% of forested land worldwide (FAO 2022). In addition, the rate of natural forest regeneration following disturbances may be inhibited by climate change, especially warming and drought (Davis et al. 2019), and by mega disturbances such as wildfires and insect outbreaks (Millar and Stephenson 2015; Seidl et al. 2017; Stevens-Rumann and Morgan 2019). Without artificial reforestation, disturbed forests may have slower rates of recovery or may never recover. In United States alone, there is about 3 million ha of identified reforestation backlog (<https://healthyforests.org/2021/04/investing-in-reforestation-and-forest-roads/>, accessed 2 February 2023). Furthermore, the Trillion Trees Initiative calls for additional forest trees to be planted with the hope of mitigating climate change by sequestering more carbon from the atmosphere (<https://www.1t.org/>). As a result, more planted forests will be established in the future and the cov-

erage is expected to grow from 7% to more than 20% over the next century (Brocknerhoff et al. 2013; Hansen et al. 2013).

With the growth of these extensive forest plantations, concern has been raised for some time over the potential negative effects of plantations on species diversity and in particular, on plant diversity (Carnus et al. 2006; Stephens and Wagner 2007). This concern is especially prevalent for the intensively managed plantations that use genetically improved or engineered tree species, dubbed “green deserts” by the media (Acosta 2011; cf. Horak et al. 2019). Preserving plant diversity in plantation understory is important as it provides a variety of ecosystem functions and services (Landuyt et al. 2019; Balandier et al. 2022a) such as nutrient cycling, soil erosion control, wildlife habitats, and maintaining healthy soil by providing organic matter (OM), reducing soil compaction, and improving soil structure (Landuyt et al. 2019; Balandier et al. 2022a, b; Deng et al. 2023). Plantations also play a significant role in carbon sequestration in vegetation and in the soil (Zhang et al. 2017). A diverse understory can increase the resilience of plantations to the impacts of climate change, such as drought, pests, and diseases (cf. Deng et al. 2023).

However, some understory species, particularly some shrubs, regenerate quickly on disturbed land, especially due to wildfires, from their prolific seed banks (McDonald and Fiddler 2011), leading to limited species diversity developing at a site. Without effective control, competing shrubs

can lead to high mortality of tree seedlings and regeneration failure (Fiske 1982). Therefore, a common practice is to control understory vegetation (especially shrubs and other woody plants) early for increased survival and establishment of tree seedlings and is typically followed by thinning the plantation trees after crown closure. Following tree thinning, understory species can re-establish (James et al. 2012; Willms et al. 2017; Li et al. 2020). Under such management practices, plantations may not lead to reduced plant diversity.

The generalization of negative effects of plantations appears to be unsupported or sometimes biased (Carnus et al. 2006; Brockerhoff et al. 2008; Hartmann et al. 2010; Horak et al. 2019). Based on numerous reviews and meta-analyses, effects of planted forests on biodiversity depend on many factors (Evans 2004; Carnus et al. 2006; Zhang and Stanturf 2008; Onyekwelu and Olabiwonnu 2016; Braun et al. 2017; Castano-Villa et al. 2019; Cifuentes-Croquevielle et al. 2020; Albert et al. 2021; Hua et al. 2022; Wang et al. 2022; Latterini et al. 2023; Vu et al. 2023). These factors include plantation type (industry, conservation, or protective), stand age (young vs. old developmental stages), species planted (native vs. exotic), species composition (monoculture vs. polyculture), management regimes (competing vegetation control, fertilization, tending, and thinning), legacy plant communities (forest, shrub, grassland, or cropland), control references used (e.g., old growth, secondary, farmland, or natural deserted land), and indicators chosen for biodiversity (plants, birds, mammals, insects, soil organisms or microorganisms, etc.). Some studies have demonstrated negative effects of plantations on biodiversity, mainly when compared to primary forests (Potton 1994; Fitzerbert et al. 2008; Gomes-Gonzales et al. 2020). However, it is generally understood that management interventions can enhance stand development by improving light, nutrients, and water availability (Balandier et al. 2006, 2022b). Therefore, plantations, if appropriately managed through manipulation of spatiotemporal heterogeneity and by mitigating natural disturbances, could help enhance biodiversity at a landscape scale (Lindenmayer et al. 2010; Horák et al. 2019).

In the Klamath Mountains, Southern Cascades, and Sierra Nevada of California, extensive inventories suggest that traditionally managed conifer plantations with practices applied, such as pre-commercial thinning and commercial tending, can maintain plant diversity and richness at a level similar to, or greater than natural forests (DiTomaso et al. 1997; Battles et al. 2001; James et al. 2012; Zhang et al. 2013a). On post-wildfire plantations in the Sierra Nevada, Bohlman et al. (2016) found that removal of specific shrub species resulted in increased richness of other plant species in plantations that used shrub control (treated) when compared to sites that were naturally regenerated or untreated forest stands. Information about differences in plant diversity between intensively managed and less-managed plantations in manipulated experiments is lacking, especially for monocultures (cf. McDonald and Fiddler 2011). To ensure forest land stays forested post-disturbance while maintaining plant diversity, land managers will need to understand the relationships between plantation treatments and understory plant diversity.

Plantation effects on soil properties and microbial communities are also inconclusive (Liao et al. 2012; Deng et al. 2017; Zhang et al. 2017), especially for the interactions between aboveground vegetation and soil organisms (Wardle et al. 2004; van der Heijden et al. 2008). In a meta-analysis, Zhang et al. (2017) found a positive effect on microbial biomass when a plantation replaces bare soil (afforestation) and a negative effect when a plantation replaces a natural forest. No significant effect on microbial biomass was detected if a plantation replaces shrubs, pasture, grassland, and cropland (Zhang et al. 2017).

In this study, we utilized a designed plantation experiment, established 35 years ago at two sites. While the original design was intended to assess plantation productivity, we used the sites to assess the treatment effects on plant diversity and soil microbial responses. The management treatments were applied during the early stages of plantation establishment and included herbicide for competing vegetation control, fertilization to enhance growth, and pre-commercial thinning to reduce competition, (Powers and Ferrell 1996; Zhang et al. 2022). Our objectives in this study were to (1) explore the inter-relationships among overstory trees, understory plants, soil chemical properties, and microbial communities, and (2) determine management regimes that can strike a balance between maximizing tree growth while maintaining plant diversity in forest plantations.

Materials and methods

Study site

The ponderosa pine (*Pinus ponderosa* Lawson & C. Lawson) plantations evaluated in this study are the Pondosa and Chester sites; these are the only two remaining plantations among the original eight Garden of Eden installations (Powers and Ferrell 1996). The Garden of Eden study was originally established to investigate basic tree and soil interactions and to address fundamental questions about the factors governing plantation growth in a Mediterranean climate (Powers and Ferrell 1996). The original eight sites covered a range of site quality with site indexes ranging from 17 to 30 m at 50 years (Powers and Ferrell 1996) including 20 m at Chester and 18 m at Pondosa (Zhang et al. 2022). Of the other six sites, two were accidentally damaged by forest operations, three were converted to second-rotation plantation studies, and one was lost to a backfiring operation during the 2016 Gap Fire (Zhang et al. 2022). The Chester site (Lat. 40.3077, Long. 121.0998, Elev. 1533 m) is located near Chester, California in the northern Sierra Nevada Range; the Pondosa site (Lat. 41.2083, Long. 121.6252, Elev. 1181 m) is 110 km north of Chester and is close to Pondosa, California in the southern Cascade Range. Chester is a cooler and wetter site with an average annual precipitation of 1200 mm. It has a weakly developed soil, classified as the Windy series (skeletal, frigid Humic Vitrixerands). Pondosa is dryer with an average annual precipitation of 760 mm. Soils are fine-loamy Vitrandic Palexeralfs of the Jimmerson series, formed from andesitic lava flows. Both sites were planted following the mechanical

clearing of a dense shrub field of *Arctostaphylos* spp. and *Ceanothus* spp.; Chester in 1987 and Pondosa in 1988.

Study design

Eight factorial treatment combinations of with and without (1) vegetation control, (2) fertilization, and (3) insect control were applied to each of three replicated plots for a total of 24 plots at both sites. Seventy-two seedlings were planted at 2.4 × 2.4 m spacing on each plot. Seedlings were raised at the USDA Forest Service Placerville Nursery using seeds from local seed zones for each respective site. Treatment history is detailed in Powers and Ferrell (1996) and Zhang et al. (2022). Treatments were applied over the first 6 years of plantation growth, with competing vegetation controlled by spraying herbicides and insects were controlled by spraying insecticides. Acephate or dimethoate insecticides were applied each spring during the first 6 years using manufacturer recommendations for insect species likely to be present (Powers and Ferrell 1996). Depending on soil and vegetation type, glyphosate, hexazinone, or triclopyr herbicides were applied each spring of the first 6 years to all competing vegetation (Powers and Ferrell 1996). Fertilization was applied using macro- and micronutrients, following a ramp schedule in which nutrient supply increases with demand in 4 of the first 6 years. The total added amounts per hectare were 1074 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. The eight treatment combinations of herbicide (H), insecticide (I), and fertilization (F) are referred to as a H, F, I, HF, FI, HI, HFI, and C for control or no treatments. There was a lack of visible insect activity anywhere in the plots and in the surrounding forest during first 12 years of the study. As a result, a decision was made for all plots with HI and HFI to be thinned by leaving 50% trees at age 12. Pre-commercial thinning (T) of industry plantations was a standard practice at the time (following canopy closure). The I and FI plots were not thinned because trees had not reached the canopy closure at that point. Therefore, the I and C plots were considered essentially the same as one another (i.e., controls), and the F and FI plots were essentially similar (i.e., F treatments). The treatment plots at age 35 are shown in Fig. 1.

Tree measurement

Once the study was installed, the inner 20 trees of each plot was established as the measurement plot with two outer rows of trees as the plot buffer. Height and diameter at breast height (dbh, at 1.37 m height) were measured for trees on the Chester plots at ages 2, 4, 6, 8, 10, 12, 24, 30, and 35, and on the Pondosa plots at ages 2, 4, 6, 8, 10, 23, 29, and 34. Crown width was measured for each tree during the first five measurement years (ages 2–10), by averaging the widths at two directions. Crown width was measured again at age 15 for plots that did not receive herbicides (e.g., C, F, FI, and I treatments). Results from measurements through age 24 have been reported elsewhere (Powers and Ferrell 1996; Zhang et al. 2022); we only report the latest measurements of overstory tree growth.

Understory vegetation survey

Understory vegetation was sampled using a line-intercept method on four parallel, 10 m transects oriented between the rows of the measurement trees. For each understory plant, plant cover was measured at the starting and ending distance of the crown along the transect. In the early surveys conducted at ages 2–15, plant cover was only recorded on non-herbicide plots because understory plants were rare on herbicide-treated plots. These early data are summarized here to demonstrate overstory and understory dynamics during plantation establishment stage. In the latest measurement in 2021, species were also identified individually across all 24 plots in addition to recording plant cover.

Understory plant cover is expressed as a percentage of transect length. Species richness was calculated as simply the number of understory species. Understory plant species diversity for the last measurement was calculated using the Shannon–Wiener Index (H') that weighs both richness and abundance of species (Shannon 1948).

$$(1) \quad H' = - \sum \left(\frac{n_i}{N} \times \ln \frac{n_i}{N} \right)$$

where n_i is number of individuals of each species (the i^{th} species), N is total number of individuals for the treatment plot, and $\ln$ is the natural log of the number. A high value of H' (maximum is 5.0 for biological communities) would be representative of a diverse and equally distributed community, and lower values represent a less diverse community. A value of 0 would represent a community with just one species.

Soil sampling and analysis

Soil samples were collected from two depths (0–10 and 10–20 cm) for soil chemical and phospholipid fatty acid (PLFA) analyses in 2022. From each plot, three systematic spots along a diagonal were chosen and pooled by depth. Then, samples were immediately placed in an ice cooler before returning to lab where samples were stored at 4 °C. Soil pH, percent OM loss on ignition (LOI %), nutrients (N, P, K, Ca, Mg), cation exchange capacity (CEC), and PLFA were analyzed with methods used by Buyer and Sasser (2012) at the Ward Laboratory (<https://www.wardlab.com/>; Kearney, Nebraska, USA). The PLFAs are biomarkers used to identify microbial biomass and community structure (Bossio et al. 1998). PLFAs are structural components of microbial cell membranes, and their presence in soil samples provides information on the types and abundance of total living microbial biomass, functional group diversity index, and community composition and stress and activity ratios (please see the details in <https://www.wardlab.com/wp-content/uploads/2019/09/PLFA-Customer-Report-9-27-2013.pdf>).

Due to the limited insect treatment effect on aboveground vegetation, we pooled soil samples from “I” treatment with “C” control and “FI” treatment with “F” fertilizer. This pooling resulted in two sites, two depths, three replications, and 2 × 2 (H × F) for a total of 48 samples. In addition, original HI and HFI plots were not combined as they were thinned at age 12. These resulted in a total of 24 samples (two treatments, two sites, two depths, and three replications). A grand total

Fig. 1. Plots of Control (C), Fertilizer (F), Thinned with HI or HFI, and Herbicide and Fertilizer (HF) treatments at Chester and Pondosa Garden of Eden sites at age 35. H plots are not included here because they look the same as HF plots.



of 72 samples per site were analyzed for chemical properties and microbial PLFAs.

Statistical analysis

We analyzed all variables with a complete randomized design with plot as our experimental unit repeated at two sites using SAS PROC MIXED (SAS Institute Inc. 2013). All treatments and sites were assigned as fixed effects and plot as a random effect. The following model was used for all vegeta-

tion = associated variables:

$$(2) \quad y_{ijl} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \varepsilon_{ijl}$$

where y_{ijl} is the dependent variable measured for the i^{th} treatment and the j^{th} site, and l^{th} plot; μ is the overall mean; α_i is the fixed effect of the i^{th} treatment ($i = 1, 2, \dots, 8$); β_j is the fixed effect of the j^{th} site ($j = 1, 2$); and ε_{ijl} is an experimental error, $\varepsilon_{ijl} \sim iidN(0, \sigma_e^2)$.

Table 1. Means and standard errors of all treatments, with (H1) and without (H1) herbicide, and Analysis of variance (ANOVA), including effect, degrees of freedom, and probability ($P < F$) of diameter at breast height (dbh), quadratic mean diameter (QMD), height, basal area (BA), and trees per hectare (TPH) by site and treatment for 35-year-old ponderosa pine trees grown at two contrasting sites in northern California.

Site	Treatment*	dbh (cm)	QMD (cm)	Height (m)	BA (m ² ha ⁻¹)	TPH
Chester	C	18.8 (1.1)	19.3 (1.1)	7.2 (1.1)	42.8 (7.4)	1458 (97)
	I	20.4 (0.8)	20.8 (0.9)	6.6 (0.7)	48.2 (5.6)	1430 (223)
	F	22.3 (1.5)	22.9 (1.4)	8.7 (0.4)	55.2 (7.2)	1346 (146)
	FI	21.2 (1.2)	21.7 (1.2)	7.7 (0.9)	55.9 (6.4)	1514 (84)
	H0 mean	20.7 (1.2)	21.1 (1.1)	7.5 (0.8)	50.5 (6.6)	1437 (137)
	H	23.1 (1.4)	23.4 (1.3)	9.8 (0.3)	61.1 (1.2)	1430 (146)
	T(HI)	27.3 (1.3)	27.4 (1.4)	10.0 (0.2)	49.8 (5.1)	841 (0)
	HF	24.7 (1.3)	25.0 (1.3)	10.3 (0.4)	70.2 (6.5)	1430 (84)
	T(HFI)	27.5 (1.3)	27.7 (1.4)	11.6 (0.4)	50.7 (5.1)	841 (0)
	H1 mean	25.7 (1.3)	25.9 (1.3)	10.4 (0.3)	58.0 (4.5)	1135 (57)
Site mean		23.2 (1.2)	23.5 (1.2)	9.0 (0.5)	54.2 (5.5)	1286 (97)
Pondosa	C	13.8 (2.9)	14.6 (2.7)	7.2 (1.1)	20.5 (7.2)	1206 (129)
	I	12.8 (2.7)	13.7 (2.3)	6.6 (0.7)	20.5 (8.4)	1346 (336)
	F	17.0 (1.5)	17.6 (1.7)	8.7 (0.4)	29.9 (6.6)	1234 (257)
	FI	14.7 (3.5)	15.6 (2.8)	7.7 (0.9)	23.9 (16.2)	1121 (620)
	H0 mean	14.6 (2.7)	15.4 (2.4)	7.5 (0.8)	23.7 (9.6)	1227 (335)
	H	18.6 (0.7)	19.1 (0.6)	9.8 (0.3)	41.8 (3.4)	1458 (129)
	T(HI)	22.5 (0.3)	22.7 (0.4)	11.1 (0.4)	34.1 (1.3)	841 (0)
	HF	19.4 (1.0)	19.8 (1.0)	10.3 (0.4)	50.2 (1.8)	1626 (97)
	T(HFI)	23.3 (0.7)	23.5 (0.7)	11.6 (0.4)	36.4 (2.1)	841 (0)
	H1 mean	21.0 (0.7)	21.3 (0.7)	10.7 (0.3)	40.6 (2.2)	1192 (56)
Site mean		17.8 (1.7)	18.3 (1.5)	9.1 (0.6)	32.2 (5.9)	1209 (196)
Effect	Num/Den DF					
Site	1/16	<0.001	<0.001	<0.001	<0.001	0.219
Treatment (trt)	7/16	<0.001	<0.001	<0.001	<0.001	<0.001
Site*trt	7/16	0.699	0.749	0.734	0.205	0.393

*Treatments: Control (C), Insecticide (I), Fertilizer (F), Fertilizer and Insecticide (FI), Herbicide (H), Herbicide and Fertilizer (HF), Herbicide and Insecticide thinned at age 12 T(HI), and combination of all three treatments also thinned at age 12 T(HFI).

For all soil associated variables, depth was added into the model.

$$(3) \quad y_{ijkl} = \mu + \alpha_i + \beta_j + \alpha\beta_{ij} + \gamma_k + \alpha\gamma_{ik} + \beta\gamma_{jk} + \alpha\beta\gamma_{ijk} + \varepsilon_{ijkl}$$

where y_{ijkl} is the dependent variable measured for the i^{th} treatment and the j^{th} site, k^{th} depth, and l^{th} plot; μ is the overall mean; α_i is the fixed effect of the i^{th} treatment ($i = 1, 2, \dots, 6$); β_j is the fixed effect of the j^{th} site ($j = 1, 2$); γ_k is the fixed effect of k^{th} depth ($k = 1, 2$); and ε_{ijkl} is an experimental error, $\varepsilon_{ijkl} \sim iidN(0, \sigma_\varepsilon^2)$.

For each variable analysis, residuals were examined to ensure that statistical assumptions of normality and homoscedasticity were met. If these assumptions were not met, a natural-log transformation was applied. During the model selection process, we selected the model with not only the minimum Akaike information criterion (AIC), but also the most appropriate Pearson's residual panels. Multiple comparisons among treatments were conducted for least squares means by the Tukey–Kramer's test by controlling for the overall $\alpha = 0.05$.

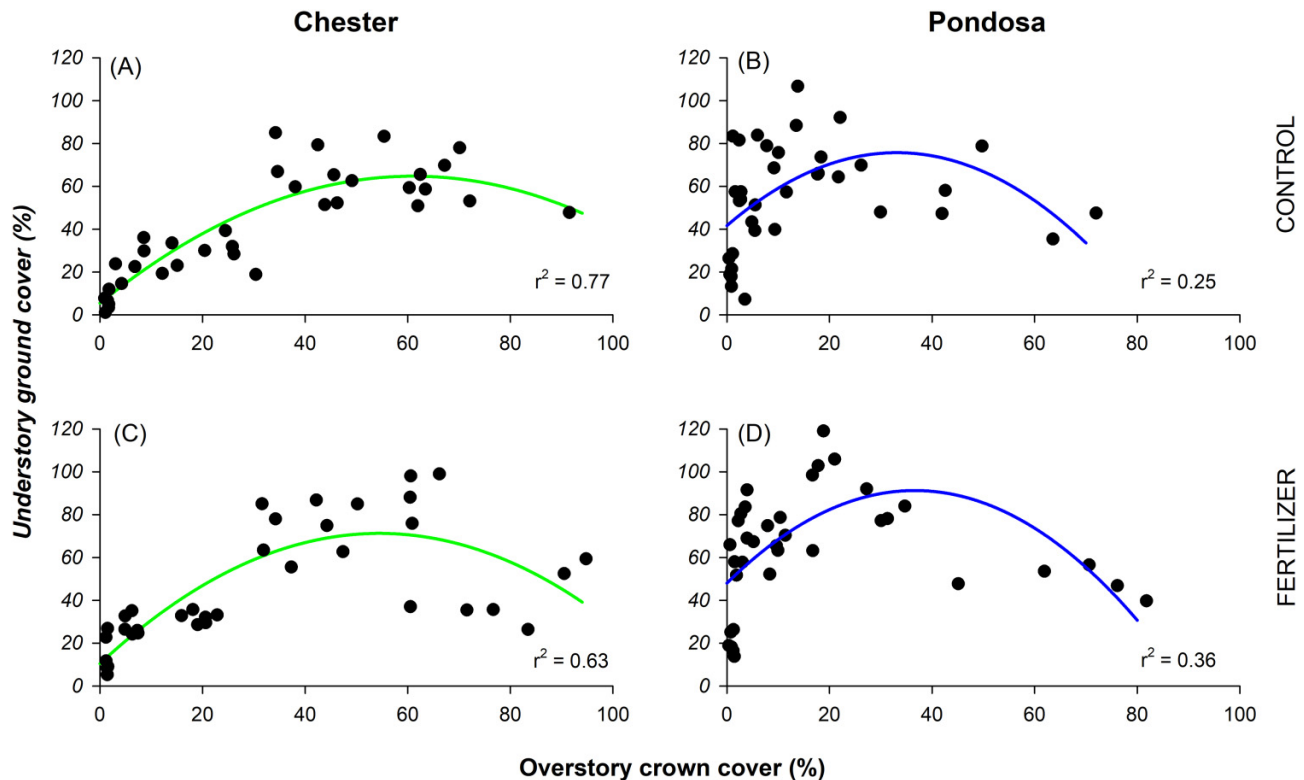
To determine the relationships among overstory trees, understory community, soil chemical properties, and microbial community, we conducted simple correlations among variables within each group to explore whether a relationship exists.

Results

Overstory conditions

Overstory response to the treatments is presented first to explain how the treatments may have affected understory responses. Herbicide treatments caused the plantation trees to grow significantly larger, both measured by individual tree level (dbh and height) and by plot level (quadratic mean diameter (QMD) and basal area (BA)), ($P < 0.001$, Table 1). Fertilizer also increased tree growth ($P < 0.001$). As expected, overall growth at the better site (Chester) was significantly higher ($P < 0.001$) than at the poorer site (Pondosa). However, there was no site difference in mortality indicated by trees per hectare (TPH) ($P = 0.22$). Treatment difference in TPH was only caused by thinning in the T(HI) and T(HFI) plots, which

Fig. 2. Effect of overstory crown cover on understory ground cover on the non-herbicide plots with and without fertilization in the ponderosa pine plantations at Chester and Pondosa during the first 15 years.



had no subsequent mortality post thin, reflected by the zero standard errors. Site by treatment interactions was not significant for any variables (Table 1).

Vegetation dynamics during plantation establishment

Our analysis suggests second-order polynomial functions best capture the relationship between overstory crown cover and understory ground cover during the first 15 years of growth (Fig. 2). The understory ground cover peaked at 60% of overstory crown cover at the Chester site and at 35% at the Pondosa site. Then, understory ground cover declined gradually with increasing overstory cover. The peaks in ground cover matched the thinning years at about age 12 when the overstory was just closing. Because these plots in Fig. 2 never received herbicide (i.e., these were Controls or Fertilized treatments with naturally colonizing vegetation), these results indicate the effect of crown cover of overstory trees on understory development without any artificial control with herbicides.

Plant diversity and vegetation cover at mature stands

Understory species richness, ground cover, and plant diversity as measured by the Shannon–Wiener Index in 2021 differed significantly between both the two sites and among the various treatments (Fig. 3). Yet, none of the interac-

tions (site by treatment) were significant. The Pondosa site showed much higher plant species diversity, richness, and cover than the Chester site (Figs. 3A, 3C, and 3E). Herbicide treatments were associated with reductions in species richness in most treatments (Fig. 3D). However, plant diversity on thinned plots T(HI) and T(HFI) was not significantly different from the I, F, and FI plots (Fig. 3B), and ground cover in T(HI) differed from in H and HF but not in T(HFI) (Fig. 3F). The greater variation in percent cover from the plot nutrient additions compared to other treatments was mainly caused by the trend changes among non-herbicide treatments, negatively at Chester and positively at Pondosa (Fig. 4). Clearly, after 15 years following cessation of herbicide treatments, understory plants have colonized the herbicide-treated plots, especially on the thinned T(HI) and T(HFI) plots.

Soil nutrients

Soil chemical analyses indicated that most differences occurred between sites and depths (Tables 2 and 3). The Chester site showed significantly higher OM and lower pH, K, Ca, Mg, and CEC than the Pondosa site. No site difference was found for N and P. The top 10 cm soil showed higher pH, OM, N, and P, and lower K, Ca, Mg, and CEC than the 10–20 cm soil. Significant treatment differences were found in pH, P, K, and Mg with the higher levels observed in HF and T(HFI), which suggests that fertilized plots without competing vegetation

Fig. 3. Plant species diversity measured by (A and B) Shannon–Wiener Index (H'), (C and D) species richness, and (E and F) ground cover (%) for understory species between sites (A, C, and E) and among eight treatments (B, D, and F) at Chester and Pondosa in northern California, USA. Individual treatments included control (C), insecticide (I), fertilization (F), herbicide (H), and their combinations, some with thinning (T). Bars (Box and Whisker plot) with different letters indicate the differences ($P < 0.05$).

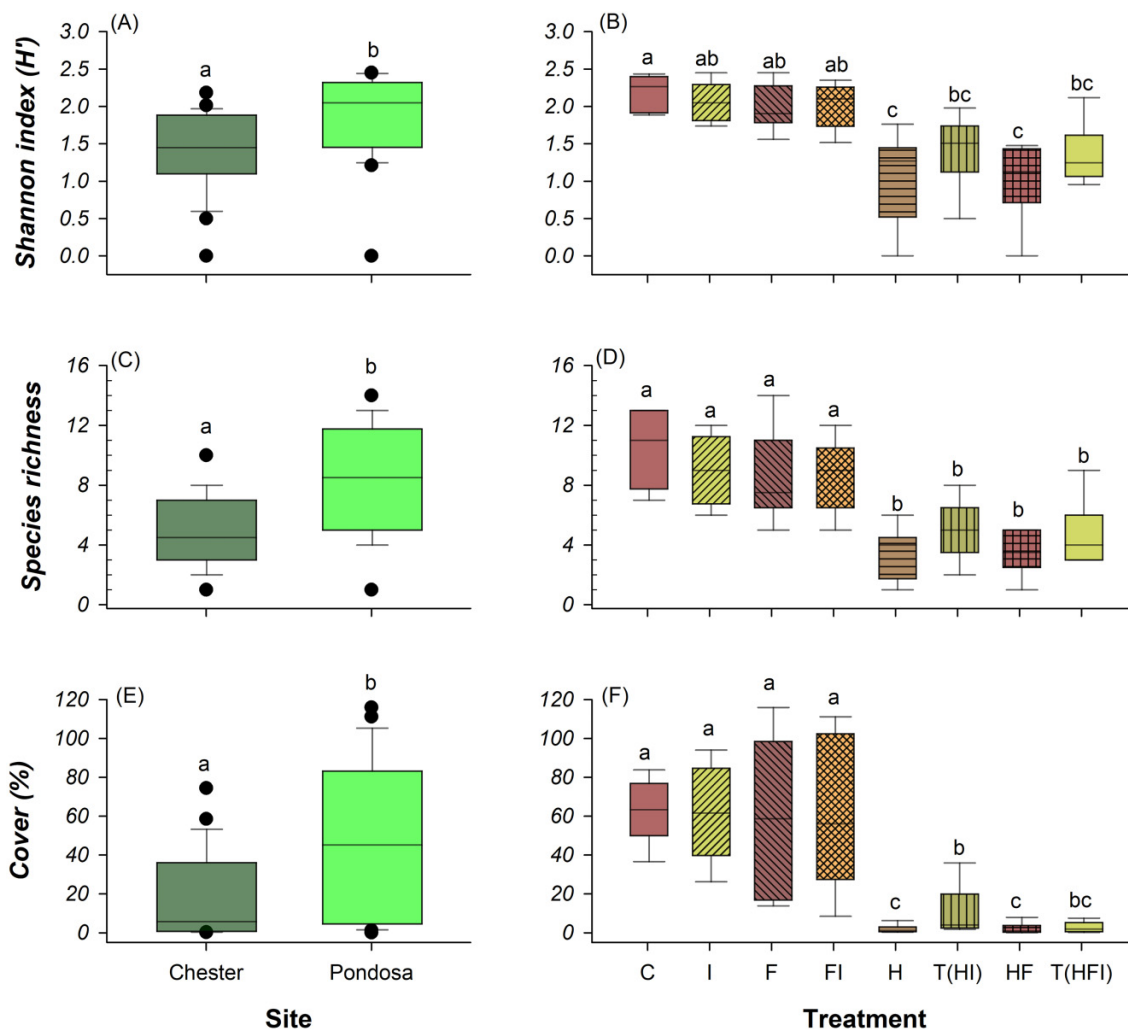
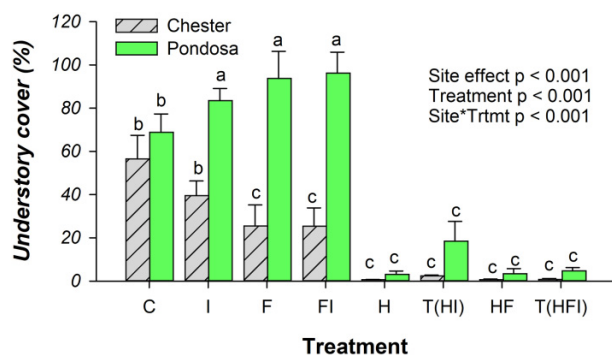


Fig. 4. Means and standard errors of understory plant cover (%) across eight treatments, including control (C), insecticide (I), fertilization (F), herbicide (H), and their combinations, some with thinning (T) at Chester and Pondosa Garden of Eden sites. Bars with different letters indicate the differences ($P < 0.05$).



still held more residual soil P, K, and Mg. Other interactions among depth, treatment, and site were lacking in general.

PLFA soil microbial community analysis

Microbial community variation was more site- and depth-dependent than treatment (Tables S1 and S2). Soil at the Pondosa site contained a significantly higher total microbial biomass (5404 vs. 3309 ng g^{-1} soil) and higher microbial diversity (1.5 vs. 1.4) than at the Chester site (Table S2). The trends were consistent with other biomass variables measured by PLFAs. None of the treatment effects was significant for any variable (Table S1). Neither were most treatment interactions. An exception was the site and treatment interactions for community composition ratios—fungi:bacteria ratio and Gram(+):Gram(−) ratio, and stress community activity ratios—sat:unsat and mono:poly (Fig. 5).

Table 2. Means of soil pH, loss on ignition (LOI) organic matter (OM) (%), soil nitrite N, P, K, Ca, Mg, and cation exchange capacity (CEC) for soil samples collected at two depths at two contrasting sites in Northern California.

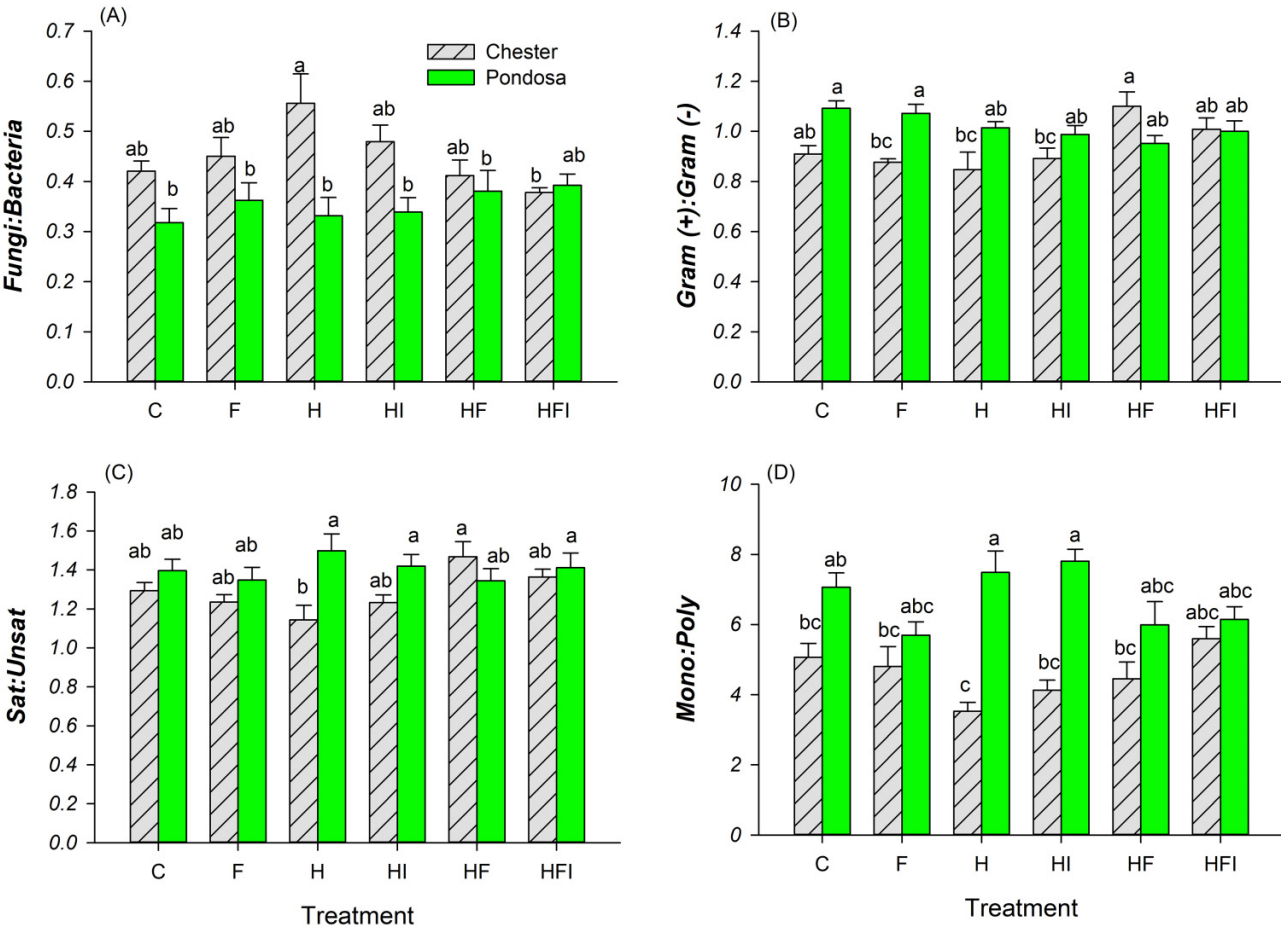
Site	Treatment*	Depth (cm)	pH	OM (%)	N (ppm)	P (ppm)	K (ppm)	Ca (ppm)	Mg (ppm)	CEC (Meq/100 g)
Chester	C	0–10	6.2 (0.0)	13.3 (0.8)	1.1 (0.7)	6.9 (0.2)	142.7 (4.7)	625.7 (30.2)	46.7 (2.7)	11.6 (0.4)
	F		6.4 (0.0)	14.4 (1.3)	1.7 (0.5)	30.4 (6.7)	199.0 (15.5)	986.0 (87.5)	91.0 (4.5)	12.1 (0.3)
	H		6.3 (0.1)	14.2 (1.5)	2.1 (1.5)	6.9 (0.7)	182.3 (25.0)	639.0 (86.0)	49.3 (4.8)	11.7 (1.0)
	HF		6.7 (0.3)	11.6 (1.6)	3.4 (1.6)	35.6 (19.1)	241.3 (27.7)	881.7 (67.9)	113.7 (19.0)	10.1 (2.1)
	T(HFI)		6.7 (0.2)	11.4 (0.2)	0.6 (0.2)	22.7 (13.6)	193.7 (10.7)	871.7 (180.4)	73.0 (9.3)	9.0 (1.4)
	T(HI)		6.3 (0.1)	13.3 (0.7)	1.6 (0.6)	7.3 (0.2)	181.0 (4.4)	660.7 (34.2)	49.3 (0.9)	10.8 (1.5)
	Mean		6.4 (0.1)	13.0 (1.0)	1.7 (0.9)	18.3 (6.7)	190.0 (14.7)	777.4 (81.0)	70.5 (6.9)	10.9 (1.1)
Chester	C	10–20	6.3 (0.2)	13.6 (1.3)	0.5 (0.0)	7.2 (0.2)	155.0 (14.1)	630.7 (15.7)	50.3 (4.8)	11.2 (1.3)
	F		6.3 (0.0)	12.9 (1.1)	0.5 (0.3)	15.6 (3.4)	167.7 (16.5)	861.0 (48.3)	76.7 (2.9)	12.8 (0.2)
	H		6.3 (0.1)	11.7 (0.5)	0.6 (0.4)	6.2 (0.6)	181.7 (17.8)	704.0 (110.6)	50.3 (8.1)	11.7 (0.3)
	HF		6.4 (0.1)	11.0 (1.3)	2.1 (1.5)	6.8 (1.2)	185.3 (18.8)	639.3 (70.1)	77.3 (21.1)	10.1 (0.1)
	T(HFI)		6.3 (0.1)	11.3 (0.6)	0.7 (0.3)	17.9 (5.4)	178.7 (17.2)	754.3 (182.7)	75.3 (17.7)	12.0 (0.6)
	T(HI)		6.3 (0.1)	11.6 (0.9)	0.2 (0.1)	7.0 (0.1)	171.0 (6.8)	626.7 (36.4)	46.3 (2.9)	10.6 (1.0)
	Mean		6.3 (0.1)	12.0 (0.8)	0.8 (0.4)	10.1 (1.8)	173.2 (15.2)	702.7 (77.3)	62.7 (9.6)	11.4 (0.6)
Pondosa	C	0–10	6.4 (0.0)	6.3 (0.1)	1.2 (0.3)	6.7 (0.3)	451.0 (21.8)	993.3 (52.4)	181.7 (8.0)	13.2 (0.4)
	F		6.4 (0.0)	6.8 (0.2)	1.8 (1.4)	18.2 (5.1)	472.3 (27.7)	970.7 (56.2)	222.0 (10.4)	13.7 (0.3)
	H		6.4 (0.1)	5.7 (0.2)	1.3 (1.1)	6.7 (0.2)	408.3 (11.6)	892.3 (49.2)	196.7 (3.2)	13.2 (0.6)
	HF		6.9 (0.3)	6.3 (0.2)	0.9 (0.6)	51.7 (17.4)	456.7 (34.2)	1119.3 (309.2)	241.7 (13.4)	11.2 (1.8)
	T(HFI)		7.0 (0.2)	6.0 (0.1)	0.5 (0.0)	19.9 (5.3)	466.0 (21.7)	989.3 (71.9)	238.3 (4.9)	9.9 (1.6)
	T(HI)		6.4 (0.0)	6.7 (0.3)	2.2 (1.0)	7.1 (0.5)	385.7 (30.8)	1001.7 (86.0)	183.7 (20.8)	13.2 (0.7)
	Mean		6.6 (0.1)	6.3 (0.2)	1.3 (0.7)	18.4 (4.8)	440.0 (24.6)	994.4 (104.1)	210.7 (10.1)	12.4 (0.9)
Pondosa	C	10–20	6.5 (0.0)	5.4 (0.2)	1.6 (0.9)	6.6 (0.1)	366.3 (22.8)	923.7 (59.3)	196.0 (15.5)	12.5 (0.5)
	F		6.4 (0.0)	5.3 (0.1)	0.9 (0.2)	6.9 (0.7)	453.3 (9.3)	929.3 (72.2)	220.3 (21.5)	13.6 (0.1)
	H		6.5 (0.1)	4.9 (0.4)	0.2 (0.0)	6.4 (0.2)	313.3 (23.3)	871.3 (62.8)	236.0 (9.9)	12.2 (0.8)
	HF		6.7 (0.3)	5.2 (0.2)	0.4 (0.1)	8.0 (0.9)	391.3 (27.4)	858.7 (153.0)	222.7 (45.0)	11.1 (1.3)
	T(HFI)		6.5 (0.1)	5.4 (0.4)	0.4 (0.1)	7.5 (1.0)	442.7 (23.0)	901.0 (39.9)	236.7 (22.9)	12.9 (0.4)
	T(HI)		6.4 (0.0)	5.3 (0.1)	1.0 (0.4)	7.1 (0.1)	332.3 (5.4)	1002.0 (60.8)	218.7 (21.9)	13.3 (0.5)
	Mean		6.5 (0.1)	5.3 (0.2)	0.8 (0.3)	7.1 (0.5)	383.2 (18.5)	914.3 (74.7)	221.7 (22.8)	12.6 (0.6)

*Treatment: Control (C), Fertilizer (F), Herbicide (H), Herbicide and Fertilizer (HF), and combination of treatments thinned at age 12 T(HFI) and T(HI).

Table 3. Sources of variation, degrees of freedom, and *P* values for soil pH, organic matter (OM), N, P, K, Ca, Mg, and cation exchange capacity (CEC) for soil samples collected from two depths at two contrasting sites in northern California.

Effect	Num DF	Den DF	pH	OM	N	P	K	Ca	Mg	CEC
Site	1	24	0.032	<0.001	0.545	0.595	<0.001	0.001	<0.001	0.005
Treatment (Trt)	5	24	0.042	0.269	0.602	0.002	0.002	0.577	0.013	0.050
Site*Trt	5	24	0.963	0.368	0.262	0.474	0.011	0.553	0.786	0.901
Depth	1	24	0.009	<0.001	0.008	0.001	<0.001	0.003	0.728	0.295
Site*depth	1	24	0.942	0.987	0.440	0.536	0.008	0.911	0.055	0.683
Trt*depth	5	24	0.004	0.085	0.525	0.002	0.549	0.042	0.068	0.043
Site*Trt*depth	5	24	0.983	0.218	0.987	0.900	0.130	0.891	0.753	0.992

Fig. 5. Effect of treatment by site interactions for phospholipid fatty acid (PLFA) microbial community composition ratios in soil collected on Chester and Pondosa plots in northern California. Individual treatments included control (C), fertilization (F), herbicide (H), and their combinations with insecticide (I). Bars with different letters indicate the differences ($P < 0.05$).



Relationships among soil properties, microbial community, overstory growth, and understory plant diversity

Because of a substantial site effect for almost every measure, we ran Pearson's simple correlations to uncover site-specific relationships between variables (Fig. 6). At Chester, where trees had much higher growth and lower understory plant diversity than Pondosa, none of correlation coefficients were significant between Shannon H' and any other variables

($|r| < 0.42$, $P > 0.05$). Overstory tree BA was only correlated with P, K, and Mg ($r = 0.50$ – 0.74 , $P < 0.05$). As for the soil chemical properties and microbial variables, only Gram +/– ratio was significantly related to OM and K.

At the Pondosa site, diversity index H' was negatively related to BA, P, and fungi/bacteria, positively related to Gram +/– ratio. Correlations between BA and P, Mg, and Gram +/– ratio reached significant levels. Correlation between OM and AM was 0.47 ($P < 0.05$).

Fig. 6. Heatmap of correlation coefficients among overstory basal area (BA), understory plant diversity (H'), soil chemical properties, and soil arbuscular mycorrhizal fungi (AM), microbial community composition ratios—fungi:bacteria (F/B) and Gram(+):Gram(−) (G+/G−) at Chester (upper right triangle numbers) and Pondosa (lower left triangle numbers) sites in Northern California. The bold, italic numbers refer to the significant coefficients ($P < 0.05$).

	H'	BA	OM	pH	P	Mg	K	Gram (+/-)	F/B	AM		Legend
H'		-0.40	0.36	-0.20	0.04	0.06	-0.42	-0.02	-0.13	0.07		r =
BA	-0.75		-0.14	0.07	0.50	0.63	0.74	0.15	0.06	-0.27		0.80
OM	0.41	-0.23		-0.53	-0.01	-0.34	-0.47	-0.65	0.39	0.40	CHESTER	0.60
pH	-0.05	0.38	-0.06		0.30	0.35	0.30	0.36	-0.25	-0.35		0.40
P	-0.64	0.47	-0.08	0.29		0.69	0.63	0.31	-0.36	0.07		0.20
Mg	-0.26	0.51	0.13	0.63	0.45		0.79	0.44	-0.39	-0.26		0.00
K	-0.05	-0.16	-0.13	0.03	0.49	0.25		0.50	-0.31	-0.26		-0.20
Gram (+/-)	0.51	-0.60	0.34	-0.16	-0.34	-0.17	-0.16		-0.72	-0.40		-0.40
F/B	-0.56	0.31	-0.19	-0.27	0.32	0.23	0.31	-0.53		-0.08		-0.60
AM	0.17	-0.11	0.47	0.00	0.08	0.04	0.07	0.27	-0.34			-0.80
PONDOSA												

Discussion

Although all treatments, except for thinning, were applied in the early (first 6 years) stages of plantation establishment over 30 years ago, results clearly show that plantations with herbicide applications for controlling understory vegetation have enhanced overstory growth and reduced plant diversity compared with those without competing vegetation control (Fig. 3). Significant increases in growth and survival of planted trees when competing vegetation is controlled is universal for most, if not all tree species, worldwide (Wagner et al. 2006), including ponderosa pine (Zhang et al. 2013b). Fertilization is also important in improving the growth in ponderosa pine (Table 1) and other species plantations (Fox 2000). While we saw no fertilizer effect on plant diversity, the response of understory percent ground cover to fertilization on non-herbicide plots was site-specific with a negative effect at Chester and a positive effect at Pondosa (Fig. 4). The discrepancy is most likely caused by an effect of an interaction between fertilizer and water availability on stand development (Powers and Ferrell 1996). Chester receives more precipitation and has more soil OM than Pondosa and subsequently, the overstory grows and develops more rapidly with fertilizer application (Zhang et al. 2016, 2022). At Pondosa, the soil is too dry for nutrients to be readily utilized (Powers and Ferrell 1996). The negative correlations in Fig. 6 between overstory growth and understory plant diversity or ground cover corroborate the lower diversity measured at Chester than Pondosa (Fig. 3).

While herbicide applications, or other methods used to control competing vegetation, simultaneously inhibit under-

story plants and enhance planted tree survival and growth in the early stage of stand development, light availability may also limit understory development after crown closure (Wagner et al. 2011; Valladares et al. 2016). In addition, overstory trees increase their ability to access soil water and nutrients relative to understory vegetation following crown closure (Balandier et al. 2022b). In this study, the crown closure at both sites occurred at about age 12 when pre-commercial thinning was conducted in HI and HFI plots. Although non-herbicide plots had not reached crown closure by age 12, as all plots eventually approached crown closure, understory cover dropped off (Fig. 2). Gradually, those shade-intolerant shrubs died (Fig. 1). In northern California, two major shrubs (*Arctostaphylos* spp. and *Ceanothus* spp.) aggressively regenerate and occupy sites after any type of disturbances (Powers and Ferrell 1996) as they did in the non-herbicide plots at both sites. These shrubs not only affect the survival and growth of planted trees, but also influence colonization of other plant species. DiTomaso et al. (1997) found that although initial native plant diversity was richer in their non-herbicide-treated plots, the diversity quickly fell as shrubs dominated plots. Within 8 years, both species richness and diversity were greater in their herbicide-treated areas as other native species were allowed to emergence and flourish (DiTomaso et al. 1997).

Pre-commercial thinning overstory trees improves light availability to the forest floor and potentially soil water and nutrient availability as well, for both residual trees and any understory plants. In addition, by opening the overstory through thinning, direct sunlight increases the temperature

below the canopy, especially on the soil surface, which may promote seed germination from the seed bank and increase litter decomposition (Comez et al. 2021). Therefore, this traditional management practice alone can increase plant diversity as our results indicate (Fig. 3F).

Regional forest practices have substantially evolved since these trees were planted, with changes in planting density as an example. In the 1980s, 1680 seedlings were planted ha⁻¹ with spacings at about 2.4 m by 2.4 m. Today, a maximum number of 750 seedlings ha⁻¹ are planted. In fact, depending on forest type and site quality, this number (750 trees ha⁻¹), which would have been the minimum count for reforestation success in the past, has been changed to 312–500 seedlings ha⁻¹ in the California forestry practice rules (California Department of Forestry and Fire protection 2020). This change has resulted from a significant improvement of seedling stock, field survival rate, rapid seedling growth, fuel management requirements, and priorities for future forest resilience to disturbance. In addition, the tendency to plant ponderosa pine monocultures has been replaced with mixed-species plantations, typically with at least three species. In addition to silvicultural tending of these stands, these changes in forestry practices all benefit biodiversity (Wang et al. 2022; Hua et al. 2022).

Despite additions of heavy loads of nutrients in the first 6 years of plantation establishment, soil nutrient concentrations in the fertilizer plots are not higher (Table 2). It is possible that this could be explained by the high tree growth rates, demand from understory plants, and (or) leaching in the fertilizer plots (Powers 2001). A strong positive relationship between K and BA was found to be significant at the Chester site ($r = 0.74$, $P < 0.001$) but not at the Pondosa site, which might be due to slower growing trees at the latter site, where BA is 41% lower than at former site at age 35 (Table 1 and Fig. 6). Clearly, potassium is more of a limiting factor for tree growth at the Chester site, while other factors such as water availability may be more limiting at Pondosa. Positive relationships between K and forest growth have been found in several previous studies (cf. Tripler et al. 2006). Working on forest soil in the Inland Northwest (USA) for many years, Moore et al. (2022) found a complex balance between underlying geology and the natural deficiency of potassium and suggests site-specific nutrient management prescriptions for forests in the region. Since K plays a significant role in maintaining intracellular osmotic balance, photosynthesis, cell extension, stomatal regulation, and cation–anion balance (Marschner 1995), its influence on stomatal regulation in particular will certainly benefit our trees in dealing with water stress during the growing season in the Mediterranean climate (Powers and Reynold 1999).

Our results suggest that soil chemical properties have limited influence on understory diversity; none of the nutrient concentrations was related to diversity (H') at Chester and only P is at Pondosa. This suggests that either their influence on plant diversity is minimal or nutrients are accessed more readily by overstory trees or soil microbes. In fact, negative relationships between overstory BA and understory plant diversity were found at both sites (Fig. 6). We know that fertilizer increases tree growth (Zhang et al. 2022). This circular

effect may be captured in chronosequence sampling of both soil and vegetation.

The relationship between plant diversity and soil microbes is complex and can be influenced by a range of biotic and abiotic factors. Assuming that there was a negative effect of treatment early on in stand development, the current lack of treatment effect observed indicates that microbial biomass may have recovered following the treatments. Moore-Kucera and Dick (2008) found that composition of the microbial community recovered from clear-cutting a Douglas-fir forest after 25 years.

Site difference was highly significant (Table S1) and Pondosa soils contained significantly higher microbial PLFAs for every functional group when compared to Chester soil (Table S2), which parallels the higher plant diversity at Pondosa (Fig. 3). However, significant variation in plant diversity among treatments did not parallel the microbial change within each site, which counters the idea that plant species shapes the structure and functional diversity of microbial communities in forest soils (Fu et al. 2015; Gunina et al. 2017). We speculate that these conflicting results are potentially due to light availability, litter type, or the small plot sizes. One possibility is that microbes have recovered but understory plants have not because of reduced light reaching the soil due to the rapid overstory growth shading the forest floor. Second, because of high tree density and herbicide treatments, the massive amount of litter produced was exclusively pine needles covering the ground and discouraging growth of understory plant species. Last, the relatively small plot size may also allow for microbes to colonize into the vegetation-controlled plots.

Although functional groups did not differ among treatments, community composition ratios show treatment by site effect (Table S1), which is supported by our study because there is significantly more soil OM (doubled) at Chester than at Pondosa (Table 2). While the positive relationships between bacterial communities and pH at Chester were not significant (Fig. 6), bacterial communities tend to do better at higher pH levels (in the soil pH interval 4–7) (Rousk et al. 2010). Therefore, the overall lower bacterial biomass found at Chester makes sense, with Chester being significantly more acidic compared to Pondosa (Table 2 and S2). Additionally, the higher amount of OM further contributes to this result with the negative correlation between pH and OM at Chester (Fig 6). Pondosa shows 84% more bacterial biomass than Chester. Although fungal biomass was also higher at Pondosa, the ratio of fungi over bacteria is higher at Chester, which suggests that this site is more productive. Fungal communities are also generally less influenced by environmental conditions such as pH compared to bacteria (Rousk et al. 2010). Ushio et al. (2013) found that when there was an increase in tannins (extracted from conifer leaves) in a tropical montane forest in Borneo, Malaysia, the fungi-to-bacteria ratio also increased. Some fungi have been found to utilize tannins better than bacteria can (Scalbert 1991), and while this study did not directly measure for tannins, tannin content has been previously measured for ponderosa pine needles having 8.6% (Hernes and Hedges 2004). Therefore, the higher OM content at Chester (resulting from primarily pine needles) could have contributed to this increase in fungi-to-bacteria. Finally, it is

possible that the Chester site having larger trees, with bigger and more active root systems, would require a larger and more active mycorrhizal association (Birch et al. 2023).

The negative relationship between Gram (+/–) ratio and overstory tree BA at Pondosa suggests that plots with lower BA are under certain environmental stressors such as drought, and Gram (+) has ability to form spores capable of surviving in dry conditions (Chodak et al. 2015). However, across the sites, the Gram (+/–) ratio was higher (i.e., either the G (+) bacteria increased, the G (–) bacteria decreased, or both) in non-herbicide treatments at Pondosa and in HF treatments at Chester, indicating that there are some forms of environmental stress that has a greater effect on G (–) bacteria. Gram (–) bacteria have been found to be less resistant to drought and subsequent soil rehydrating stress compared to Gram (+) bacteria (Chodak et al. 2015), which is also reflected in our study. For the other two stress and community activity ratios, substantially higher ratios of the monounsaturated to polyunsaturated fatty acids (mono/poly), along with higher ratio of saturated to unsaturated fatty acids (sat/unsat) ratio at Pondosa indicate less stress than at Chester. Because of trees' high growth rate and intertree competition onset occurring much earlier at Chester, both trees and microbes have experienced a prolonged stress due to conditions such as moisture, pH, or nutrient starvation.

Conclusions

The study demonstrates that early control of competing vegetation and application of fertilizers enhances planted tree growth and plantation development while also reducing understory plant richness, diversity, and cover. This reduction may last a long time, not because of early treatments directly, but due to the treatments promoting rapid overstory crown closure. Rapid crown closure in turn inhibits understory plant emergence and (or) creates increased competition for soil nutrients and water. Similar indirect effects may also occur for soil microbes. To mitigate the negative effect on biodiversity in plantations, foresters can intervene by reducing overstory tree cover with traditional pre-commercial thinning and tending.

Acknowledgements

We acknowledge the late colleague Dr. Robert Powers, who initiated the Garden of Eden experiment, and thank many former and current staff who helped in installing, maintaining, and measuring these plots during the last 35 years. We appreciate the generous support from landowner of Roseburg Resources CO., and Sierra Pacific Industries. We also thank Drew Gilberti for helping measure the latest understory plant species cover and diversity, and Kim Mattson for collecting soil samples. The comments from Drs. Kim Mattson and Brianna Finley, associate editor, and anonymous reviewers for improving the manuscript are greatly appreciated. Use of trade names in this paper does not constitute endorsement by the United States Department of Agriculture Forest Service. The findings and conclusions in this publication are those of the authors and should not be construed to

represent any official USDA or US government determination or policy.

Article information

History dates

Received: 19 April 2023

Accepted: 5 January 2024

Accepted manuscript online: 11 January 2024

Version of record online: 25 March 2024

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Data availability

Data used in this study are available upon prior request by interested parties.

Author information

Author ORCIDs

Jianwei Zhang <https://orcid.org/0000-0003-3492-2356>

Author contributions

Conceptualization: JZ

Data curation: JZ

Formal analysis: JZ

Funding acquisition: JZ

Investigation: JZ, KF

Methodology: JZ

Project administration: JZ

Supervision: JZ

Writing – original draft: JZ

Writing – review & editing: JZ, KF

Competing interests

The authors declare there are no competing interests.

Funding information

The authors declare no specific funding for this work.

Supplementary material

Supplementary data are available with the article at <https://doi.org/10.1139/cjfr-2023-0088>.

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