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Effect of overstorey trees on understorey vegetation in California (USA) ponderosa pine plantations

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Understorey vegetation plays a significant role in the structure and function of forest ecosystems. Controlling understorey vegetation has proven to be an effective tool in increasing tree growth and overstorey development. However, a long-term consequence of the practice on plant diversity is not fully understood. Here, we analysed early development of overstorey and understorey vegetation of four ponderosa pine plantations established decades ago in northern California, USA. These experiments were intended to examine the effect of understorey control on tree growth, including additional effects of tree density or fertilization. Over the years, trees and understorey vegetation were measured repeatedly for height and crown width. We found that responses of understorey vegetation to overstorey varied at different developmental stages. First, understorey cover increased with overstorey cover until it peaked at a certain age or overstorey height and cover, which varied with site quality. Second, herbaceous species reached their peak earlier than shrubs; shrubs subsequently suppressed herbaceous species. Fertilizer effects on plant species diversity were site specific, and density effects were non-significant except at the highest density. These results demonstrate that both fertilization and density manipulation influenced understorey cover and diversity. Such differences are relevant in vegetation management planning efforts.

Introduction

Understorey vegetation plays a significant role in the structure and function of forest ecosystems. Following regeneration harvest or stand-replacing disturbance, understorey shrubs and other species can be more aggressive than tree seedlings in occupying the site (Tappeiner *et al*., 2007; McDonald and Fiddler, 2011). These thickets of plants not only hinder tree regeneration but also become hazardous fuels for wildfires. Controlling understorey vegetation has proven to be an effective tool in plantation establishment by increasing tree growth and accelerating overstorey crown closure (Powers and Reynolds, 1999; Wagner *et al*., 2006; Zhang *et al*., 2013b). However, the practice may alter plant diversity, wildlife habitat and water and nutrient cycling. For example, understorey vegetation, if not controlled, contributes significantly to overall plant diversity in a 60-year-old ponderosa pine plantation (Zhang *et al*., 2013a). Therefore, potential impacts of intensive management practices on plant diversity are a concern (Roberts, 2002). Uresk and Severson (1989) found that ponderosa pine forests provide important habitat for various wildlife species and forage for livestock grazing. Similar results were also found in the Cascades region (Riegel *et al*., 1995) and the southern Rockies (Moore *et al*., 2006). Some understorey species are important sources of nutrition for cattle and deer (Sindel, 1962). In addition, some species can facilitate tree seedling establishment under drought conditions in the first growing season (Keyes and Maguire, 2005). The understorey may also contain a significant fraction of total ecosystem biomass or carbon, especially in a young stand (Campbell *et al*., 2009; Ponder *et al*., 2012) and plays an important role in nutrient (Moore and Allen, 1999) and water cycling (Black and Kelliher, 1989). Therefore, foresters face a great challenge in managing vegetation to balance wood production, fire hazard and other ecosystem services.

While plenty of information is available on the effects of understorey on overstorey growth and development (Wagner *et al*., 2006; Zhang *et al*., 2013b), the effects of overstorey on understorey strata have not been fully explored (Balandier *et al*., 2006). Although some studies have focused on understanding the interactions of overstorey trees and understorey productivity and composition, these studies were conducted either in existing mature plantations and natural stands (Uresk and Severson, 1989; Riegel *et al*., 1995; Battles *et al*., 2001; Zhang *et al*., 2013a) or in very young plantations (McDonald and Fiddler, 2011). Fewer studies have monitored long-term effects of overstorey on understorey composition and species diversity from the seedling stage through overstorey canopy closure, which is crucial for determining the stand developmental processes (Halpern and Lutz, 2013). In this paper, we analysed data collected during the early development of both tree overstorey and understorey vegetation of four ponderosa pine (*Pinus ponderosa* C. Lawson var. *ponderosa*) plantations established decades ago in northern California, USA. These research plots were established originally to determine responses of stand growth and development to understorey vegetation control and also to examine influences of tree stand density or fertilization on those responses. Here, we address questions opposite from the original goals in that we examine how understorey vegetation responded to overstorey dynamics. The two specific objectives are to (1) examine the relationships between understorey vegetation and overstorey trees in the early stand development phase and (2) determine whether and how site quality or stand density affects the relationships. The answers to these questions will help forest managers in planning different vegetation management strategies for different forest stands.

Materials and methods

Two long-term studies were included in the analysis. The 'Garden of Eden' study was established on lands cleared of brushfields or natural forest over a range of site qualities in northern California from 1986 to 1988 (Powers and Ferrell, 1996). Each plot measuring 19.7 × 21.9 m was hand-planted at a standard square spacing of 2.4 m. Following planting, 8 combinations of with and without herbicide, fertilizer and insecticide applications were applied to 24 plots in a completely randomized design. For this analysis, three of eight sites were chosen representing the highest (Feather Falls), intermediate (Whitmore) and lowest (Elkhorn) productivity sites. The location and site characteristics are presented in Table 1. Within each site, we focused only on three control and three fertilized plots where understorey had freely developed. Plots with insecticide application were not considered because plots were thinned at Feather Falls and Whitmore during this period. After installation, trees were measured five or six times during 20 years of stand development. Each tree was measured for diameter (DBH, at 1.37 m height), total height, height to the base of the live crown (defined as having three or more live branches) and crown width at the base of the crown. Understorey vegetation was sampled using a line-intercept method on three parallel 10-m transects. Beginning at the southern end, each plant crown was measured for average height, and the starting-to-stopping distance was recorded along the transect for estimating shrub cover. Species were identified individually for all woody plants including naturally regenerated conifers, and herbaceous species were only grouped as grasses and forbs.

The Challenge Initial Spacing study (ISS) provided a second data set (Table 1). This study was established with planted ponderosa pine seedlings on the west slope of the northern Sierra Nevada in 1966 (Oliver, 1990). The previous stand comprised 70-year-old ponderosa pine and was clear-cut for this experiment. Logging slash was raked, piled and burned. There were two blocks; each block contained five plots that were planted at square spacings of 1.8, 2.7, 3.7, 4.6 and 5.5 m. Each plot was split into two adjacent subplots. On one subplot, understorey vegetation was controlled by hand and/or herbicide for 7 years. On the other subplot, shrubs were allowed to develop naturally, and these were the subplots used in this paper. Each subplot contained 12 measurement trees that were buffered from adjacent plots by at least 7 m, minimally 2 rows of trees. Because the same number of trees was used among plots, subplot size with buffer varied among treatments, covering 0.02 ha for 1.8-m spacing plots to 0.13 ha for 5.5-m spacing plots.

Height and DBH (once tree height reached 1.37 m) were measured every year from 1968 to 1975, every 2 years from 1975 to 1985, and every 4 years from 1985 to 2006. Other measurements included height to live crown and crown width. Woody understorey vegetation was sampled three times in 1976, 1980 and 1986. Circular 0.001-ha plots were established at random locations within the tree measurement plots. The number of shrub sample plots, varying with tree plot size, covered ~22–25 per cent of tree measurement plot areas within each density treatment. Within each plot, shrubs and naturally regenerated tree species were measured for mean maximum crown diameter and mean crown height.

After data were collected, two variables were derived for overstorey trees: (1) canopy cover was calculated by dividing total crown areas of all trees in the plot by plot size and (2) individual tree volume was estimated using Oliver and Powers (1978) for the Garden of Eden trees and using Zhang *et al.* (2006) for trees at Challenge. Plot-level volume was calculated by adding all trees in the plot and converting to volume per hectare. Two variables were also derived to characterize the understorey vegetation. Plant cover was estimated as a percentage of measured intercept length for each plant divided by total transect length at three Garden of Eden sites. In Challenge, individual plant cover was calculated by dividing the total areas calculated from canopy diameter measurement by understorey vegetation plot area. Plant species diversity was calculated by the Shannon–Wiener Index (H′) that weighs both richness and abundance of species (Shannon, 1948).

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

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)

Table 1 Geographic locations and site characteristics of four *Pinus ponderosa* plantations in northern California

	Elkhorn	Whitmore	Feather Falls	Challenge
Latitude (N)	40.0825	40.6259	39.6198	39.4754
Longitude (W)	122.742	121.899	121.197	121.217
Elevation (m)	1545	756	1246	810
Geologic province	Klamath	Cascade	Sierra	Sierra
Site index (m at age 50)	17	23	30	34
Annual mean T_{max} (°C)	16.4	21.4	18.3	20.4
Annual mean T_{min} (°C)	2.4	7.6	5.7	6.3
Annual precipitation (mm)	1015	1140	1780	1730
Parent material	Metasediment	Volcanic	Volcanic	Volcanic
Soil group	Xerochrept	Haplohumult	Haplohumult	Haplohumult
Soil type	Sandy loam	Loam	Loam	Loam
Previous vegetation	Plantation	Brushfield	Natural stand	Natural stand
Year planted	1988	1986	1988	1966

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.

All variables were analysed based on a completely randomized design for the Garden of Eden study and a randomized complete block design for the Challenge ISS, with treatments as the fixed effect and site or block as a random effect and using age as a repeated measure with SAS PROC MIXED (SAS Institute Inc., 2013). An autoregressive model with varying measurement times (i.e. SP(POW)) was used in all models to account for serial correlation resulting from repeated plot measurements over time. All understorey variables were analysed using a covariate derived from overstorey cover such as quadratic or logarithmic form that was chosen by comparing AICc and residuals during model fittings. For each variable that was analysed under the mixed model, residuals were examined to ensure that statistical assumptions of normality and homoscedasticity were met for the data. A square root or a log transformation was applied for those dependent variables when assumptions were not met. Multiple treatment comparison was conducted by the Tukey–Kramer test by controlling for the overall $\alpha = 0.05$ after adjustment for the age covariates. The trends of overstorey tree cover and understorey shrub cover along tree height were fitted with the SAS TRANSREG procedure.

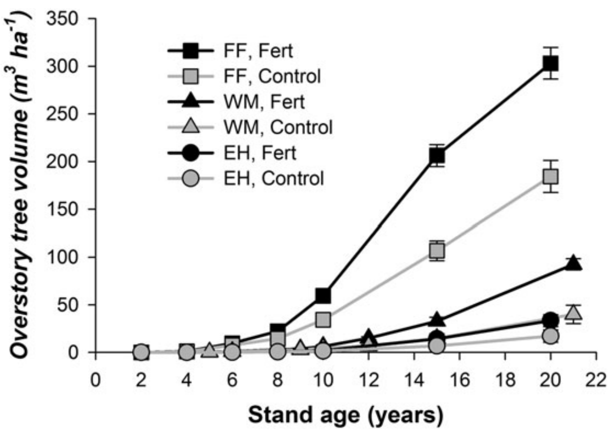

Figure 1 Volume trends for ponderosa pine grown under fertilized and control plots at Elkhorn, Whitmore and Feather Falls Garden of Eden sites in northern California.

Results

Garden of Eden study

To demonstrate differences among site qualities, we included volume trends for planted ponderosa pine trees in fertilized and control plots at the Garden of Eden sites over 20 or 21 years (Figure 1). Volume varied significantly between treatments and among sites (Table 2). Significant age-site-treatment interaction suggests that site and treatment effects changed with stand developmental stages. At the end of 20 or 21 years, fertilization doubled wood production compared with controls for all sites (Figure 1). Site differences in volume were also substantial. Trees at Whitmore (Fert: 92.5, control: 40.1 m^3 ha^{-1}) produced >100 per cent more volume than trees at Elkhorn (Fert: 33.4, control: 17.3 m^3 ha^{-1}). Trees at Feather Falls (Fert: 303.2, control: 184.3 m^3 ha^{-1}) had over an order of magnitude more volume production compared with trees at Elkhorn.

Cover of overstorey trees showed similar results (Table 2). Again, fertilization increased canopy cover; the differences were not significant until the age of 10 at Feather Falls ($P < 0.04$), 15 at Whitmore ($P < 0.021$) and 20 at Elkhorn ($P < 0.05$) and thereafter (Figure 2A–C). The magnitude of site differences in both fertilized treatment and control was not as large as for volume.

Except for shrub cover, age × treatment × site interactions were significant for all measured variables ($P < 0.001$). The interactions between site and treatment were significant for all understorey variables. At the poorest site quality, shrub cover peaked at ~40

Table 2 *P*-values of fixed effects from the best fitting model with a covariate derived from overstorey cover for: understorey cover (%) by strata including naturally regenerated (NR) trees and *Ceanothus prostratus*, and the Shannon–Wiener species diversity index (H′); tree volume production (m^3 ha^{-1}) and overstorey cover were analysed without a covariate; plots are without artificial control of understorey vegetation; treatment consists of fertilization (with *vs* without) at the three Garden of Eden sites and density (5 levels) at the Challenge ISS site in northern California

Site	Variable	Source of Variation							
		Treatment	Site	Treatment × Site	Age	Age × treatment	Age × site	Age × treatment × site	Covariate
Garden of Eden	Volume	0.009	<0.001	0.67	<0.001	<0.001	<0.001	0.026	
	Tree cover	<0.001	<0.001	0.662	<0.001	<0.001	<0.001	<0.001	
	Shrub cover	0.004	0.005	0.037	<0.001	<0.001	<0.001	0.477	0.014[a]
	Herbaceous cover	0.275	<0.001	0.02	<0.001	<0.001	<0.001	<0.001	0.037[b]
	NR tree cover	0.61	0.017	0.003	0.003	0.027	0.016	<0.001	0.001[b]
	Shannon–Wiener H′	0.14	0.016	0.005	<0.001	<0.001	<0.001	0.013	0.001[a]
Challenge ISS	Volume	0.884			<0.001	0.008			
	Tree cover	<0.001			<0.001	0.714			
	Shrub cover	0.001			0.01	0.026			0.732[b]
	NR tree cover	0.146			0.087	0.147			0.116[b]
	C. prostratus	0.209			<0.001	<0.001			0.031[b]
	Shannon–Wiener H′	0.28			0.119	0.841			0.343[a]

[a]Log (overstory cover) as a covariate.
[b](Overstory cover)^2 as a covariate.

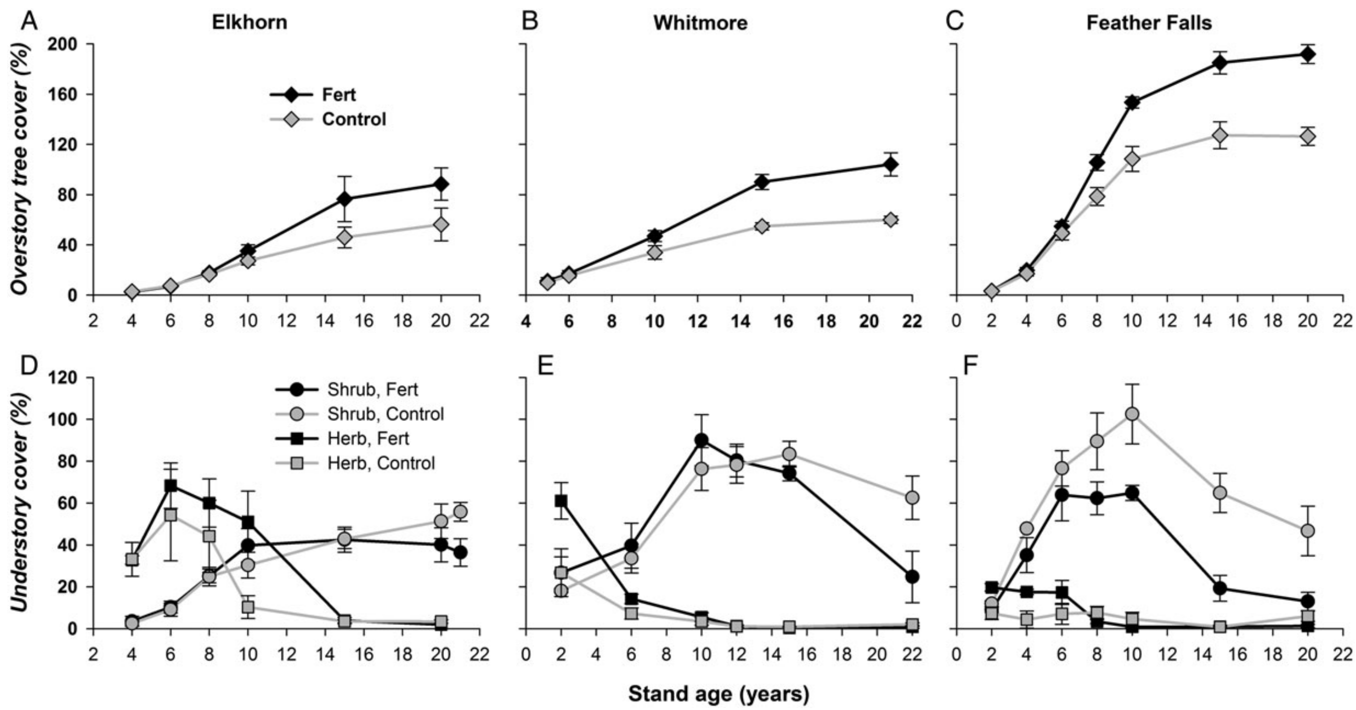

Figure 2 Cover of overstorey planted ponderosa pine trees and understorey shrubs and herbaceous species freely grown on fertilized and control plots at Elkhorn (A and D), Whitmore (B and E) and Feather Falls (C and F) Garden of Eden sites in northern California.

per cent in ∼20 years (Figure 2D). However, at the site with better site quality, shrub cover reached 80–100 per cent within 10 years before decline (Figure 2E and F). Fertilization promoted the development of shrub and herbaceous cover so that understorey cover was higher in the earlier years and lower in the late years than the cover in the unfertilized control, except for the shrub cover at Feather Falls where shrub cover was always lower in the fertilized plots. Herbaceous species reached the maximum cover much earlier than shrubs on all three sites. Fertilization increased herbaceous cover as well as accelerated the development process, resulting in the herbaceous cover reaching peak cover earlier than the shrubs. It appeared that gains in shrub cover significantly affected herbaceous species. All three sites had similar herbaceous cover levels after two decades, regardless of fertilization.

Understorey vegetation cover (shrubs, herbaceous species and natural regeneration) and the Shannon–Wiener H′ were significantly related to overstorey cover ($P < 0.04$) (Table 2). In the earlier years, tree height and shrubs had a linear relationship with time before shrub cover reached its peak (Figure 3). Then, shrub cover rapidly declined. Both the turning point and decreasing slope were site-specific. The turning point was at a tree mean height of ∼4 m at Elkhorn and Whitmore, and ∼5 m at Feather Falls. At these stand heights, both shrub cover and overstorey cover were ∼50 per cent at Elkhorn and 80 per cent at Feather Falls. At Whitmore, shrub cover was 80 per cent whereas overstorey cover was ∼50 per cent.

Understorey species diversity (H′) differed among sites and interacted with fertilization ($P < 0.01$). For example, a significant fertilization effect in H′ was only found at Whitmore, but not at Elkhorn and Feather Falls from the Tukey–Kramer test (Figure 4). An age effect was significant ($P < 0.001$) and so were the interactions among age, treatment, and site ($P \leq 0.013$). Although the fertilizer effect was not statistically significant at Elkhorn, H′ appeared to be higher in fertilized plots than in controls, especially during 10–15 years after planting (Figure 4A). However, the trend was completely reversed at Whitmore where H′ was higher in control than that in fertilized plots (Figure 4B). A crossover pattern was found in H′ at Feather Falls, with H′ being higher before the age of 9 and lower after 9 in fertilized plots *vs* controls (Figure 4C). Understorey species diversity in these plantations ranged from 1.0 to 2.0. In general, the number of herbaceous plants tended to be dominant in the earlier years and the number of woody plants was dominant in the later years (Supplementary data, Table S1). Similar patterns were observed for cover (Figure 2D, E and F). *Ceanothus prostratus*, a N-fixer, occurring frequently at Whitmore, disappeared much more quickly in the fertilized treatment than in control (Supplementary data, Table S1). In addition, a few shade-tolerant species such as *Rubus ursinus*, white fir (*Abies concolor*), incense cedar (*Calocedrus decurrens*) emerged in later years of the study.

Challenge initial spacing study

At Challenge, tree volume did not differ among densities ($P > 0.88$) before 28 years (Table 2, Figure 5A), but the age effect and age by density interactions were significant ($P < 0.01$). The results from multiple comparisons showed that the highest density produced significantly more volume than the two lowest densities starting at age 12. At age 20, stem volume was 66.3, 58.7, 40.6, 23.4 and 29.2 $m^3\ ha^{-1}$ from the highest density to the lowest density plots, respectively.

Planted tree canopy cover differed significantly among densities ($P < 0.01$) and stand ages ($P < 0.01$), but not among interactions

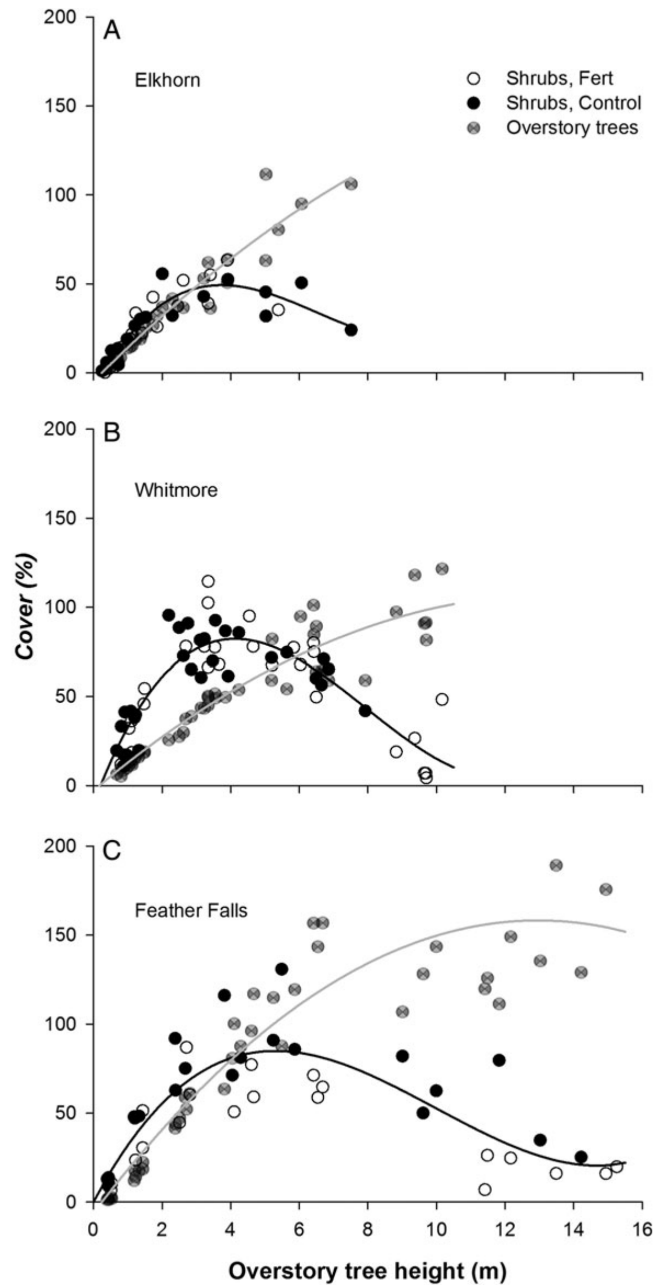

Figure 3 Relationships between shrub cover and overstorey tree height on fertilized and control plots grown on (A) Elkhorn, (B) Whitmore and (C) Feather Falls in northern California. The overstorey tree canopy cover with height was also plotted.

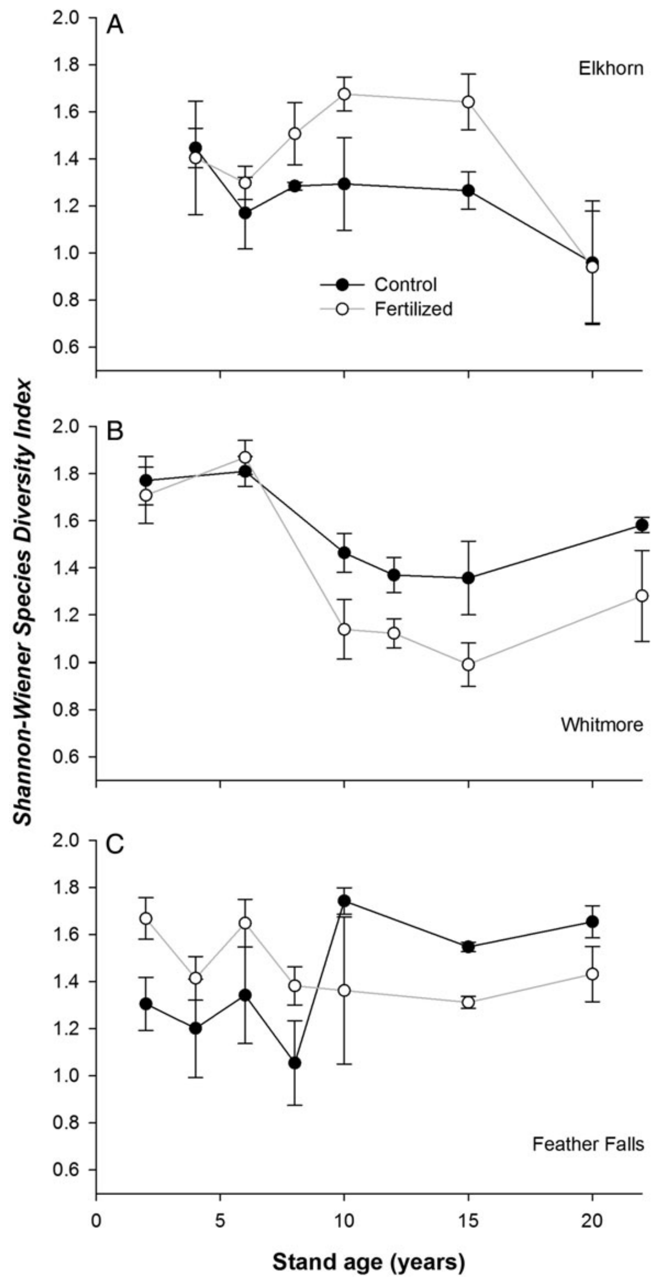

Figure 4 Plant species diversity measured by the Shannon–Wiener Index (H′) for understorey species naturally developed on fertilized and control plots across stand age in three Garden of Eden sites in northern California.

($P > 0.71$) (Table 2). The trends were the same as volume among densities *vs* stand age except for the two highest density plots where canopy cover peaked at age 20–25 (Figure 5B) and began declining from incipient mortality.

Three fixed effects were all significant for shrub cover ($P < 0.03$) although only the age effect and age by density interaction were significant in *C. prostratus* ($P < 0.01$). For non-planted trees, mainly tanoak (*Lithocarpus densiflorus*) and California black oak (*Quercus kelloggii*), cover was not significant among densities and among stand ages ($P < 0.08$). It appeared that shrubs regenerated and grew more in the lower density plots, although shrubs consistently covered more on the 480 stems ha^{-1} plots than the 330 stems ha^{-1} plots and on the 2745 stems ha^{-1} plots than the 1330 stems ha^{-1} plots (Figure 6A). However, *C. prostratus* only occurred on the highest density plots at age 10, and afterward was absent; it covered much more on the intermediate density plots (1330 and 750 stems ha^{-1}) prior to 15 years (Figure 6B).

Understorey woody species diversity was lower in the higher density plots ($2745 < 1330$ stems ha^{-1}). But, it appeared to peak

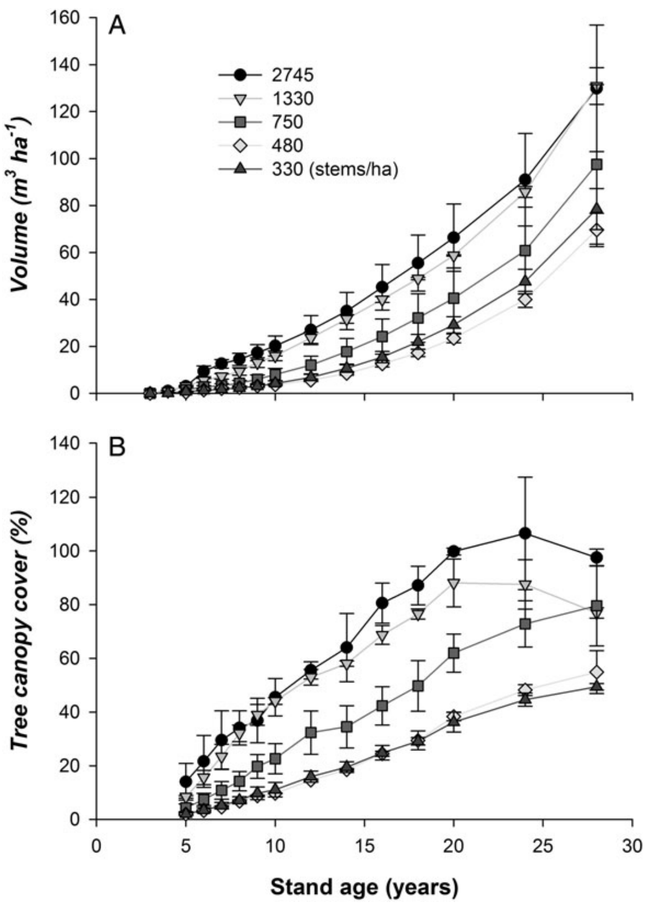

Figure 5 Stem volume (A) and canopy cover (B) of ponderosa pine grown in five stand densities (stems ha^{-1}) over 30 years on the Challenge ISS in northern California.

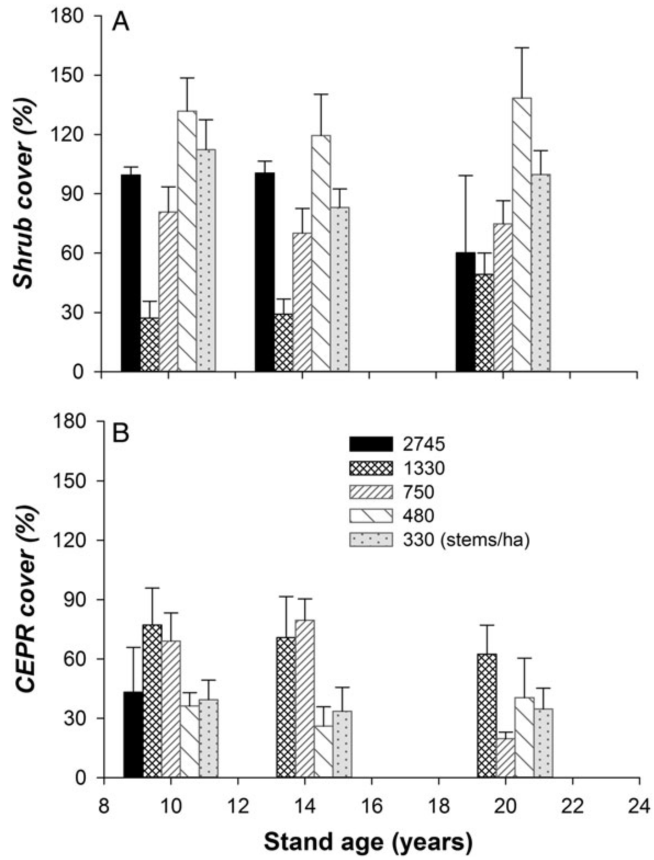

Figure 6 Cover % of (A) shrubs and (B) *Ceanothus prostratus* (CEPR) free-grown in the five stand densities at age 10, 14 and 20 on the Challenge ISS in northern California.

at the middle density plots (750 stems ha^{-1}) or to keep a similar level between 1.5 and 2.0 within the two higher density plots (Figure 7). Nonetheless, the difference in H′ was not significant among densities ($P > 0.28$) (Table 2). Neither were the age and age by density interactions significant ($P > 0.11$).

Overall, there were 18 species occurring at the sites; 90 per cent of total number of individual plants was from seven species. These included two *Arctostaphylos* (*viscida* and *mewukka*), two *Ceanothus* (*integerrimus* and *prostratus*), *Chamaebatia foliolosa*, *Toxicodendron diversilobum* and *Rosa spithanea*. In addition, tanoak emerged only at the age of 20. California black oak had more sprouts at the age of 10 than at the age of 20.

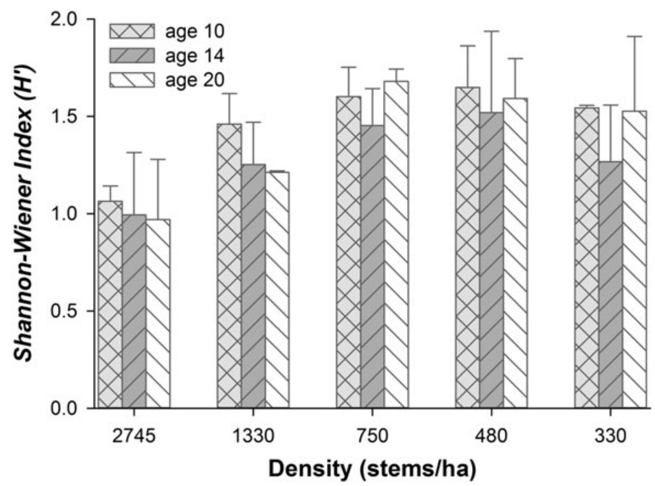

Figure 7 Plant species diversity measured by the Shannon–Wiener Index (H′) for understorey species naturally developed on five stand-density plots at age 10, 14 and 20 years in the Challenge ISS in northern California.

Discussion

Direct evidence of overstorey response to the treatments demonstrated the consistently higher volume and canopy cover in the fertilized plots than that in controls regardless of site quality (Figures 1 and 2A–C), which was the same trend as previously reported (Powers and Ferrell, 1996; Wei *et al*., 2014). Volume did not differ among different densities overall, which differed from the previous report (Oliver, 1990; Zhang *et al*., 2006). The discrepancy was likely caused by analysing only the no-vegetation-control split-plots within only two replications; the variation among trees and between plots tended to be larger in controls *vs* the vegetation-controlled treatment (personal observations). In addition, significant interactions between density and age suggest that difference among densities varied with stand developmental stages. Because fertilization and density manipulation significantly affected overstorey development in ponderosa pine plantations (Zhang *et al*., 2013a), we hypothesized that they would also influence the understorey development and possibly the overstorey–understorey relationships. This hypothesis has been confirmed with the results of this study where there were strong connections between overstorey development and understorey species diversity (Bartels and Chen, 2010), species composition and ground cover in ponderosa pine plantations (Figures 2–5, 6 and 7).

Fertilizer effects

The results from the Garden of Eden sites indicated that the effect of fertilizer on understorey cover was not always significant (Table 2). Yet, fertilizer and age interactions were, suggesting that the fertilizer effect was age specific (Figure 2). Shrub cover was not influenced by fertilization at Elkhorn until the age of 21 (Figure 2D), decreased at Feather Falls across ages (Figure 2F), but increased prior to and decreased after the age of 12 at Whitmore (Figure 2E). Over the 20 years, shrub cover showed a general trend of a bell-shaped curve at Whitmore and Feather Falls (Figure 2E and F). The Elkhorn site appeared to reach an asymptotic level after ~10 years (Figure 2D). Herbaceous species, however, showed a general trend of higher cover in fertilized plots than that in controls in the earlier years except at Elkhorn at the age of 4. Then, cover declined quickly towards a similar cover for both fertilized and control plots (Figure 2D–F). During the same periods, fertilization increased overstorey cover consistently and eventually reached an asymptotic level that varied among the three sites (Figure 2A–C), due to the increased leaf area by fertilization (Powers and Reynolds, 1999).

Lack of a general pattern in shrub cover *vs* stand age might indicate that an inappropriate independent variable (i.e. stand age) was used. After we plotted shrub cover with stand height, the most reliable measurement besides diameter in a typical stand examination, we found that tree height and shrub cover showed a linear relationship before shrub cover reached its peak (Figure 3). The peak point was at tree height of ~4 m at Elkhorn and Whitmore, and >5 m at Feather Falls. At these stand heights, both shrub cover and overstorey cover were ~50 per cent at Elkhorn and 80 per cent at Feather Falls. At Whitmore, shrub cover was 80 per cent whereas overstorey cover was ~50 per cent. The difference in Whitmore might reflect that this plantation was initiated from a pure brushfield (Powers and Ferrell, 1996), which might have a richer shrub seed bank. The results also suggested that the relationships between understorey shrub and overstorey trees cannot be explained by tree height (shade) alone because the turning points differed in overstorey cover among sites. In fact, other mechanisms for overstorey control of understorey productivity include, but are not limited to, direct competition through the accumulation of a dense litter layer (White *et al*., 1991), reduced below-ground resource availability (Uresk and Severson, 1989) and interactions of litter depth, soil nutrient status, light and moisture.

The effect of fertilization on understorey has been previously studied. Agee and Biswell (1970) reported that nitrogen application significantly increased herbaceous biomass production in a second-growth ponderosa pine plantation. Turner (1979) found that in a young Douglas-fir (*Pseudotsuga menziesii*) stand, fertilizer additions increased understorey growth. When trees overgrow the understorey, increased shade effect may lead to larger understorey plants and lower plant diversity. In this study, we found that the Shannon–Wiener index was higher in the fertilized plots at Elkhorn, lower at Whitmore, and from higher to lower along developmental age at Feather Falls (Figure 4). From other ecological studies, fertilization usually reduced plant species diversity (Thomas *et al*., 1999; Bobbink *et al*., 2010). In a comprehensive analysis with herbaceous plant communities from several long-term ecological research sites, Gough *et al*. (2000) found that nitrogen application with 9–13 g m^{-2} year^{-1} increased net primary productivity by ~50 per cent and reduced species density by ~30 per cent over control. Our results suggest that forest plantations showed the similar trends although the magnitude of fertilizer effect depends on site quality and overstorey stand developmental stages.

In the understorey communities' developing years, it appeared that herbaceous species were inhibited by shrubs (DiTomaso *et al*., 1997), which were occurring earlier at more productive sites *vs* the lower quality site (i.e. Feather Falls > Whitmore > Elkhorn in time sequence; Figure 2D–F).

Density effects

Our hypothesis for the Challenge ISS was that shrub cover would be much higher in the lower density plots than in the higher density plots before shrub cover reached its highest peak. The results showed it was not always true, especially in the highest and the lowest density plots (Figure 6). However, because understorey vegetation was not measured until the stand reached 10 years, when the shrub cover with 2.4-m spacing should have already reached the maximum cover, based on Feather Falls Garden of Eden with a similar site index, shrub cover might have passed the peak point in the highest density plots with 1.8-m spacing at the Challenge ISS before it was first measured. Therefore, these results should be used with a caution. Similarly, the lack of differences in species diversity (Table 2 and Figure 7) could have occurred for the same reason. In addition, species diversity is well related to plot size (Stohlgren, 2007). Although ~25 per cent tree plot area was used for sampling understorey species, these plots might be too small to reliably characterize the plant diversity.

Three groups of studies examined the understorey community in ponderosa pine stands. The first groups' objective was to determine the best control of competing understorey vegetation using either existing young plantations or new plantings with a common spacing (from 2 × 2 m to 4 × 4 m) used at the time. If understorey species were monitored, these studies were more interested in the vegetation community development itself and its effect on overstorey growth (Tappeiner *et al*., 2007; McDonald and Fiddler, 2011). The most notable results from these studies were (1) competing vegetation had a significantly negative effect on plantation growth and (2) understorey community was complex in a young conifer plantation and this vegetation would embrace one or more successional pathways of facilitation, tolerance and inhibition (McDonald and Fiddler, 2011). The complexity of the overstorey and understorey relationships is shown in this study.

The second group was aiming to increase forage production under existing mature stands or plantations through density manipulation, i.e. thinning. Mixed results have been reported for responses of understorey cover and abundance to overstorey density in various forest ecosystems (Hughes and Fahey, 1991; Harrington and Edwards, 1999; Ares *et al*., 2009; Cole *et al*., 2010). Some explanations for these results were proposed such as competition for light, water, nutrients or pre-treatment history. In ponderosa pine stands, Moore and Deiter (1992) found a significant negative relationship between stand density index and forage production. This relationship was also reported for aboveground biomass in the Black Hills Level-of-Growing-Stock installations (Uresk and Severson, 1989) and elsewhere in ponderosa pine forests (McConnell and Smith, 1965; Clary and Ffolliott, 1966; Riegel *et al*., 1995; Carr and Krueger, 2011). However, delayed or no response of shrubs to thinning was also found in Washington (McConnell and Smith, 1965) and Oregon (Riegel *et al*., 1995). Unfortunately, herbaceous species were not measured in our Challenge ISS, and therefore it is hard to relate to these findings.

The third group was to study understorey responses to fuel reduction thinning in recent years (Moore *et al*., 2006; Laughlin *et al*., 2008). Some general trends were that overstorey tree density and understorey productivity and diversity were negatively related; the response of the understorey to fuel reduction can take several years to decades before the understorey stabilizes.

Responses of understorey to various densities in young ponderosa pine plantations were also found to be species specific (Folkard *et al*., 2012). We also observed that understorey species changed along years of development. These studies are among the few long-term ones to determine the impacts of planted tree density on understorey plant species diversity in ponderosa pine plantations started from seedlings.

Conclusions

Results indicated that responses of understorey vegetation to overstorey trees varied at different developmental stages. First, understorey cover increased with overstorey cover until it peaked at a certain age or overstorey height and cover, which varied with site quality. Second, herbaceous species reached the peak point earlier than shrubs; shrubs subsequently suppressed herbaceous species. Fertilizer effects on plant species diversity were site specific, but density effects were non-significant except for the highest density. These results demonstrate that both fertilization and density manipulation not only affected the overstorey growth and canopy cover but also influenced understorey cover and diversity. The effects varied with stand age, i.e. stand development. These differences are relevant considerations in vegetation management planning efforts.

Supplementary data

Supplementary data are available at *Forestry* online.

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Conflict of interest statement

None declared.

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