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Long-term effects of silviculture on soil carbon storage: does vegetation control make a difference?

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Forests and the soils beneath them are Earth's largest terrestrial sinks for atmospheric carbon (C) and healthy forests provide a partial check against atmospheric rises in CO_2. Consequently, there is global interest in crediting forest managers who enhance C retention. Interest centres on C acquisition and storage in trees. Less is directed to understorey management practices that affect early forest development. Even less is paid to the largest ecosystem reservoir of all – the mineral soil. Understorey vegetation control is a common management practice to boost stand growth, but the consequence of this on ecosystem C storage is poorly understood. We addressed this by pooling data from five independent groups of long-term studies in the western US. Understorey control increased overstorey biomass universally, but C contents of the forest floor and top 30 cm of mineral soil largely were unaffected. Net soil C increment averaged 1.3 Mg C ha^{-1} $year^{-1}$ in the first decade. We conclude that soil C storage is not affected adversely by vegetation management in forests under a Mediterranean climate. However, understorey shrubs can profoundly affect stand susceptibility to wildfire. We propose that C accounting systems be strengthened by assessing understorey management practices relative to wildfire risk.

Introduction

Forests and forest soils are the primary terrestrial sinks for atmospheric carbon (C) and more than half of ecosystem C commonly occurs in the upper horizons of mineral soil.[1] Because forests store vast amounts of atmospheric C, intensive management has been questioned based on perceptions about carbon budget impacts including losses of C from mineral soil.[2,3] Mineral soil C comes from the decomposition of plant products produced in net primary productivity. While some compounds enter the soil solution as dissolved organic C, the largest share enters through comminution by micro- and mesofaunal shredders that reduce the particle size and increase the surface area of forest floor and root detritus, favouring further processing by fungi and bacteria. In this way, organic C is added to the soil where it resides in varying states of stability.[4] Under a temperate climate, turnover time of C averages from 1–2 years for low-molecular-weight compounds in fresh detritus near the soil surface (a loss of a quarter to two-thirds of the initial organic C) to as much as a millennium for organic matter complexed with mineral matter deeper in the soil profile.[5] Carbon sequestration in soil is a slower and less-visible process than that in vegetation, but this does not diminish its importance nor our need to understand how it is influenced by management.

Vegetation management consistently accelerates overstorey development and early productivity.[6–10] However, most C assessments centre on above-ground dynamics and ignore soil chemical changes. Findings for soil chemical changes[11–13] usually are short term and tend to show early C losses due to soil respiration, followed by gains as perennial vegetation reestablishes.[14] Longer-term studies centre on impacts of overstorey removal. Meta-analyses of published data[15,16] offer general summaries but lack the specificity possible with controlled, long-term experiments. Nave *et al.*[17] concluded that overstorey removal reduced forest floor C mass. But depending on the soil type, declines in mineral soil C usually recovered within 2 decades. Consensus holds that detrimental management impacts are apt to be greatest on soils low in initial C and in low general fertility, particularly in regions where climate accelerates decomposition and soils depend on a steady recruitment of C from plant detritus.[18] However, reports of long-term impacts of understorey vegetation management on soil C are rare.

The question of how management intensity – particularly understorey vegetation control – influences soil C storage is particularly complex and long-term effects have not been broadly addressed. Concerning C budgets, both advocates and critics of active vegetation management often base their arguments on anecdotes, short-term findings and simplistic assumptions. But some field experiments lasting a decade or longer have tackled the issue directly.

Coleman *et al.*,[19] comparing soil beneath short-rotation *Populus* in the US South with that in nearby agricultural fields,

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found no significant differences in C after 10 years due partly to soil variability. In a more controlled experiment, Shan *et al.*[20] summarized soil C findings for three 17-year-old plantations of *Pinus elliottii* Engelm. on poorly drained sites in Florida. They found a significant reduction of 45 Mg C ha^{-1} (32%) in soil where vegetation had been controlled and concluded that total ecosystem productivity and soil C sequestration were lowered when understorey vegetation was excluded, attributing it to reduced detrital inputs from understorey plants. Hoepting *et al.*[21] reported 15-year findings of a gradient of herbaceous management intensities on several conifer plantations in southern Ontario. They concluded that forest floor and soil nutrient pools beneath *Pinus banksiana* Lamb. and *P. resinosa* Ait. were not affected adversely by high-intensity vegetation management, but that forest floor C and nitrogen (N) masses beneath *Pinus strobus* L. and *Picea mariana* (Mill.) BSP were less after 15 years. Differences were attributed to lower growth rates and detritus production in the latter two species. Another controlled experiment[22] reported 35-year effects of repeated understorey removal in an established ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stand in Oregon. Suppressing understorey vegetation increased tree growth but led to lower C and N contents in the forest floor (21 and 36%, respectively) and upper 24 cm of mineral soil (18 and 16% for C and N, respectively). Declines in these properties were attributed to reduced litterfall and fine root production. More recently, McFarlane *et al.*,[23,24] studying 2 decades of repeated vegetation control on three ponderosa pine plantations in California, found that effects varied with site quality. Soil C and N concentrations and absolute quantities in the upper 20 cm increased substantially with site index (SI), but largely were unaffected by vegetation control. However, the nature of soil C was affected. On the poorest site (Elkhorn), the proportion of light fraction (labile) C was slightly but significantly greater where vegetation had been controlled,[24] possibly reflecting more recalcitrant organic C compounds in detritus from the predominant understorey shrub, *Arctostaphylos* sp. (manzanita).[25]

Carbon sequestration phenomena are drawing world attention and – as a simple check of the World Wide Web shows – a new industry of C accounting systems, services and software has been born. Accounting systems, however, are only as good as their fundamental assumptions concerning components and their fate following management. Bird *et al.*[26] point to the relative importance of organic soil C to ecosystem C stock changes and to the variability in international accounting systems in dealing with this. We wish to replace speculation with fact. Here, we report C stored at varying soil depths from five separate data sets of vegetation management experiments on a broad sweep of field sites in California and Oregon, USA. The experiments have lasted a decade or more and focus mainly on plantations of ponderosa pine apt to be managed intensively for wood production. Specifically, we address the issue of whether sustained control of understorey vegetation increases aboveground forest growth at the sacrifice of soil C sequestration.

Methods

Our data are from five groups of field studies spanning three geomorphic provinces, 6° N latitude, and a narrow longitudinal band of only 2.2° (119.5–121.7° W) in California and Oregon (Table 1). They encompass a broad mix of geology and a threefold span in both annual precipitation (610–1900 mm) and SI (13–35 m at 50 years). Four of the five groups are plantations, and all study groups are linked by three common traits: (1) the overstorey species are entirely or predominately Pacific ponderosa pine; (2) each field study involves strong contrasts between understorey vegetation control and no control; (3) treatment responses have been followed for at least a decade. Characteristics of the five groups of long-term field studies follow.

Pringle falls

The study area is located on the Pringle Falls Experimental Forest in central Oregon east of the crest of the volcanic Cascades. Soil is a Xeric Vitricryand derived from dacite pumice. SI is the lowest of any site in this study (SI ~13 m at 50 years). The stand at the start of the

Table 1. Characteristics of the five groups of long-term studies with sustained vegetation control

Study group	No. of sites	Latitude (deg.)	Elev. (m)	Geomorphic provenance (geology)	Ann. ppt (mm)	Site index (m)	Stand age at treatment (years)	Period of observation (years)
Pringle Falls	1	43.7N	1340	Cascades (volcanic)	610	13	55	35
Mt. Shasta	1	41.3N	1269	Cascades (volcanic)	940	18	5	34
Garden of Eden	3	39.6N–40.6N	730–1490	Cascades (volcanic) Sierra Nevada (metavolcanic) Coast Ranges (metasediment)	1015–1780	17–35	1	19–20
Challenge	1	39.5N	810	Sierra Nevada (metavolcanic)	1730	34	1	28
LTSP	12	37.2N–40.7N	790–1959	Cascades (volcanic) Sierra Nevada (granitic, metavolcanic)	670–1900	15–30	1	10

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experiment consisted of 40- to 70-year-old ponderosa pine saplings released by harvesting an overstorey of old-growth pine, leaving a stocking density of ~17 284 stems ha^{-1}. Annual precipitation of 610 mm $year^{-1}$ falls mainly as snow in October through April, and the droughty, cool climate is described best as continental. Thirty 0.08-ha plots were established in 1958 and thinned to six replications of five approximate tree spacings: 2.0, 2.8, 4.0, 5.7 and 8.0 m (2469-154 stems ha^{-1}) arranged in a completely randomized design. Three replications were chosen randomly from each of the five spacings for vegetation control, and all understorey vegetation was removed in 1959 both manually and with 2,4,5-T herbicide. Understorey control was repeated at 3- to 4-year intervals thereafter using combinations of 2,4-D herbicide and manual removal methods. Details and growth responses were reported by Busse *et al*.[22]

Diameters and heights of all trees were measured periodically from 1959 through 1994 for all stocking levels and vegetation control treatments. In summer 1994, forest floor samples were collected at 10 random locations per plot using a 10-cm diameter corer and composited for laboratory analyses. Mineral soil samples were taken from the 0–4, 4–8, 8–12 and 12–24 cm depths at an intensity of 20 samples per plot (256 samples ha^{-1}) and composited by depth for each plot. Samples were analysed for organic C and other properties.[22]

Mt Shasta

Possibly the first plantation experiment in western North America involving strong vegetation control was established by McDonald in 1962 on a single site near the city of Mt Shasta in northern California.[27] The site is on the western flank of the Cascades and the soil is a Vitrandic Xeropsamments developed on glaciofluvial deposits from igneous rock. Climate is predominately Mediterranean, but the site occupies an ecotone between the warm Sacramento valley to the south and the drier, cooler continental climate to the north in the rain shadow of the Cascades. The site probably had been timbered into the late 19th century, but lumbering and wildfires led to a dense, tall brushfield of *Arcostaphylos*, *Ceanothus* and *Prunus* sp. that persisted through 1960. The following year, some 12 ha were cleared by bulldozer with both brush and topsoil pushed into windrows, creating scalped bays of ~30 m width. The area was planted the following spring with ponderosa pine at a spacing of 2.4 by 3.0 m. During 1962, 0.07-ha plots were established and a pioneering series of herbicide trials were applied through 1964 to regenerating shrubs.[28]

Shrubs reinvaded these plots at densities varying with the effectiveness of the herbicide treatments. In 1966, the plots were revisited and classified into four conditions of shrub cover (none, light, moderate and heavy) and both tree heights and diameters and shrub heights and cover were measured regularly in the fall of 1992.[27] SI was estimated at 18 m. Nine years later, the site was revisited. Most of the treatment replicates had been destroyed because the land managers had masticated the shrubs, thinned the trees and used a bulldozer to spread the previously windrowed topsoil back onto the plots. However, we relocated two adjacent treatment plots originally classified as 'none' and 'moderate' shrub densities which had not been disturbed. All trees were remeasured and mineral soil was collected by volumetric sampler at 10-cm intervals to a depth of 30 cm on these paired plots. Ten samples were taken randomly per plot (143 ha^{-1}) and composited by depth for chemical analysis. At four random locations, forest floor was sampled using a 0.25-m^2 frame and composited for laboratory analyses. Details are reported in McDonald and Powers.[29]

Garden of Eden

Eight research plantations were established between 1986 and 1988 in the Cascades, Sierra Nevada and Coast Ranges of northern California where the dominant climate is Mediterranean. The objective was to determine ponderosa pine response to repeated combinations of insect, soil fertility and understorey competition control. Genetically superior pine families were planted at a 2.4 m spacing. Eight factorial combinations of treatments were replicated three times per plantation to 0.04-ha plots in a completely randomized design.[30] Growth measurements of trees, understorey vegetation and foliar chemistry were made at 2-year intervals and reported through year 10.[8]

Three plantations spanning a broad range of site qualities were selected for a more detailed study. In ascending order of site quality, these are Elkhorn (SI 17 m, loamy-skeletal Typic Dystroxerepts from metasedimentary rocks) in the eastern slope of the Coast Range, Whitmore (SI 23 m, Xeric Haplohumults) on a volcanic mudflow in the southern Cascades and Feather (SI 35 m, fine-loamy Ultic Haploxeralfs) on metamorphosed basalt in the northern Sierra Nevada. Following the 2005 growing season when the three plantations were 19, 20 and 19 years old, respectively, forest floor was collected at five locations per plot using a 0.25-m^2 sampling frame and composited for laboratory analysis. Mineral soils were sampled with a coring device to a depth of 1 m and composited by depth increments. The sampling intensity varied with soil depth: 12 sampling points $plot^{-1}$ for the first 15 cm, 8 $plot^{-1}$ for the next 15, cm, and 3 $plot^{-1}$ for all depths thereafter (300, 200 and 75 ha^{-1}, respectively). Details and soil chemistry findings are described by McFarlane *et al*.[23] Tree and shrub dimensions also were measured and biomass was determined by destructive sampling.

Challenge

In 1966, a research plantation was established at Challenge Experimental Forest on the western slope of the Sierra Nevada with the purpose of testing how initial tree spacing and competition from understorey vegetation affect stand development.[31] The site is characterized by a Mediterranean climate and mild growing conditions. The soil is deep and derived from metamorphosed basalt (mesic Xeric Haplohumults). SI is high (34 m). An overstorey of 90-year-old mixed conifers was clearcut, slash was removed and ponderosa pine from local seeds were planted at five spacings varying between 1.8 and 5.5 m. Each spacing plot was split and understorey shrubs were killed by sprays of 2,4,5-T herbicide through years 2 and 4 on one split and allowed to develop naturally on the other. Thereafter, woody shrubs on the treated split were removed manually. Split plot size varied by spacing and ranged between 0.045 ha at the narrowest tree spacing and 0.146 ha at the widest. Each spacing treatment was assigned randomly and arranged in two blocks. Tree measurements were recorded periodically and growth results were published.[31]

Following the 28th year, two replicates each of three spacing treatments – the narrowest (1.8 m), intermediate (3.7 m) and widest (5.5 m) – were chosen for a more detailed study. Forest floor samples were collected at five random locations per plot using a 0.25-m^2 frame and composited for laboratory analyses. Mineral soil cores were taken from the 0–10 and 10–20 cm depths and 10 samples per treatment plot (68–222 ha^{-1}) were composited by depth for the shrubs present and shrubs absent split plots. Standard tree dimensions (height, diameter, crown dimensions by sector) were measured as well on all trees.

Long-term soil productivity

The long-term soil productivity (LTSP) experiment was chartered in 1989 to determine how pulse changes in site organic matter, soil porosity and understorey diversity might affect the long-term net primary productivity of forests.[32] Beginning in 1991 and continuing for 7 years, 12 installations were established on harvested mixed-conifer sites spanning 3.5° of latitude in California's Sierra Nevada and Cascade mountains. Treatments involved three levels of surface organic matter removal/retention

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crossed with three levels of soil compaction in a completely randomized design. Plots were planted at a 2.4 m spacing with equal numbers of ponderosa pine, *Abies concolor* (Gord. & Glend., Lindl. ex. Hildebr.), *Pinus lambertiana* (Dougl.) and either *Pseudotsuga menziesii* (Mirb., Franco) or *Sequoiadendron giganteum* (Lindl.) Buchholz), depending on the approximate natural southern extension of *P. menziesii* and the northern extension of *S. giganteum*. Each 0.4-ha treatment plot was split and competing vegetation was controlled with herbicides on one half and left to develop on the other. Details and descriptions of the broad array of soil types are found in Powers.[32]

Vegetation was measured at 5-year intervals and living understorey vegetation was clipped at ground line from four random 3.5 m^2 subplots per treatment plot at year 10 and transported to the PSW lab in Redding, CA, US, for drying and weighing. On some of the sites at year 20, forest floor was collected with a 0.25-m^2 frame and composited for laboratory analyses. Soil cores were drawn from the 0–10, 10–20 and 20–30 cm depths at the start of the study and at year 10 on plots with and without continuous vegetation control. Sampling intensity was 10 cores per split plot (50 ha^{-1}) and samples were composited by depth. Lab data from three of the lowest site qualities were not available at the time of this writing.

Biomass estimation

Trees were measured through complete inventories taken at the time of soil sampling. Whole-tree biomass was estimated by an equation developed specifically for ponderosa pine plantations.[33] On the LTSP plots, understorey vegetation was clipped on fixed-area subplots and air-dried over the summer at the PSW lab in Redding, CA, US. Air-dry weights of the whole field samples were determined on a platform scale and processed through a commercial chipper. Processed chips were collected, mixed thoroughly and a subsample taken and weighed immediately, then dried at 70°C for a minimum of 3 days to a constant weight. Field biomass was estimated by applying the ratio of oven-dry weight to air-dry weights of subsamples and multiplying by the fresh weight of whole samples. Results were expanded to mass per hectare. Forest floor collections were oven-dried, weighed, and expanded to mass per hectare.

Laboratory analyses

Soils were treated by a similar protocol, with some variation depending on the principal investigator (each group of studies was conducted at varying times and by several investigators as described in the original publications). Regardless of nuances in technique, all samples from a given study group were processed similarly at each collection date. Each composited volumetric sample by depth zone was oven-dried at 105°C for at least 24 h and sieved to pass a particle size of 2 mm or less (the fine fraction). Sieved samples were weighed and converted to fine fraction bulk densities by dividing oven-dry weight by the total volume of the composited sample and expressed as mass m^2 by 10-cm depth increment. Subsamples were analysed for organic C and other elements by dry combustion at >1300°C and carbon, nitrogen, and sulfur (CNS) elemental analyses.[34] Two study groups, Pringle Falls and the Garden of Eden, had not been sampled at discrete 10-cm depth increments, so C masses were interpolated by plotting depth trends for those sites. The Challenge study group had only been sampled to 20 cm. Masses of C m^{-2} by depth increment were expanded to Mg ha^{-1}.

Statistical analyses

The five study groups in Table 1 could be seen as analogous to blocks in a randomized block experiment comparing two treatments: the presence or absence of an understorey of competing vegetation with varying numbers of observations among blocks. A randomized block analysis of variance was applied to test the hypothesis that responses of either biomass or soil C were not affected by sustained control of understorey vegetation. The dataset also conforms to 24 paired observations when all the combinations of the study group, site and spacing are considered individually. A paired *t*-test is a more effective means of detecting smaller real differences between treatments whenever the variance between experimental units (study groups) is greater than the variance between treatments paired by field sites. Therefore, a pair-wise Student's *t* approach was applied to all 24 field plot pairs to test the hypothesis. Differences were considered statistically significant if α probability in a two-tailed test was 0.05 or less. Significant trends in soil C were analysed by regression and analysis of covariance against hypothesized slopes and intercepts. Methods followed principles described by Sokal and Rohlf.[35]

Results

Vegetation control effects on standing biomass

On average, sustained control of understorey vegetation nearly doubled standing tree biomass at the time of soil sampling ($P = 0.03$). The effect was proportionally less for the older, natural stand at Pringle Falls than for younger, planted stands of the other study groups (Tables 2 and 3). Variability within a study group measured by coefficient of variation ranged from a low of 9% for Challenge to 89% for the Garden of Eden group (the single replication surviving at Mt Shasta precludes any

Table 2. Mean standing biomass (and % coefficient of variation) for the overstorey trees and forest floor by study group at the time that soil samples were taken

Study group (Block)	Field plots (reps)	Stand age (y)	Biomass (Mg ha^{-1}) above-ground when understorey is				$P > t$
			Present		Absent		
			Trees	Forest floor	Trees	Forest floor	
Pringle Falls	5	90	53.4 (42.3)	24.7 (26.1)	69.0 (28.8)	19.4 (25.6)	0.05
Mt Shasta	1	39	10.0 (–)	34.0 (–)	85.0 (–)	30.0 (–)	–
Garden of Eden	3	19–20	69.6 (88.6)	16.9 (57.1)	116.5 (40.4)	18.1 (37.6)	0.07
Challenge	3	28	82.6 (15.5)	17.9 (8.0)	120.3 (9.1)	15.1 (13.8)	0.05
LTSP	12	10	10.7 (62.3)	11.9 (17.5)	21.2 (52.5)	10.5 (12.8)	<0.01

Exception: LTSP forest floor data based on 3 of 12 reps at year 20. P = probability of chance differences in tree biomass.

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estimate of treatment variation). In general, forest floor mass increased with years since treatment, although the trend was confounded by site quality differences among study groups (Tables 1 and 2). Forest floor mass averaged 15% greater on plots with an understorey ($P = 0.03$) and in two cases, equalled or exceeded the biomass in standing trees (Table 2).

Randomized block analysis of variance by study group also revealed a strong block effect ($P = 0.04$), which is not surprising considering that each study group (block) differed greatly in SI, soil type, stocking density and years since treatment. Applying a *t*-test to paired stand data shows that biomass response to sustained control of understorey vegetation was consistent and highly significant among all 24 field sites (Figure 1, $P < 0.01$). Increases due to vegetation control averaged 22.1 Mg ha^{-1} among the 24 field pairs, but varied between 2.5 and 75.0 Mg ha^{-1} (Table 3). Mean annual increments (MAI) in biomass were only 0.44 Mg ha^{-1} year^{-1} at Pringle Falls, but 2.21 Mg ha^{-1} year^{-1} at Mt Shasta, second in MAI only to the Garden of Eden plantations.

Assuming that approximately half of biomass is C, sustained vegetation control produced an average of ~10 Mg C ha^{-1} in overstorey trees for the 24 field sites in our dataset, and that is where many studies stop. This is short-sided from the aspect of C budgets because it centres simplistically on trees as a single component of a forest ecosystem. Appreciable biomass also occurs in understorey vegetation when it is not controlled silviculturally. Analysis of all living vegetation on the 12 field sites in the LTSP study group indicates that at the decadal mark, the biomass in understorey vegetation usually exceeds that in overstorey trees, regardless of treatment (Figure 2). Combined, understorey and overstorey biomass at 10 years more than doubled than that of trees free of understorey competition.

Vegetation control effects on soil carbon

Randomized block analysis of variance of C storage in the upper 30 cm of mineral soil revealed no significant effect of vegetation control among study groups ($F < 0.01$), although the block effect

Table 3. Stand biomass response to vegetation control by study group

Study group	Site index (m)	Age treated (years)	Observation period (years)	Difference in tree biomass owing to understorey control			
				Mean (Mg ha^{-1})	Gain (%)	Range (Mg ha^{-1})	MAI (Mg ha^{-1} year^{-1})
Pringle Falls	13	55	35	15.6	37	3.6–37.3	0.44
Mt Shasta	18	5	34	75.0	750	75.0	2.21
Garden of Eden	17–35	1	19–20	46.9	126	24.2–69.2	2.43
Challenge	34	1	28	37.6	48	19.4–47.9	1.34
LTSP	15–30	1	10	10.4	109	2.5–24.3	1.04

All treatment plots responded positively to vegetation control, but the magnitude of response varied by site quality and period of observation.

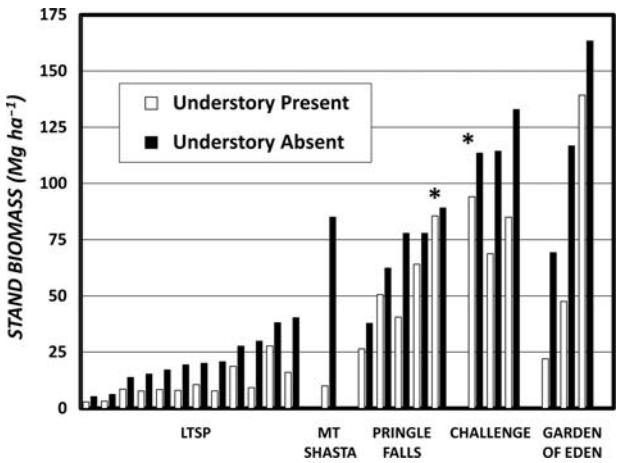

Figure 1 Above-ground biomass for stands at the 24 field sites in our five study groups at the time of soil sampling. Stand biomass was doubled on average when understorey vegetation was absent. Pringle Falls and Challenge Study Groups represent replicated spacing trials. Asterisks indicate stands at unusually narrow spacings.

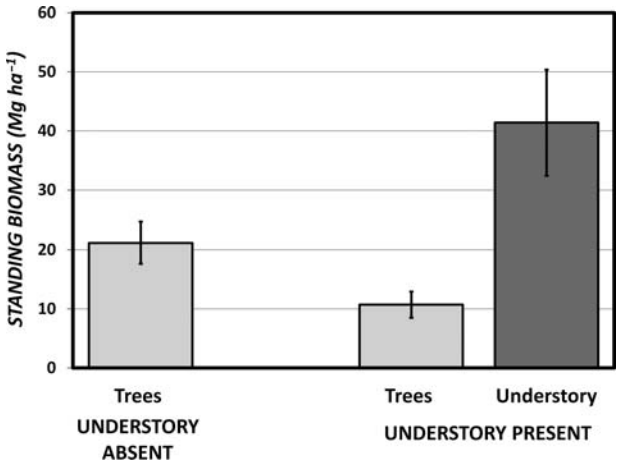

Figure 2 Means and standard errors in standing biomass for 12 LTSP sites at a plantation age of 10 years. Standing biomass was doubled in trees when understorey vegetation was absent. The total ecosystem biomass was 2.5 times greater when tree biomass and understorey biomass were combined on understorey present plots. On average, this amounts to ~25 Mg C ha^{-1} in standing vegetation.

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was highly significant ($P < 0.01$) with the lowest storage at Pringle Falls and the greatest in the LTSP dataset. However, inherent site differences among the five study groups could mask significant treatment differences within each group – particularly differences with soil depth. We addressed this by studying soil C trends by depth increments for each study group (Figure 3). Results describe a typical inverse J-shaped trend with absolute quantities greatest near the surface, reflecting inputs from surface litter and comminution by soil fauna and from fine root turnover.

Variation in soil C storage by depth was low within three of the five study groups, but the Garden of Eden and LTSP groups showed high variability. Unlike the Pringle Falls and Challenge groups which had multiple silvicultural treatments all on the same two sites, the Garden of Eden and LTSP groups include by design a broad array of distinct sites across a vast geographic region. Therefore, treatments among all sites are better examined as individual paired plots. Figure 4 depicts soil C storage by depth zone for the 21 field sites with laboratory soil data. The diagonal slope bisecting the figures represents the 1:1 trend if there are no differences in soil C storage due to vegetation control.

Figure 4 shows the clustering of similar values for the Pringle Falls and Challenge sites where all stocking treatments were within close proximity. The greater spread in values for the Garden of Eden and LTSP field sites indicates the geographic separation of each field site within a study group and the differences in site properties among them. Trends clearly were linear.

$$\text{C mass}_a = 1.125\ \text{C mass}_p - 4.561, \quad r^2 = 0.93$$

Where subscripts a and p represent C mass in the 0–10 cm zone with understorey absent or present, respectively.

Covariance analysis indicates that this equation did not differ appreciably from a hypothetical slope of 1.00 ($P = 0.10$). However, the intercept of −4.561 did differ significantly from zero ($P = 0.05$). Although soil C averaged 0.92 Mg ha^{-1} higher

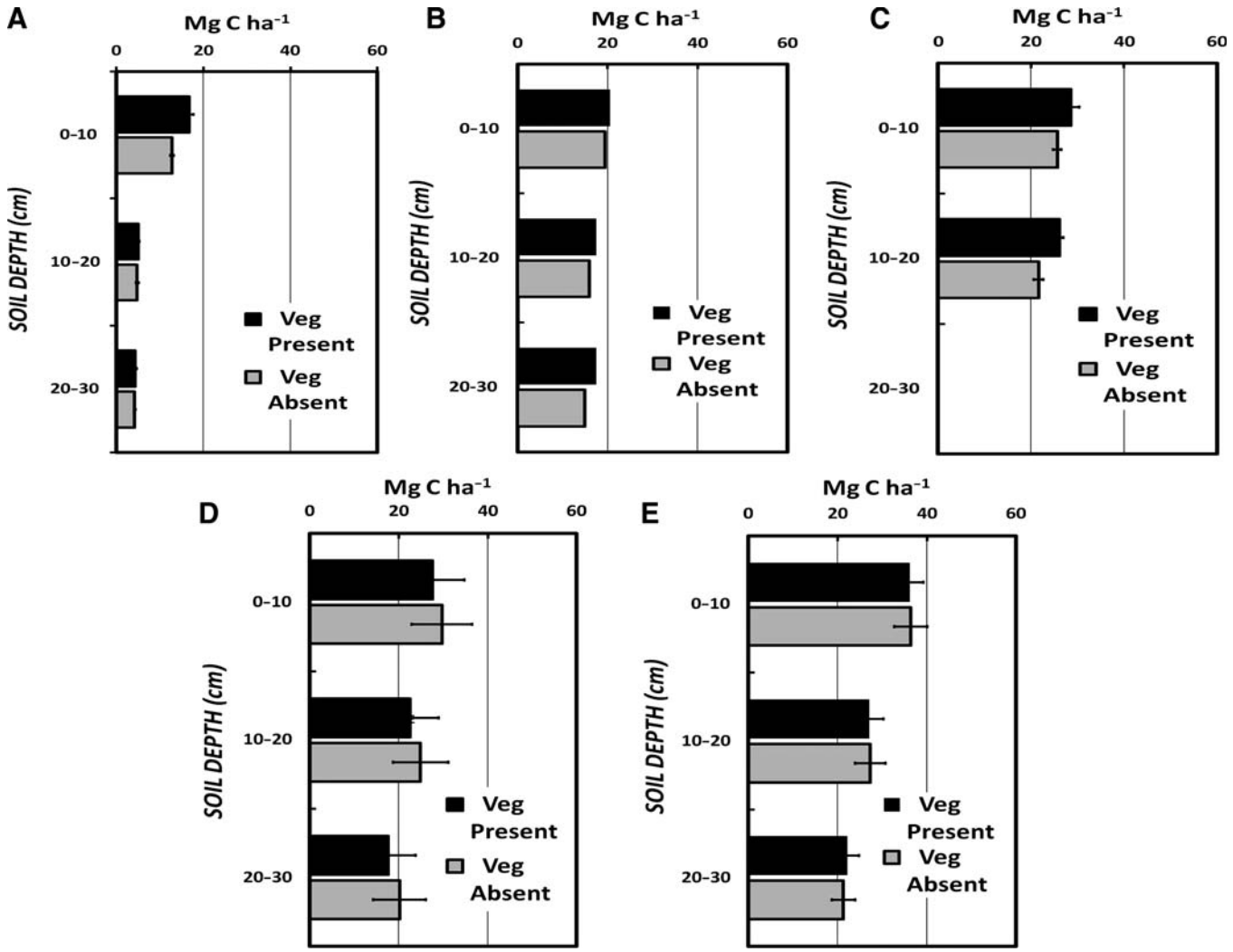

Figure 3 Effect of the presence or absence of understorey vegetation on soil carbon storage in the upper 30 cm of mineral soil averaged by study group. (A) Pringle Falls after 35 years; (B) Mt Shasta after 34 years; (C) Challenge after 28 years; (D) Garden of Eden after 19–20 years; (E) LTSP after 10 years. Bars = standard error.

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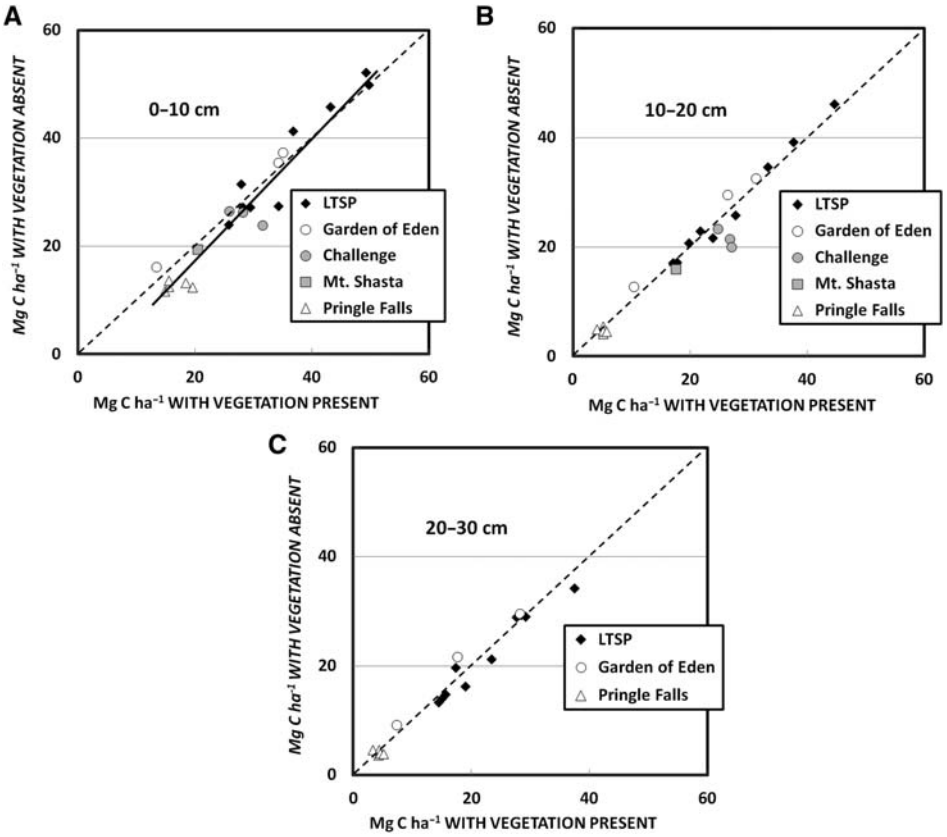

Figure 4 Effect of the presence or absence of understorey vegetation on soil carbon storage in the upper 30 cm of mineral soil by individual field site in the five study groups. Dashed line indicates 1:1 trend. (A) Surface 10 cm; (B) 10–20 cm; (C) 20–30 cm. Solid line on (A) represents linear regression fit.

overall in the 0–10 cm zone where understorey vegetation was present, differences were not statistically significant ($P = 0.22$).

Figure 4 suggests that soil C storage may have been lowered by vegetation control on soils with <37 Mg C ha^{-1}, but the effect was confined to the surface 10 cm. To test the generality of this, we examined an independent validation dataset from four dissimilar sites in the Canadian and US LTSP network where soil C was measured a decade or more after treatment. Ontario, Canada data represent site replicates in two *Pinus banksiana* plantations sampled at 15 years (P.W. Hazlett and R.L. Fleming, unpublished data). Climate is boreal moist and soils are Humo-Ferric Podzols and Dystric Brunisols derived from glacial outwash. Idaho data are from a 10-year-old mixed-conifer plantation on an Andic Fragiudalf at the Priest River Experimental Forest (D. Page-Dumroese, unpublished data) where the climate is cool, temperate moist. Soil data from Missouri (F. Ponder Jr, unpublished data) were collected from 15-year-old plantations of *Pinus echinata* Mill. growing on a Typic Paleudult formed from dolomitic chert where the climate is warm, temperate moist. 'Louisiana' averages 10-year data from seven LTSP sites planted with *Pinus taeda* L. in Louisiana and Mississippi (D.A. Scott, unpublished data). The climate is subtropical moist and soils mainly are Paleudalfs, Paleudults and Dystraquerts derived from marine sediments. More details of these independent sites are in Powers.[32] Figure 5 shows the validation dataset superimposed on the full set of soil C pairs from Figure 4.

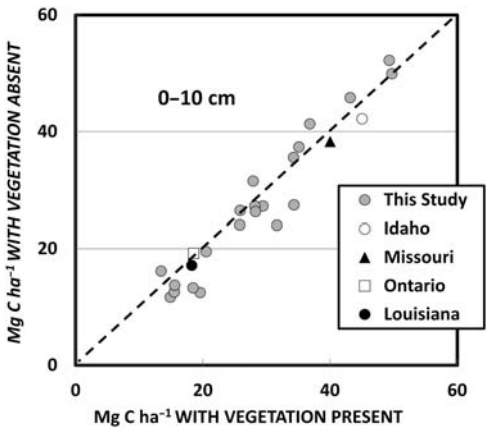

Figure 5 Comparing soil carbon storage trends from California and Oregon sites at 0–10 cm with those from four independent installations in the LTSP network in the US and Canada. Dashed line indicates 1:1 trend.

Again, the trend for the validation data was strongly linear ($r^2 = 0.99$) and conformed closely to the trend in our current study. Differences between the two datasets are not statistically significant.

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Table 4. Means and standard errors for 10-year increments in soil C on eight LTSP field sites with both pre- and post-treatment sampling data

Soil depth (cm)	Initial C (Mg ha^{-1})	Increment (Mg C ha^{-1}) when understorey is		Difference (Mg C ha^{-1})	Probability of chance differences
		Present	Absent		
0–10	31.0±2.5	5.3±1.2	6.5±1.7	1.2±0.9	0.249 ns
10–20	23.6±2.6	3.8±1.3	4.4±1.5	0.6±0.4	0.241 ns
20–30	19.5±1.9	3.0±1.2	2.4±1.2	−0.6±0.6	0.306 ns

Inconsistent discrepancies between treatments may partly be due to slight initial differences in soil C between treatment plots. Homann *et al.*[36] found that the precision in detecting changes in soil chemical properties could be improved by considering the variation in starting values. Most of the experiments in our five study groups were not aimed specifically at soil issues and initial soil samples unfortunately were not taken. However, eight of the field sites in our LTSP study group did have both initial and 10-year soil data, affording a means for estimating net C increment (Table 4). Net changes were positive and declined with depth, averaging 5.9 Mg C ha^{-1} in the 0–10 cm zone ($P=0.01$), 4.1 Mg C ha^{-1} at 10–20 cm ($P=0.03$) and 2.7 Mg C ha^{-1} at the 20–30 cm zone ($P=0.07$). Incremental differences in soil C from the presence or absence of understorey vegetation were not statistically significant for any depth ($P=0.24$–0.31; Table 4).

Discussion

Understorey influence on ecosystem components

Our five study groups showed consistent positive response to understorey control, with biomass gains ranging between 0.44 and 2.43 Mg ha^{-1} year^{-1} (Table 3). This range spans post-treatment observation periods from 10 to 35 years. Other factors being equal, gains due to vegetation control should diminish with time as tree canopies close and suppress the undergrowth, occurring sooner on better sites than on poorer sites. But variation in biomass response also reflects site quality differences and stand condition differences at the time of treatment. Pringle Falls and Challenge study groups contrasted strongly in site quality, but both showed proportionally less response to vegetation control than sites in the other groups (Table 3). Three explanations are likely. First, site quality at Challenge is very high. Even with dense understorey vegetation, trees dominated the site rapidly despite an understorey so that competitive effects were lessened.[31] Second, silvicultural treatments at Pringle Falls and Challenge included plots at very high stocking densities where understorey vegetation was diminished simply because of overstorey cover. Third, the natural stand at Pringle Falls already was 55 years old and trees were in a dominant position when vegetation control treatments were applied. The importance of stand condition at the time of treatment is particularly evident when Pringle Falls is compared with Mt Shasta. Although similar both in site quality and in post-treatment response period, they contrast strikingly in both suppressive effects of understorey (Table 2) and in response to vegetation control (Table 3). At Mt Shasta (and all other study groups), planted trees were affected by shrub competition essentially from the time of planting. Similar effects to those at Mt Shasta were noted at Elkhorn[23] and other droughty, low productivity sites in California.[10] Lacking vegetation control on poorer, droughty sites, plantations may lag decades before trees assume dominance.

That sustained control of understorey vegetation enhanced above-ground tree productivity is not unusual. Consistent growth responses are common beyond this study, although the usual response measure is bole volume or basal area,[7,9,37,38] rather than whole-tree biomass. Responses reflect a shift in soil resources to trees. The effect is proportionally greatest in the early stages of stand development before overstorey canopies have closed to extinguish the understorey.[38] Consequently, differences are greatest in very young stands in the crown-building stage, on poor sites (because soil resources are scarce and it takes longer to attain canopy closure) and at low stocking densities (because overstorey canopies can be open). Indeed, Figure 1 indicates only marginal differences in understorey effects on growth at the narrowest tree spacings (2.0 m at Pringle Falls, 1.8 m at Challenge). Upon release by thinning or overstorey removal, older, densely stocked stands such as those at Pringle Falls must adjust to release by building leaf area before a sizable bolewood response appears. Trees already stressed by low site quality as at Mt Shasta and Elkhorn fall further behind when moisture and nutrient stress is compounded by understorey competition. Such trees may never dominate the site. Forest floor mass averaged 15% greater where understorey vegetation was present, but only those of the Challenge study group differed at a near-significant level of probability ($P=0.09$). Forest floors comprised a surprisingly high proportion of above-ground mass (19–77%) where understorey was present, compared with where it was not (11–33%). Such effects occurred only where understorey shrubs had suppressed tree growth early and substantively as at Elkhorn and Mt Shasta (Table 3).

Influence on carbon retention

What are the implications of this for C sequestration? Seldom do we consider the biomass that may persist for an extended period in understorey vegetation (Figure 2). This is particularly significant when the understorey consists of woody shrubs or trees as was the case at our study sites. At Challenge, the understorey was a tall, sprouting community of *Arbutus*, *Quercus* and *Lithocarpus* trees and *Arctostaphylos* and *Ceanothus* shrubs. Elsewhere, woody communities of *Arctostaphylos*, *Ceanothus*, *Prunus* and *Purshia* shrubs dominated. Assuming that half of biomass is C, twice as much (~10 Mg C ha^{-1}) is sequestered above-ground in trees free of understorey vegetation than in those competing with an understorey on the average LTSP site in the first decade (Figure 2). But more than twice as much C is stored in vegetation when the understorey is included in the budget analysis (Figure 2), and the effect can persist for decades on poor site qualities.[29,38] This sizable and persistent difference would seem to be a source of detritus to fuel the forest floor and soil C pools. However, Tables 2 and 4 show that

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understorey vegetation had a meagre effect on the forest floor or mineral soil. This paradox may be explained by the biochemical nature of understorey detritus and the dominant effect of a Mediterranean climate on microbial decomposition. Quideau *et al.*[25] found that surface detritus of manzanita (predominant on all of our sites) decomposes very slowly due to its peculiar organic C composition, and the organic compounds that do transfer to mineral soil may be more resistant to decomposition than that of broadleaves or pine. In their California study of litter decomposition using mesh bags, Hart *et al.*[39] found that decomposition rates of ponderosa pine needles were among the lowest reported for any temperate and boreal forest and attributed this largely to constraints of moisture and temperature. Slow decomposition rates point to a steady buildup of forest floors beneath young pine forests in California until inputs are balanced at some point by microbial respiration or removed by fire.

Understorey vegetation and forest floors are relatively ephemeral in fire-prone regions, and neither draws much interest in C accounting systems. However, woody shrubs are not necessarily benign concerning C sequestration. Shrub competition for soil resources reduces tree growth, keeping crowns short and in contact with fuel ladders for extended periods. Detritus from understorey shrubs supplement a forest floor mass that ignites quickly. This can extend ground fire upwards to dry shrubs and into the low crowns of drought-stressed trees. To test the generality and consequences of this, Zhang *et al.*[33] applied popular fire simulation models to stand data from several pine plantations in California. Where understorey vegetation had been controlled, tree mortality from simulated wildfire varied between 13 and 42% (less for older stands, greater for younger). Where understorey shrubs were present, mortality varied between 78 and 100%. A consequence of stand-replacing wildfire is substantive C loss from the ecosystem that may take a half-century to rebuild.[40]

Why soil C was unaffected

Given the relative mass of understorey vegetation (Figure 2), the absence of a consistent effect on soil C in Figure 4 seems counterintuitive. Why is this not reflected in greater quantities of C in surface horizons where an understorey is present? We offer four possible explanations.

(1) Our sample size is inadequate to detect significant changes.
(2) Not enough time has passed for changes to appear.
(3) Detritus from understorey decomposition truly has no appreciable effect on soil C in a Mediterranean climate.
(4) The increment due to understorey is small, relative to the mass of C already present in the soil.

Explanation 1 refers to the inherent variability in soil properties on a particular treatment plot or among plots, and it i's possible that our sampling intensity was not sufficient to detect sizable differences between treatments. Absolute C content is a function of both soil C concentration and fine-fraction bulk density. Page-Dumroese *et al.*[41] addressed the spatial variability in soil bulk density within plots treated alike, finding it greatest in the top 10 cm. On average, between 43 and 83 soil samples ha^{-1} would estimate the plot mean within $\pm$15% with 90% confidence on soils receiving moderate machine traffic. Sanchez *et al.*,[11] examining C contents of the upper 10 cm in Louisiana, concluded that 28 soil samples ha^{-1} could estimate the plot mean within 5% at 95% confidence. For our study groups, plot sampling intensity varied from a low of 50 samples ha^{-1} (LTSP) to a high of 300 ha^{-1} (Garden of Eden). Therefore, we believe that plot means were characterized adequately.

If plot means are accurate, the question expands to whether sufficient paired samples were drawn to distinguish meaningful differences between vegetation management treatments. In addressing this, we calculated the number of paired samples (n) needed to test whether a difference of 1 Mg C ha^{-1} (the average difference observed for all of our sample sites) is a real measure of the treatment effect using the following formula:

$$n = \frac{t^2 s_d^2}{D^2}$$

where t is the t-table value for $\alpha = 0.05$ and 20 degrees of freedom, s_d^2 the variance of individual paired sample differences and D the true difference we wish to detect (1 Mg C ha^{-1}).

Results indicate that testing the hypothesis that a difference of 1 Mg C ha^{-1} is not due to chance with 95% confidence requires fewer than 10 paired samples. Because our sample size of 21 exceeds that, we reject Explanation 1. Sampling deficiencies cannot account for the lack of a significant understorey treatment effect on soil C storage.

We also reject Explanation 2. Except for the youngest sites (LTSP), 11 of our field sites had two or more decades to adjust to the presence or absence of understorey vegetation. Further, the potential influence of an understorey on soil C will be limited to the period of its presence as either a growing or senescing community. The better the site quality or the narrower the spacing of trees, the more rapid the canopy closure of the overstorey and the briefer the period of understorey inputs to the soil. Busse *et al.*[22] showed that understorey cover can persist for at least 35 years when trees are spaced widely, but understorey shrubs senesce rapidly when stocking densities are high. The third explanation seems plausible for surface detritus which, in our case, consists mainly of materials from sclerophyllous, drought-adapted vegetation such as manzanita that may be resistant to decay. McFarlane *et al.*,[23] studying the same Garden of Eden plantations as included here, reported greater forest floor mass and C content where vegetation had been controlled, but this held for only the poorest site quality (Elkhorn, $P = 0.04$) where trees were definitely stunted and no differences were found on the better sites. Understorey presence produces a more diversified litter of course, and theoretically, this might hasten decomposition, reducing the mass of the forest floor. In their leaf litter decomposition studies in the Mediterranean region of Spain, Moro and Domingo[42] concluded that leaves of an N-fixing shrub decomposed at five times the rate of needles of pine. And Quideau *et al.*[25] suggest that manzanita litter resists microbial decay due to its biochemical composition.

The presence or absence of understorey vegetation also would affect soil microbial conditions. Wang *et al.*,[43] working with a mixed species plantation in the subtropical monsoon region of southern China, concluded that understorey removal altered organic C inputs, soil temperature and soil moisture sufficiently that heterotrophic soil respiration was reduced by half. For our Pringle Falls site, consistently higher microbial biomass

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was found throughout the year where a light understorey that included N-fixing shrubs and herbaceous vegetation was present,[22] although the differences were confined to the upper 4 cm of mineral soil. In their more recent studies of LTSP sites in California and subtropical North Carolina and Louisiana, Busse *et al*.[44] found that vegetation control had a greater and more consistent impact on soil microbial biomass, activity and community structure than either soil compaction or organic matter removal. All microbial measures were heightened by the presence of understorey, although differences were smaller and less consistent in California than in the subtropical sites. Lesser effects in California were attributed to shrub communities with lower growth rates and more recalcitrant detritus, compared with predominantly herbaceous communities in North Carolina and Louisiana. In contrast, Slesak *et al*.[13] reported results for two *Pseudotsuga menziesii* plantations in a moderately high rainfall region of Oregon and Washington, but found no differences in potential microbial respiration between understorey treatments. They concluded that any additional inputs of detrital C from the presence of an understorey were rapidly consumed in place and respired as CO_2.

We believe that pine sites under California's Mediterranean climate fare similarly to those studied by Slesak *et al*.,[13] but possibly for different reasons. In an altitudinal gradient study of N mineralization in northern California, Powers[45] found that decomposition and mineralization were hindered by cold winter temperatures and by dry conditions in the summer – both precluding long periods of heightened microbial activity. Active mineralization was confined to a brief period in the spring. Thus, it seems likely that C in surface detritus respires quickly as CO_2 during brief periods (melting snow cover, autumn rains) when conditions favour decomposition.

Compared with litter of broadleaves such as *Quercus*, forest floors beneath pines decompose slowly in a summer-dry climate. Consequently, C incorporation into the surface mineral soil is comparatively slow.[46,47] We argue that in forests influenced by a Mediterranean climate, mineral soil C originates more from fine root turnover than the incorporation of surface detritus. If fine roots are the main progenitors of soil C, one would expect appreciably greater fine root production when an understorey is present. Clearly, this was the case on the poorly drained soils in the Florida study.[20] Yet, McFarlane *et al*.,[23] studying living fine roots on our three Garden of Eden plantations, found no significant difference in the total biomass of fine roots when all species were combined, regardless of understorey presence ($P = 0.46–0.85$) and no differences were found in soil C concentrations even after nearly 2 decades.[24] We hypothesize that in regions where soil drought is common, soil volumes are fully exploited by fine roots after a decade or more, regardless of whether they are roots of pines or shrubs. Climatic conditions in winter and spring that do favour decomposition of the forest floor likely lead to CO_2 efflux through microbial respiration.

The two groups with appreciably greater masses of soil C where an understorey was present (Pringle Falls and Challenge; Figure 3) may reflect the nature of the understorey. Two of the three persistent shrubs at Pringle Falls were N-fixing species[22] and it is feasible that their N-rich senescing roots might hasten the decomposition of organic C to a small particulate level that persists in the soil.[48] At Challenge, the understorey was far more massive than for any other study group, producing a nearly impenetrable jungle. Conceivably, the sheer mass of detritus from an extraordinarily massive understorey could account for the differences apparent for Challenge in Figure 4. Thus, we reject Explanation 3 with two caveats: that the phenomenon is confined to near-surface conditions and that it depends on the mass and biochemical nature of understorey detritus.

Explanation 4 has some validity. Regardless of subsequent treatment, all forest soils contain sizable reserves of C at the start of a study period. Worldwide soil profile assessments[49] show that warm, coniferous forest soils of temperate North America average 186 Mg C ha^{-1} to a depth of 1 m. Based on McFarlane' *et al*.'s[23] findings from the Garden of Eden sites, a mean of 62% (67 Mg C ha^{-1}) is in the top 30 cm of mineral soil. Thus, any net increment to soil C from detritus over several decades could be small, relative to the amount already present.

Homann *et al*.[36] pointed out that variability in initial soil contents among plots at a location can mask subsequent treatment effects if incremental changes are small and that soil chemical changes due to treatments can be assayed more effectively if starting values are known. Unfortunately, starting values of soil C were not taken for many of the study sites in our dataset because the experiments were not established to test soil changes. But we did have starting soil data for eight of our LTSP sites. There, 10-year gains in soil C in the top 10 cm averaged 17–21% where understorey vegetation was present or absent, respectively. Differences between vegetation control treatments were not statistically significant ($P = 0.25$; Table 4), but increments are sizable relative to the initial mass of soil C. From this, we conclude that there was positive net increment averaging 5.9 Mg C ha^{-1} in the top 10 cm (12.7 Mg C ha^{-1} $decade^{-1}$ in the top 30), but that sustained vegetation management did not affect this.

One problem with assessing whether vegetation management has an influence on soil C is that net gains in fine-fraction C are due only partly to inputs from a developing stand. Sanchez *et al*.[11] reported significant gains in the upper 30 cm in the first year following harvesting on an herbicided North Carolina site and showed that gains increased through 5 years even where all surface organic matter had been removed. They attributed gains to natural densification of mineral soils in a subtropical climate following harvest, to root exudates from the new stand and to decomposition of root systems left from the previous stand. The latter phenomenon probably occurs commonly and may persist for at least a decade.[50] Therefore, not all soil C increments in the fine fraction can be attributed to detritus from regrowth following harvest. Some undoubtedly traces to the decomposition of coarse organic residues of the previous stand that now are fine enough to pass a 2 mm sieve for subsequent detection. From this, we agree that net increments in soil C may be small, relative to the mass of C present at the start of treatment, but our results suggest that they can be sizable too. Accordingly, we reject the explanation that changes in this study were too small to detect.

Conclusions

Despite vast differences in total above-ground biomass in the early stages of stand development, sustained control of understorey vegetation had no clearly detrimental long-term effect

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on soil C storage beyond the upper 10 cm under temperate western conditions. Sampling intensities and procedures reported here for estimating plot means are sufficient to detect meaningful differences among treatments, but more precise assessments are possible if researchers account for plot differences in soil C at the start of the experiment and if they are aware of the contribution of residual detritus as it decays from coarse- to fine-fraction soil C. From a soil C sequestration perspective, understorey management has negligible impact once trees dominate the site.

However, indirect effects may be severe because vegetation management decisions may affect the fate of sequestered ecosystem C in respect to wildfire. Simulation models suggest that retaining a shrub understorey increases the risk of stand-replacing wildfire in young stands prone to drought and with it, the loss of site C to combustion. Such losses far outweigh any short-term gains in ecosystem C through understorey retention. We conclude that sustained control of understorey vegetation has no detrimental effect on long-term C sequestration or forest productivity. Our findings have implications to C accounting systems that overemphasize the value of shrub understories and ignore belowground C storage and the risk of C losses to wildfire.

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Conflict of interest statement

We report no conflict of interest. Mention of any herbicide types are for information purposes, only.

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