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Forests in the northern Sierra Nevada of California, USA, store large amounts of carbon in different patterns

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Abstract. To better understand forest carbon (C) storage patterns, C budgets were constructed and contrasted among four stands of different vegetation, elevation, and disturbance histories from the northern Sierra Nevada of California, USA. The True-fir stand, considered to be undisturbed and at a higher elevation (1820 m), stored substantially more C than the three stands at lower elevation (1360–1430 m) and that had sustained various levels of disturbance. The Mixed Conifer stand was minimally disturbed by thinning 27 yr ago. The Oak stand was moderately disturbed by two fires in the past 17 yr. The Pine Plantation stand was considered the most disturbed having been cleared and subjected to site preparation and windrowing 50 yr ago and thinned again 17 yr ago. Total C mass to a 30 cm soil depth (Mg C/ha) was True-fir 531, Mixed Conifer 317, Oak 310, and Pine Plantation 253. Adding in soil C to 1 m depth increased total C mass to 595, 349, 404, and 345, respectively. True-fir had significantly larger C mass than the other three stands in nearly all pools measured. The three low-elevation stands, while similar to each other in total C, stored C differently in patterns that reflected their disturbance histories. Oak and Pine Plantation were very similar in detrital C stores, whereas Mixed Conifer had at least twice the C mass in both the forest floor and woody debris pools. Mixed Conifer had higher concentrations of soil C but had very low soil C mass due to considerably lower fine-soil bulk densities and higher rock contents. C pools in the forest floor and soil showed observable patterns over distances of 10–100 m that paralleled the patterns of C in the live vegetation. Total C in True-fir was equal to the large masses of old-growth conifer forests of the U.S. Pacific Northwest and likely represents a high-equilibrium level of C storage for forests of this region. The three low-elevation stands represent typical forests in various states of recovery from disturbance that are in C accumulating stages.

Key words: carbon budget; detrital carbon; disturbance; forest; mixed conifer; roots; soil carbon; soil pits; woody debris.

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Introduction

Forests store considerable amounts of carbon (C) and are important in the global carbon balance. Calls are being made for forests to be managed for C storage (Bellassen and Luyssaert 2014) as a means to slow the rise of atmospheric CO_2 (Hall et al. 1975, Keeling 2008) and mitigate climate change. The California cap-and-trade program (CARB 2015) accepts forest projects in the United States to sell additional C as offsets to California industries as a way to meet their legislated caps of CO_2 emissions. The Clean Development Mechanism allows C offsets from new forest projects in developing countries to be used for developed countries to help meet their C emission commitments via the Kyoto Protocol (Iversen 2016).

C budgeting is a way to quantify how forests store and release C. C budgeting has been classed as either process-level or regional/empirical (Heath and Joyce 1997). Process-level techniques involve field measures of pools such as biomass or soil and processes such as photosynthesis or respiration. Forest process-level C budgets were first initiated by the International Biological Programme in the 1960s (Kira and Shidei 1967, Whittaker and Woodwell 1969, Whittaker et al. 1974, Harris et al. 1975). These studies were recognized for their value in describing forest behavior, and C budgeting continues up to the present day (Grier and Logan 1977, Kinerson et al. 1977, Harmon et al. 2004, Fahey et al. 2005, Giasson et al. 2013). The regional or empirical approach builds upon the process-level studies and is a calculation or summation process that relies on disparate data sets, such as forest inventories, soils, and land classes combined with general relationships (e.g., wood to carbon ratios) to extrapolate C contents to regions (Delcourt and Harris 1980, Homman et al. 2005, Potter 2010), countries (Birdsey and Heath 1995, Turner et al. 1995, Kurz et al. 2009), and the globe (Houghton 1996, 2003). Computer models of C behavior can also be classed as either process-level or empirical. Computer models developed from process-level budgeting include models of C for individual trees (Agren et al. 1980), specific stands (Sollins et al. 1976, McMurtrie and Wolf 1983, Cropper and Ewel 1984), and general models (Parton et al. 1988, Running and Coughlan 1988). Most of the regional estimates rely on empirical models to make their calculations.

Recent studies suggest that forests may be more important as storage mechanisms or sinks of C than originally thought (Pan et al. 2011). Global carbon budgeting efforts have recently re-evaluated the terrestrial land sink to be 3 Pg C/yr (Le Quéré et al. 2015), which is equal to approximately half the anthropogenic C inputs to the atmosphere. Eddy covariance studies have provided direct evidence that most forests are sinks for atmospheric CO_2 (Luyssaert et al. 2007). These two findings by themselves do not explain how C is being stored in forests and this raises the interest in process-level studies. However, internal or process-level C budgets for specific forest sites are still relatively rare where all pools are measured (Pregitzer and Euskirchen 2004), partly because of the labor and expense involved, and the lack of standardized measurement methods of detrital pools. Most site-specific C budgets have focused on a single stand or site. C budgets using multiple stands are more informative and have been used with as chronosequence studies (Gholz and Fisher 1982, Law et al. 2003), across watersheds (Fahey et al. 2005), in elevation transects (Moser et al. 2011), and in comparison of sites recovering from fires (Powers et al. 2013).

We chose four forest stands in the northern Sierra Nevada Range of California to develop carbon budgets based on detailed site measures. The stands are from the same geographic region but have different stand disturbance histories and vegetation types. Use of multiple stands in a single project avoids the problems that arise by comparing results from studies that used different methods (Yanai et al. 2003). To reduce sampling error and examine spatial patterns, we sampled detrital pools using three points in each of 12 plots per stand. We excavated the topsoil using small pits as an attempt to homogenize microscale soil variation. This budgeting effort is part of an ongoing project where the pools and measured fluxes between pools will parameterize a bookkeeping model of C dynamics. The Mixed Conifer (MC) stand had at least two thinning harvests and represents the common forest and disturbance type in this region. The True-fir (TF) stand is the stand type that transitions from mixed conifer forests at higher elevations, and this stand has had minimal disturbance. The Oak (OK) stand at the same elevation as MC has been maintained by fire. The Pine Plantation (PP) stand was also at the same elevation and had been clear-cut and debris and topsoil piled into windrows as a site preparation step before planting to pine followed by the common practice of stand thinning.

We expected the aboveground C in the four stands to vary in C stores from highest to lowest as TF > MC > OK > PP. This pattern was based on the conceptual models (Chapin et al. 2002, Luo and Weng 2011) where stands are thought to slowly accumulate C via internal processes until a disturbance causes C to be lost or

internal processes disrupted. We expected the different pools to be affected in varying ways as described by Luo and Weng (2011). In general, it has been shown that the live vegetation increases with stand age (Shugart 1984, Hudiburg et al. 2009, Gray and Whittier 2014, Zald et al. 2016) as does detrital and total C (Pregitzer and Euskirchen 2004). We considered time since disturbance combined with the level of disturbance would be the largest control on C stores. TF had the longest time since disturbance and at a higher elevation was also expected to have lower rates of decomposition and greater detrital C stores (Fahey et al. 2005, Moser et al. 2011). MC had the next longest time since disturbance and the thinning operations appeared to have been moderate. The thinning would have mostly removed live vegetation with less physical disturbance to the detrital pools and may even have caused increases in woody debris from the operations. OK had two fires in the past 17 yr and likely other fires before that. The canopy did not appear to have been highly disturbed by the recent fires but the surficial detrital pools were partially consumed. PP had been thinned moderately 17 yr ago. PP also was the most disturbed by the forest clearing and site preparation and associated disturbance to the forest floor and topsoil in the mid-1960s or about 50 yr ago.

We focused on the detrital pools particularly soil C as this has been thought to deviate most strongly from steady state as affected by the legacies of past events (Chapin et al. 2002) and its behavior is less clear that live vegetation as shown in empirical studies. Conceptually, large-scale detrital C accumulations appear to be related to climate (Schlesinger 1977, Meetemeyer et al. 1982, Burke et al. 1989) and this may lead to the expectation of a general equilibrium level of detrital C stores among the stands since they are within 10 km of each other. Studies show that detrital C can be highly variable over distances as short as 1–2 m (Gilmore and Rolfe 1980, McNabb et al. 1986, Hammer et al. 1987, Muukkonen et al. 2009). Soil C does not correlate well with stand productivity (Peterson and Lajtha 2013) or to multiple years of experimental carbon inputs (Lajtha et al. 2014). Finally, soil C has been suggested to be immune to harvest disturbance (Johnson and Curtis 2001) or from carbon inputs from woody debris (Johnson and Todd 1998). Given these different findings in light of its important role, we were interested in detrital C behavior.

Site description

The study stands were located in the Lassen National Forest in the northern Sierra Nevada. Here, the Sierra Nevada transitions to the Cascade Range and is a 100 km wide uplift of partially melted magma that ranges from 1200- to 2000-m elevation with peaks to 2400 m (Fig. 1). There are scattered wet meadows and wetlands, but the landscape is composed mostly of moderate to deep valleys carved by smaller streams and rivers that drain to the Sacramento Valley to the west. The climate is Mediterranean with hot, dry summers and cold, wet winters. Annual average temperature is 8.2°C. Daily maximum temperatures in August average 29°C; daily minimum temperatures in January average −7°C; and annual precipitation is 870 mm, with approximately 85% occurring between November and April with much of it as snow (from Chester, California, long-term weather records). The 2016 climate data from nearby Humbug Summit at 2040-m elevation had similar January temperatures and slightly higher precipitation than the Chester long-term means; Humbug summit had a 10°C lower temperature in August averaging 19°C and lower annual temperature of 6.7°C.

Stand types and disturbance histories

Four contrasting forest stands were chosen as representative forest types of this region (Table 1, Fig. 2). The True-fir (TF) stand was considered to undisturbed forest; past harvests in the TF area may have been selective logging of large sugar pine in the 1940s and a sanitation sale in the 1970s (L. Corral, *personal communication*). However, no cut stumps or skid trails were observed in the stand. Aerial photographs from 1967 showed some nearby areas of open canopies with shrub vegetation that appeared to be fire effects. However, the TF stand itself appeared to have escaped these disturbances as indicated by the closed canopy forest shown in 1967. If fire had occurred in TF, we thought it to have been over 100 yr ago, as we observed no fire scars on stems.

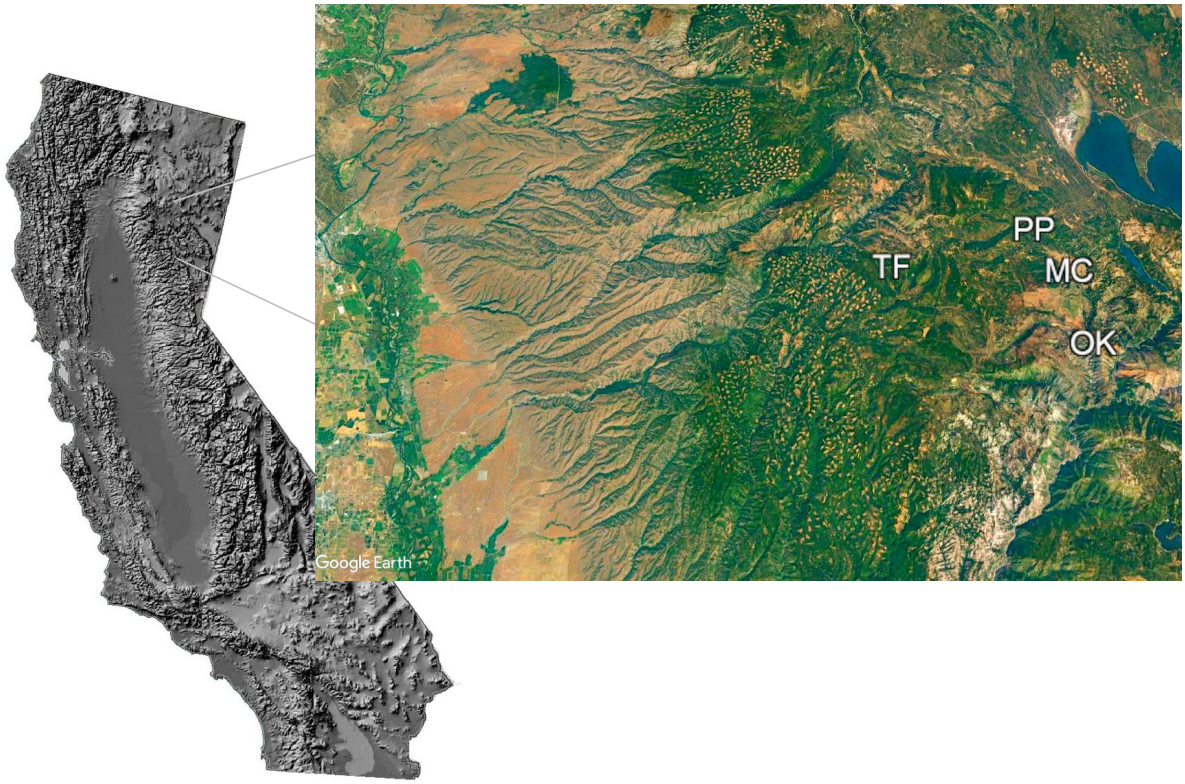

Fig. 1. Project location in the northern Sierra Nevada Range of California, USA, on left. Google Earth image on right shows the stand locations in the mixed conifer forests visible as the green at elevations above 1000 m. The burn scar to the south of the stands is from the Storrie and Chips Fire (from Google Earth version 7.3.2.5776, 10 May 2019, 40° 07′ 30″ N, 121° 17′ 00″ W; image date 30 December 2016).

The Mixed Conifer (MC) stand was minimally disturbed being thinned from below, removing a selection of the smaller stems (<48 cm diameter) in 1990 as a stand-improvement project. Cut stumps were evident from this harvest and large, old stumps were present that indicated earlier, undocumented harvest entries. We had no descriptions or evidence of recent fires in MC, and the last fire was likely more than 50 yr ago and perhaps more than 100 yr ago.

The Oak stand (OK) was a mix of California black oak (*Quercus kellogii*) and conifers typical of the mixed conifer forest. The Oak stand was considered to be moderately disturbed as conifers were prevented from encroaching and overtopping the oak by fires. Many of the oak were multiple stems and appeared to be even-aged, where regeneration was via stump sprouting following what was likely a stand-regenerating fire over 50 yr ago. There were signs of charring from the recent Chips Fire of 2012 on live and dead stems and open gaps in the canopy. The Storrie Fire of 2000 is also thought to have burned through this stand at a low intensity that left the larger stems intact.

The Pine Plantation (PP) stand was considered to be the most disturbed, being established following forest clearing and had woody debris and topsoil piled into windrows before planting to evenly spaced pines in the mid-1960s. The original forest was likely mixed conifer that was clear-cut and harvested some years earlier. Pine Plantation had been thinned about the year 2000 to favor other species and to achieve 6 × 6 m stem spacing.

Methods

Field procedures

Rectangular grids were established in each stand defining at least 24 plots. Plots were 65 m

Table 1. Four forest stands used for carbon budgets in the northern Sierra Nevada of California.

Stand and soil depth	Elev (m)	Stem basal area† (m^2/ha)	Canopy closure (%)	Fine-soil bulk density (Mg/m^3)	Rock content‡ (m^3/m^3)	Soil % C	Disturbance history
Mixed conifer	1430	50	70				Stems thinned in 1990 (27 yr ago) and selective logging harvests prior to that
0–10 cm				0.42	0.21	7.4	
10–20 cm				0.56	0.23	4.2	
20–30 cm				0.61	0.25	3.3	
Oak	1360	49	69				Lightly scorched by Chips Fire in 2012 (5 yr ago) and by Storrie Fire in 2000 (17 yr ago)
0–10 cm				0.53	0.12	6.4	
10–20 cm				0.70	0.16	3.4	
20–30 cm				0.75	0.15	3.3	
Pine Plantation	1420	48	70				Clear-cut, site prepped, and planted to pine about 1964 (53 yr ago). Organic horizons and topsoil cleared and piled into windrows. Thinned to 6-m stem spacing about 2000 (17 yr ago)
0–10 cm				0.55	0.18	6.2	
10–20 cm				0.67	0.20	5.3	
20–30 cm				0.78	0.19	3.6	
True-fir	1820	74	72				No evidence of logging or fires in the past 100 yr
0–10 cm				0.41	0.20	15.5	
10–20 cm				0.51	0.20	9.9	
20–30 cm				0.49	0.19	7.4	

† J. Zhang, *unpublished data*.
‡ Rocks plus smaller amounts of roots, and wood that did not pass a 2-mm sieve.

on a side in the TF and MC and 50 m on a side in OK and PP. The plots were organized as three treatment blocks, each to receive four levels of canopy thinning and two types of residue treatment to be implemented in the future.

In each of the 24 plots, as a separate effort, live stems were measured and volume calculated using dbh-based allometric equations for species in northern California (Zhang et al. 2010, Powers et al. 2013). These estimates included all wood, bark, and foliage growing above the mineral soil. The contribution of C in the root wad (belowground portion directly beneath the stump plus coarse roots out to 2 m from the stem) was estimated by using the ratio of total belowground to total aboveground mass of 0.22 (Burrill et al. 2018). From this value, we subtracted mean live root C mass from samples collected at distances over 2 m from the tree stems. We used the vegetation data from the 12 plots used for detrital C measures.

Detrital C pools were measured in 12 of the 24 vegetation plots: four plots in each of the three blocks. In each plot, three sampling points were established at 10-m intervals in the MC and TF plots and at 8-m intervals in the smaller OK and PP plots. The sampling points were moved as needed if they fell near objects that may unduly affect C measures: within 2 m of trees, within 1 m of large woody debris, or on top a boulder. At each point, forest floor and soils to 30 cm depth were sampled to ensure all C was collected in one of the sampled layers. The forest floor was collected in a 600-cm^2 area as two layers, the Oi+Oe (L+F) layer combined and the Oa (H) layer. Three mineral soil layers to 30 cm depth were sampled directly below the forest floor sample areas. The 0–10 cm soil was collected by

Fig. 2. Four forest stands selected for carbon budgets. True-fir is less disturbed at 1830-m elevation. The others are at about 1400-m elevation. Mixed Conifer was thinned most recently in 1990. Oak had fires in 2000 and 2012. Pine Plantation had forest floor and soil cleared into windrows and planted to pine in the mid-1960s and thinned in 2000.

first probing the soil to avoid buried boulders, and then carefully excavating a uniformly shaped 15 cm diameter by 10 cm deep pit using a chisel to break rocks at the pit boundary. The pit volume was measured as a frustum of a cone and by displacement by small pebbles contained in a mesh bag leveled to the top of the pit. The difference between the two types of measures was typically <5% with no bias with respect to each other, and the average of the two estimates was used. Using data from individual pits allowed soil C to be calculated on each pit as opposed to using mean values of bulk density for the stand or using bulk density collected on a different soil sample. We expected that use of soil pits would reduce errors in soil C, rock volumes (Huntington et al. 1988), and root C (Park et al. 2005) common for core samples in rocky soils.

Cores were chosen to sample the deeper soil layers as a time-saving step. Soil at the 10–20 cm depth was collected using a 5.6 cm core driven into the bottom of the excavated pit. Soil at the 20–30 cm depth was collected using a 3.5 cm diameter core (5.6 cm core in the Oak stand). Deep soils (from 30 cm to 1 m) were sampled in a single, large pit in each forest where fine-soil

bulk density, rock content, wood, roots, and soil carbon at selected depths were determined and the resulting estimates were interpolated for the soil layers in between.

Dead standing stems, down woody debris, and large surface rocks were sampled using three, 25-m transects (75 m total) arranged in the shape of a triangle in each plot. The diameters of down woody debris pieces ≥1 cm diameter lying on top of the Oi layer were tallied and converted to volume (Van Wagner 1968, Brown 1974). Tallies were made of species, diameter, decay class, and percent fragmentation for large woody debris ≥7.5 cm diameter over the three transects. Diameters only were recorded for medium woody debris 2.5–7.5 cm diameter over the first 6 m of each transect, and fine woody debris pieces 1–2.5 cm diameter over the first 3 m of each transect. Standing dead stems (rooted and ≥45° upright) were tallied using the same measures as large woody debris along a 4 m wide band centered on the 75-m transect except that dbh and height were recorded. Representative dead wood samples were collected, and density and C concentration were determined on the samples and extrapolated to the dead wood volumes to estimate woody debris C. Surface rock volume was measured by tallying exposed rock surfaces greater than 15 cm diameter in the same bands used for standing dead stems. The proportion of surface area occupied by rocks was assumed an unbiased estimate of belowground rock volume (typically <2%). This appeared to be valid based on observations of cut banks along roads.

Laboratory procedures

Moist forest floor and soil samples were partially air-dried in paper bags until they reached appropriate friability for sieving. The forest floor and soil samples were separated into their constituent components in the laboratory using progressively smaller sieves. The Oi+Oe layer was separated into either wood or fine organic matter by sieving through a 6-mm mesh. The Oa layer was separated into wood, live roots if present, or fine organic matter fine by sieving through 6-mm then 4-mm mesh.

Soils were sieved through 6-mm, then 4-mm, and finally 2-mm mesh. Moist processing facilitated separation of live from dead roots using color, textural, and tensile strength differences. Roots, rocks, and woody debris on top of the larger sieves were separated by hand. Dead roots often broke and passed the larger sieve and were collected by the smaller sieves. Roots, woody debris, and rocks from the 2-mm sieves were separated from each other using air dispersion similar to the method described by Santantonio et al. (1977) who used a North Dakota seed blower. We placed material from the top of the 2-mm sieve onto a 50 × 70-cm metal tray. By tipping with gentle shaking, the heavier rocks and woody debris were allowed to roll to the bottom of the tray while the roots could be winnowed free and blown by mouth up toward the top that was fitted with a screen to prevent loss of roots over the top. The rocks and wood could be separated by a subsequent separation and the process could be repeated until the sorter was satisfied with the separation. Volumes of rocks, wood, and roots were measured using weight-to-volume ratios determined on subsamples. These were used to calculate the volume of non-soil material and volume of sieved soil. Fine-soil bulk density was estimated as the volume of fine soil divided by the dry mass of fine soil (Huntington et al. 1989).

The separated components were weighed moist, and a subsample of 1–10 g was then taken for moist-to-dry weight determinations at 105°C and then loss-on-ignition (LOI) at 450°C for at least 6 h. Carbon determinations on representative samples by the Colorado State University Soils Laboratory were used to derive carbon-to-LOI ratios of 0.49 for live stems and 0.55 for detrital C. Ratios for soils ranged from 0.42 for topsoil to as low as 0.32 for deeper soils. Soil carbon-to-organic matter ratios can vary by site (Nelson and Sommers 1982) and by depth (Huntington et al. 1989). Low values occur from additional loss of hydrated water particularly for soils high in fine particles (Veres 2002) and from subsoils low in organic matter (Rowell and Coetzee 2003). Young volcanic soils with amorphous minerals are also reported to be highly hydrated (Torn et al. 1997). A test of LOI of soil with increasing ignition temperatures showed a small additional weight loss of soils above 350°C that was largely absent in nearly pure organic matter such as wood, forest floor, or charcoal. This additional loss was consistent with hydrated water

loss. Additional small losses from ashing soils have been shown as the non-zero positive intercept in regression equations of LOI vs. C determinations (David 1988, Huntington et al. 1989). To be conservative and avoid overestimates of soil C, we assumed our soils to have carbon-to-organic matter ratios similar to the detrital organic matter (0.55). Our calculations then showed that soils lost an extra 6.0%, 7.3%, and 8.1% mass with LOI for depths 0–10, 10–20, and 20–30 cm, respectively. This additional loss was subtracted from the observed LOI values before using the 0.55 ratio obtained for detrital samples.

Statistical analysis

Detrital C pools were analyzed for statistically significant differences among the four forest stands via one-way ANOVA and Bonferroni pairwise comparisons using Stata software (StataCorp LLC, College Station, Texas, USA). All detrital data except soil C and sums of component C pools showed varying degrees of skewness and were transformed as $\ln(x + 1)$. Means and confidence intervals were estimated by back-transforming these values from the ANOVA outputs. Back-transformed means are geometric means which are less sensitive to large values and are considered to be better as representative values (i.e., they approximate medians) of log-normal data. Geometric means are the same as arithmetic means in normal distributions but will be lower than arithmetic means as the degree of skewness increases (Rothery 1988). In these data, the geometric means were at least 10% lower than arithmetic means for most detrital pools but were up to fourfold lower for some of the live root data. Since transformed were needed for some of the data, all data were transformed so the means were comparable in the summaries of the ANOVA results. However, for assembling the budgets, arithmetic means were used, as they are better estimates when summing a series of mean values or when extrapolating to areal estimates (Baskerville 1972).

Results

Patterns in stand carbon pools

The relative sizes and the patterns of C storage are shown as static budgets for the four stands in Figs. 3–6. Total C (Mg C/ha) to a 30 cm soil depth in TF, MC, OK, and PP was 531, 317, 310, and 253, respectively. Deep soil C to 1 m depth held significant C mass and including deep C increased the totals C by 32 Mg C/ha in MC to as much as 92 in PP and 94 Mg C/ha in OK.

As expected, TF being the least disturbed stand had the largest stores of total C and stores were generally larger in all pools. However, MC had similar amounts of C as TF in aboveground woody debris and forest floor. Compared to TF, MC had considerably more C in down large wood pieces and less in the standing dead stems. Despite the similarities in the aboveground and forest floor detrital C pools, MC had only half the soil C as TF.

The three low-elevation stands differed slightly from our expectations of their C stores. As expected, OK and MC both had at least 30 Mg C/ha greater C mass in the live vegetation than the more recently established PP. MC had over twice the C mass in the surface detrital pool of forest floor and woody debris as OK and PP. OK had the smallest forest floor mass. However regardless of depth, soil C in MC was less C than both OK and PP.

Tests for stand differences of various components of the detrital C pools (buried wood, roots, and fine organic matter of the forest floor and soil) to 30 cm depth showed that the larger detrital C masses in TF were significant in most of the forest floor and soil detrital components (Table 2). TF and MC had similar component C masses in the fine material of the forest floor and similar mass of buried wood in all depths. Detrital C pools of OK and PP were quite similar, though the C in the forest floor of OK tended to be lower than PP and this was this significant in the Oi+Oe.

Comparing the three stands at the lower elevation, OK, PP, and MC had very similar total C summed over all detrital pools contained by the forest floor and soil to 30 cm (bottom of Table 2). But MC had significantly greater fine-material forest floor C and this was offset by the consistently lower mean fine-soil C in the three soil layers in MC, and often significantly less than OK or PP.

C in dead roots was a relatively small pool with greater spatial variation. MC had a lower mean C in dead roots, but there were no statistically significant differences in dead root C pools among the three low-elevation stands (Table 2). However, TF had over twice the C in dead roots

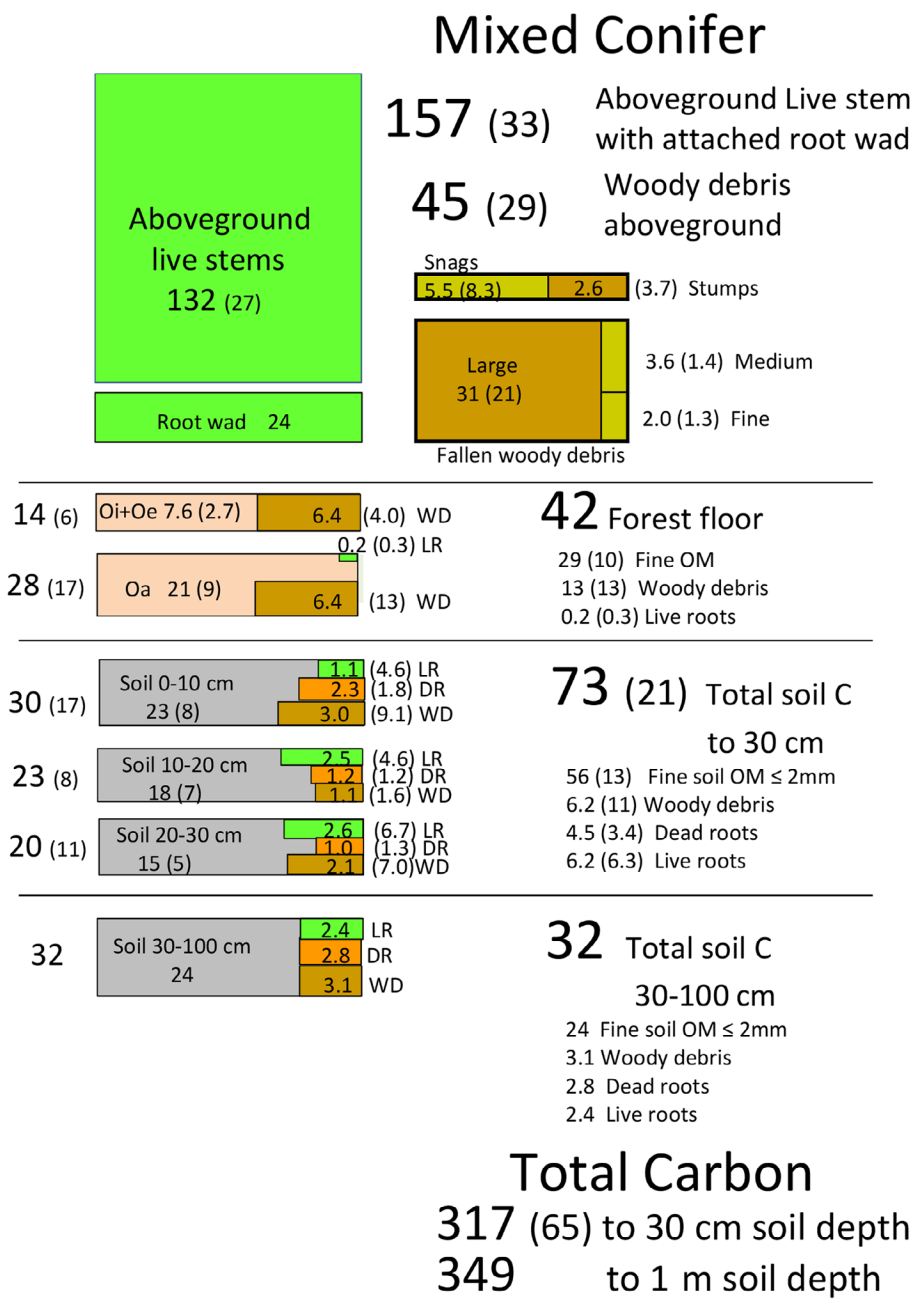

Fig. 3. Carbon static budget for the Mixed Conifer stand. Box size represents relative C pool size. Values displayed are means (Mg C/ha) with standard deviations in parentheses. Sample sizes: vegetation, aboveground woody debris = 12, forest floor and soil to 30 cm = 36, soil 30–100 cm = 1.

as the low-elevation stands and this was statistically different. C in live roots was nearly the same or slightly less compared to C in dead roots and also showed considerable spatial variation and few statistical differences. Notable trends in live root C were that by far, most was contained in the smallest diameter class and OK had the most live root C followed by MC with considerably smaller mean pool sizes in PP and TF (Table 3). The differences in live root C were

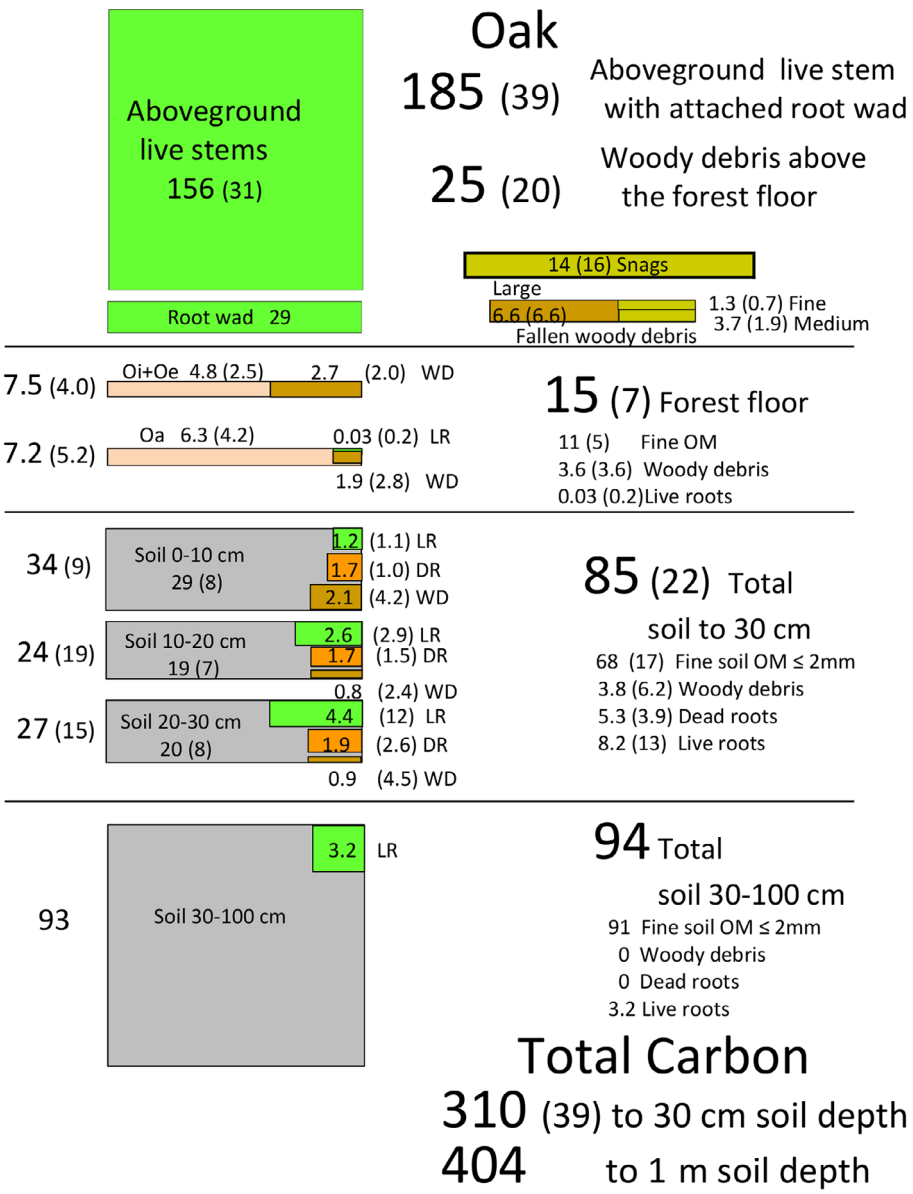

Fig. 4. Carbon static budget for the Oak stand. Box size represents relative C pool size. Values displayed are means (Mg C/ha) with standard deviations in parentheses. Sample sizes: vegetation, aboveground woody debris = 12, forest floor and soil to 30 cm = 36, soil 30–100 cm = 1.

most pronounced in the upper soil layers, particularly the 0–10 cm soil layer (Table 3, Figs. 3–6). The root masses were more variable than the other detrital masses, and differences of about twofold were needed in order to be statistically significant.

As a single deep soil pit (30–100 cm) was excavated in each stand, comparisons among stands are not as robust. Still, as was found for the upper soil layers, MC had a considerably smaller mass of soil C in the deep soil C (Figs. 3–6). The lower soil C in MC was the not so much the result of lower soil C concentrations but lower fine-soil bulk densities and higher rock contents (Tables 1, 4). Roots were observed in the deeper soils to 1 m depth, but very little

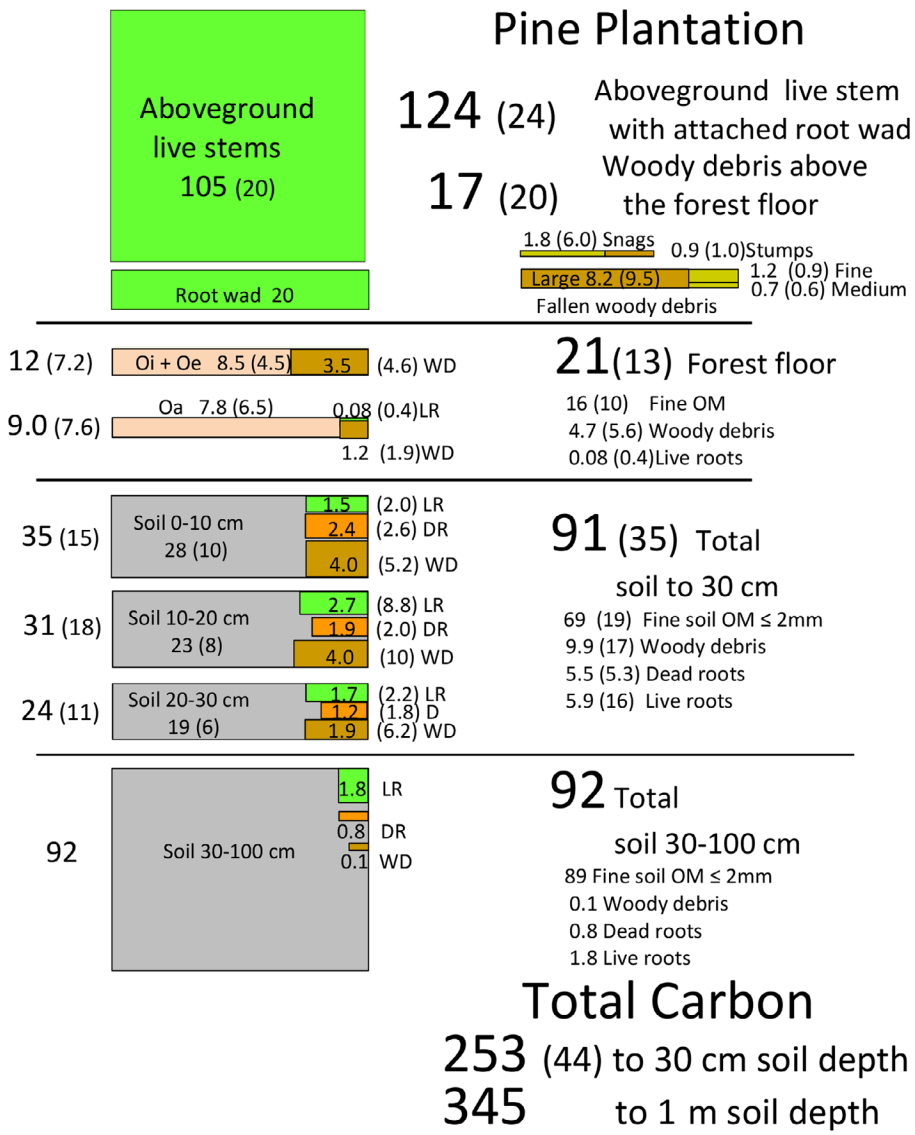

Fig. 5. Carbon static budget for the Pine Plantation stand. Box size represents relative C pool size. Values displayed are means (Mg C/ha) with standard deviations in parentheses. Sample sizes: vegetation, aboveground woody debris = 12, forest floor and soil to 30 cm = 36, soil 30–100 cm = 1.

buried wood debris was observed below 40 cm and only in MC. Given the relatively large mass of carbon in these deeper soils, they deserve closer examination as high C accumulations in deep soils have been shown elsewhere (Trumbore et al. 1995).

Figs. 3–6 show the relative importance of aboveground dead wood as a component of the total C budget, comprising 8% to 13% of total C to 30 cm in MC and TF. The C in both aboveground and buried dead wood comprised 22% of the total detrital C pool in TF and 37% in MC. These same measures were 16% and 15%, respectively, for OK and PP.

Soil carbon mass and fine-soil bulk density

Greater soil masses in the individual soil pits were associated with lesser soil C concentrations (Fig. 7). This pattern was the result of a negative relationship of soil percentage C and fine-soil

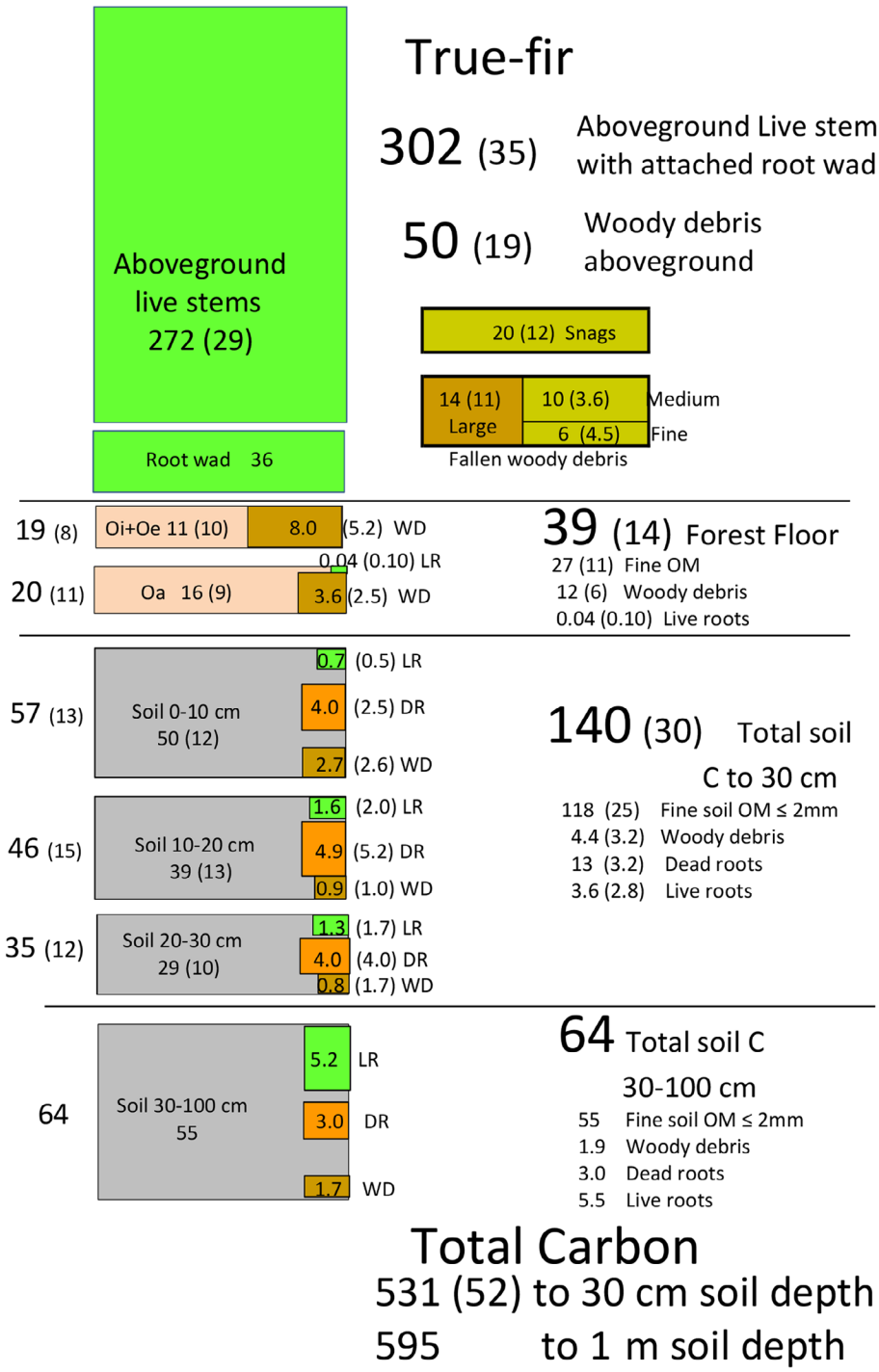

Fig. 6. Carbon static budget for the True-fir stand. Box size represents relative C pool size. Values displayed are means (Mg C/ha) with standard deviations in parentheses. Sample sizes: vegetation, aboveground woody debris = 12, forest floor and soil to 30 cm = 36, soil 30–100 cm = 1.

Table 2. Carbon pools (Mg C/ha) in forest floor and soil for four forest stands in northern California.

	MC		OK		PP		TF		All stands	
Carbon pool and layer	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
Wood†										
Oi+Oe	5.4	1.5^{B}	2.1	0.6^{A}	1.8	0.5^{A}	7.1	2.0^{B}	3.9	0.6
Oa	2.7	1.5^{B}	0.3	0.2^{A}	0.5	0.3^{A}	2.6	1.4^{B}	1.6	0.3
0–10 cm	1.0	0.5^{A}	0.8	0.5^{A}	2.1	0.9^{A}	1.7	1.0^{A}	1.7	0.4
10–20 cm	0.8	1.2^{AB}	0.3	0.2^{A}	1.3	0.6^{B}	0.9	0.5^{AB}	0.8	0.2
20–30 cm	1.9	1.7^{A}	0.2	0.2^{A}	1.2	0.7^{A}	0.6	0.4^{A}	0.5	0.2
Subtotal	14.2	3.6^{B}	5.3	1.2^{A}	8.3	2.3^{A}	14.8	1.7^{B}	9.9	1.4
Dead roots‡										
Oi+Oe	0		0		0		0		0	
Oa	0		0		0		0		0	
0–10 cm	1.8	0.6^{A}	1.5	0.4^{A}	1.8	0.6^{A}	3.3	0.8^{B}	2.0	0.3
10–20 cm	1.0	0.4^{A}	1.3	0.5^{A}	1.4	0.5^{A}	3.4	1.0^{B}	1.6	0.3
20–30 cm	0.7	0.3^{A}	1.4	0.5^{A}	0.8	0.5^{A}	3.0	1.0^{B}	1.3	0.3
Subtotal	3.3	1.2^{A}	4.3	1.1^{A}	4.1	1.1^{A}	10.3	2.5^{B}	5.0	0.8
Fine organic matter§										
Oi+Oe	7.3	0.9^{B}	4.3	0.8^{A}	7.6	1.1^{B}	10.1	1.2^{C}	7.1	0.6
Oa	18.0	3.9^{B}	5.0	1.3^{A}	5.9	2.0^{A}	13.9	3.1^{B}	9.4	1.3
0–10 cm	22.4	1.4^{A}	28.0	2.6^{B}	25.3	3.8^{AB}	49.0	3.0^{C}	29.8	1.2
10–20 cm	16.3	3.0^{A}	17.4	2.6^{A}	21.0	2.8^{A}	37.1	4.7^{B}	21.7	2.0
20–30 cm	13.4	2.6^{A}	19.8	2.7^{B}	19.4	3.1^{B}	28.2	3.7^{C}	18.9	1.5
Subtotal	83.2	5.0^{A}	77.0	6.1^{A}	83.8	6.3^{A}	142	10.0^{B}	93.7	5.3
Total C¶										
Oi+Oe	13.1	2.0^{B}	6.6	1.1^{A}	10.3	1.6^{B}	17.6	2.7^{C}	11.4	1.1
Oa	22.4	5.5^{B}	6.3	2.1^{A}	7.7	2.3^{A}	18.4	3.4^{B}	11.1	1.8
0–10 cm	27.6	4.2^{A}	33.4	4.8^{A}	35.1	4.7^{A}	55.7	5.9^{B}	36.1	2.6
10–20 cm	21.0	3.7^{A}	22.3	3.9^{A}	30.3	4.4^{A}	44.3	5.3^{B}	27.5	2.4
20–30 cm	18.2	3.4^{A}	25.9	4.3^{B}	24.5	4.0^{AB}	33.6	4.6^{C}	24.0	2.0
Total	112	8.0^{A}	96.9	8.6^{A}	107	$(10.7)^{A}$	175	11.5^{B}	119	6.5

Notes: MC, Mixed Conifer; OK, Oak; PP, Pine Plantation; TF, True-fir. Sample sizes = 36 per stand; most P values were <0.01; wood and fine organic matter in 0–10 cm were <0.05). Superscripted letters are tests of differences.

† Wood pieces buried in the forest floor or soil.

‡ Dead roots are all diameter classes.

§ Forest floor and soil material that passed sieves.

¶ Total carbon includes the sum of above plus live root masses from Table 3.

bulk density similar to that reported by others (Huntington et al. 1989, Federer et al. 1993, Jurgensen et al. 2018). Fig. 7 shows that total soil carbon in MC, OK, and PP was more influenced by the relatively wide range of fine-soil bulk density vs. the more narrow range observed in soil % C. The MC data points cluster toward the area of the graph with low fine-soil bulk density and only slightly higher soil percentage C when compared to the data points of OK or PP. The very high accumulations of soil C in TF are evident in its very different pattern of very high soil percentage C despite moderately low soil bulk density. The mean concentration of soil C between stands decreased as the level of stand disturbance increased.

Carbon patterns within stands

We examined patterns of variability by plotting measures of detrital C against the plot number of the stand. The plot numbers were surrogates for position on the landscape as the grid used for the stands was generally rectangular and the plots were numbered from lowest on one end of the stand to highest on the other end over distances of 500–700 m. Total detrital C in the forest floor C and total detrital C in the topsoil (0–10 cm) graphed against the C in live vegetation showed subtle spatial parallel patterns (Fig. 8). TF showed a tendency of higher C mass in both vegetation and soil in the center of the stand; TF plots were general at the same elevations and the center plots were in the center of

Table 3. Carbon pools in live roots (Mg C/ha) for four forest stands in northern California.

	MC		OK		PP		TF		All stands	
Size class and layer	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI	Mean	95% CI
≤1 mm										
Oa	0.13	0.07^{B}	0.02	0.03^{A}	0.05	0.06^{AB}	0.03	0.03^{ab}	0.06	0.06
0–10 cm	0.71	0.18^{B}	0.95	0.29^{B}	0.18	0.07^{A}	0.37	0.08^{A}	0.52	0.09
10–20 cm	0.94	0.29^{AB}	1.37	0.52^{B}	0.72	0.24^{A}	0.67	0.17^{A}	0.91	0.16
20–30 cm	0.60	0.29^{A}	1.04	0.38^{B}	0.77	0.31^{A}	0.54	0.23^{A}	0.73	0.16
Subtotal	2.59	0.64^{AB}	3.54	1.03^{B}	1.92	0.50^{A}	1.72	0.36^{A}	2.38	0.32
1–10 mm										
Oa	0.03	0.03^{B}	0.00	0.00^{A}	0.00	0.00^{A}	0.00	0.00^{A}	0.01	0.01
0–10 cm	0.18	0.12^{AB}	0.03	0.03^{A}	0.09	0.08^{A}	0.31	0.11^{B}	0.15	0.05
10–20 cm	0.29	0.24^{A}	0.10	0.11^{A}	0.29	0.16^{A}	0.43	0.18^{A}	0.27	0.09
20–30 cm	0.30	0.24^{A}	0.23	0.20^{A}	0.27	0.19^{A}	0.38	0.21^{B}	0.30	0.10
Subtotal	0.81	0.47^{AB}	0.33	0.20^{A}	0.67	0.33^{A}	1.26	0.34^{B}	0.73	0.18
≥10 mm										
Oa	0.00	0.01^{A}	0.00	0.00^{A}	0.00	0.00^{A}	0.00	0.01^{A}	0.00	0.00
0–10 cm	0.04	0.05^{A}	0.00	0.00^{A}	0.14	0.21^{A}	0.00	0.00^{A}	0.04	0.05
10–20 cm	0.18	0.22^{A}	0.12	0.16^{A}	0.17	0.24^{A}	0.11	0.14^{A}	0.14	0.11
20–30 cm	0.13	0.19^{A}	0.24	0.33^{A}	0.06	0.09^{A}	0.00	0.00^{A}	0.10	0.11
Subtotal	0.39	0.41^{A}	0.38	0.46^{A}	0.29	0.37^{A}	0.11	0.14^{A}	0.29	0.18
All roots										
Oa	0.16	0.08^{B}	0.02	0.03^{A}	0.05	0.06^{A}	0.03	0.03^{A}	0.06	0.03
0–10 cm	0.92	0.25^{B}	0.97	0.30^{B}	0.38	0.30^{A}	0.68	0.15^{AB}	0.52	0.09
10–20 cm	1.42	0.59^{A}	1.72	0.66^{A}	1.18	0.53^{A}	1.19	0.37^{A}	0.91	0.16
20–30 cm	1.07	0.61^{A}	1.67	0.83^{A}	1.18	0.46^{A}	0.95	0.36^{A}	0.73	0.16
Total	4.16	1.35^{A}	4.82	1.75^{A}	3.31	1.13^{A}	3.19	0.69^{A}	3.84	0.61

Notes: MC, Mixed Conifer; OK, Oak; PP, Pine Plantation; TF, True-fir. Sample sizes per stand = 36; P values are <0.05. Superscripted letters are tests of differences.

the undisturbed TF stand visible on the 1967 aerial photograph. MC and PP showed a trend of reduced C mass in the vegetation and forest floor in the higher numbered plots. In MC, the plot numbers increased uphill from a lower bench that was not thinned as heavily, to a slope, then a ridge top. The PP plots decreased in vegetation and soil C with increasing plot number. The highest numbered plots in PP were located in a separate block located 3 km from the first eight. OK showed no apparent spatial trend.

The variability of soil and forest floor C within plots is shown as the vertical separation of three points for each plot number. The vertical spread demonstrates that variation within a plot is not constant among plots within a stand and not constant across stands. Pine Plantation showed considerable variability within plots up to plot number 8, whereas TF and OK showed less within-plot variability. MC showed more variability in the lower plot numbers. Several TF plots had soil C averaging about 50 Mg C/ha (plots 4, 8, 17, and 28) and other plots averaging 75 Mg C/ha (plots 10, 16, and 19). The forest floor in MC showed the lower elevation bench (plots 3–8) with high accumulations of FF averaging 50 Mg C/ha. Those plots on mid-slope (plots 11–16) had lower C stores averaging 30 Mg C/ha. The plots on the ridgetop that had been more heavily thinned averaged 25 Mg C/ha. The soil C in PP in plots 1, 5, 8, 11, and 13 fell on top of windrows and tended to have higher live vegetation and soil C masses. Forest floor trends were not apparent across plots in PP, OK, and TF.

Discussion

High C accumulations in these stands

These stands stored high amount of C compared to other forests in northern California and the Pacific Northwest. TF total C stores to 1 m soil depth of 595 Mg C/ha are comparable to the large stores of C in the old-growth forests of the Pacific Northwest (totals in Mg C/ha): 619 in Wind River, Washington (Harmon et al. 2004),

Table 4. Carbon pools in deep soil (Mg C/ha) and soil properties.

Stand and soil depth (cm)	Buried wood	Live roots	Dead roots	Soil <2 mm	Total C	Soil % C	Fine-soil bulk density (Mg/m^3)	Rock content (m^3/m^3)
MC								
30–40	1.19	0.27	1.06	5.4	8.0	1.62	0.66	0.58
65–75	0.04	0.42	0.13	1.4	2.1	1.22	0.40	0.89
90–100	0.14	0.14	0.00	3.5	3.8	1.32	0.53	0.58
Total	3.1	2.4	2.8	24.1	32.3			
OK								
30–40	0.00	0.65	0.00	12.9	13.5	3.21	0.85	0.57
50–60	0.00	0.40	0.00	10.3	10.7	2.32	0.86	0.53
70–80	0.00	0.38	0.00	19.9	20.3	2.77	0.94	0.24
90–100	0.00	0.85	0.00	15.0	15.9	1.52	1.12	0.12
Total	0.0	2.5	0.0	90.5	93.7			
PP								
30–40	0.00	0.23	0.02	12.5	12.8	1.41	1.11	0.21
40–50	0.10	0.13	0.00	14.0	14.3	1.30	1.15	0.06
50–60	0.00	0.00	0.00	12.4	12.4	1.34	0.97	0.05
60–70	0.00	0.03	0.17	14.6	14.8	1.71	0.87	0.02
70–80	0.00	0.00	0.00	14.0	14.0	1.52	0.92	0.0
80–90	0.00	1.46	0.59	12.2	14.2	1.39	0.88	0.01
90–100	0.00	0.00	0.00	8.9	8.9	1.07	0.83	0.01
Total	0.1	1.6	0. 8	88.5	91.2			
TF								
30–40	0.96	0.40	2.51	10.8	14.7	2.81	0.68	0.50
60–70	0.00	0.91	0.00	7.6	8.5	1.79	0.82	0.60
80–90	0.00	0.65	0.00	6.7	7.4	1.65	0.66	0.42
90–100	0.00	1.00	0.26	7.7	9.0	1.80	0.66	0.38
Total	1.0	5.5	3.0	54.8	64.3			

Notes: MC, Mixed Conifer; OK, Oak; PP, Pine Plantation; TF, True-fir. Totals are interpolated values for the entire 30–100 cm profile.

635 for *Abies amabilis* in the Washington Cascade Range (Grier et al. 1981), 500–750 for *Pseudotsuga menziesii* at H.J. Andrews Forest in the Oregon Cascades (Grier and Logan 1977). Though C as high as 1127 was reported for stands along the Oregon Coast (Smithwick et al. 2002). The large masses accumulated in conifer forests of the Pacific Northwest region are considered the result of evergreen, needle-leaf vegetation adapted to the wet winters, the large size of individual trees is thought to be a buffer against environmental stress, and the long-periods between destructive storms or fires allow large accumulations (Waring and Franklin 1979). Precipitation in Oregon and Washington is often over 2000 mm. Higher net primary productivity in Oregon is related less to precipitation and more to water availability during the growing season (Waring and Schlesinger 1985). In California, the Mediterranean climate with dry summers has a more severe drought during the growing season than more northerly sites and fire return intervals are shorter (Arno 2000) contributing to lower forest growth rates and shorter periods between disturbances to accumulate C.

Hudiburg et al. (2009) estimated live biomass for all forest types in the Sierra Nevada for a continuum of stand ages out to 600 yr using inventories from state, federal, and their own site data. At stand age of 200 yr, they estimated live carbon to average approximately 140 Mg C/ha and the upper bound to be just over 300. By comparison, our MC stand had live aboveground vegetation C of 132 Mg C/ha and our TF stand had 272. Powers et al. (2013) reported total ecosystem C including soils to a depth of 30 cm in mixed conifer stands that were recovering from the Storrie Fire of 2000 as 206 Mg C/ha for a stand that burned lightly with surviving canopies (GC) and 282 for a stand with 100% stem mortality (NS). The higher C in the more heavily burned stand was due to large amounts of incompletely burned C left over. By comparison, our MC total C for the same pools and soil layers was 317 Mg C/ha.

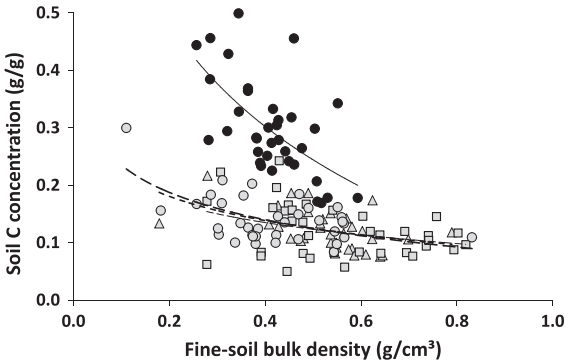

Fig. 7. Soil carbon concentration as a function of fine-soil bulk density from small soil pits excavated in the top 10 cm of mineral soil in four forest stands in northern California. Solid circles, True-fir; open circles, mixed conifer; open squares, oak; and open triangles, pine plantation.

Fine-soil C does not appear to be particularly high in our stands. For example, two other stands studied by Powers et al. (2013) were young ponderosa pine plantation and non-burned mixed conifer stand. Their plantation that had soil ripping had low soil C. However, Power et al.'s mixed conifer stand likely had little soil disturbance and it had similar fine-soil C as NS and GC, and the three stands ranged from 88 to 100 Mg C/ha. By comparison, our MC fine-soil C to 30 cm was 56 Mg C/ha and our OK, PP, and TF stands were 68, 69, and 118 Mg C/ha, respectively.

PP total C of 345 Mg C/ha is higher than those reported for ponderosa pine stands in eastern Oregon. Total C in four ponderosa pine stands including soils to a 1 m depth and aged from 300 to 500 yr old ranged from 158 to 232 Mg C/ha (Smithwick et al. 2002). Total C to 1 m depth in ponderosa pine stands ranged from 79 to 304 Mg C/ha in stands aged 9–316 yr (Law et al. 2003). The lower C stores in Law et al.'s stands are due to lower detrital C in most pools and especially the soil C which ranged from 41 to 126 Mg C/ha compared to the fine-soil C to 1 m depth in our PP of 158 Mg C/ha. The average annual precipitation in eastern Oregon is lower than our PP site (e.g., 550 mm vs. 870 mm), and lower growth rates are most likely the reason for the lower total C (Gray and Whittier 2014).

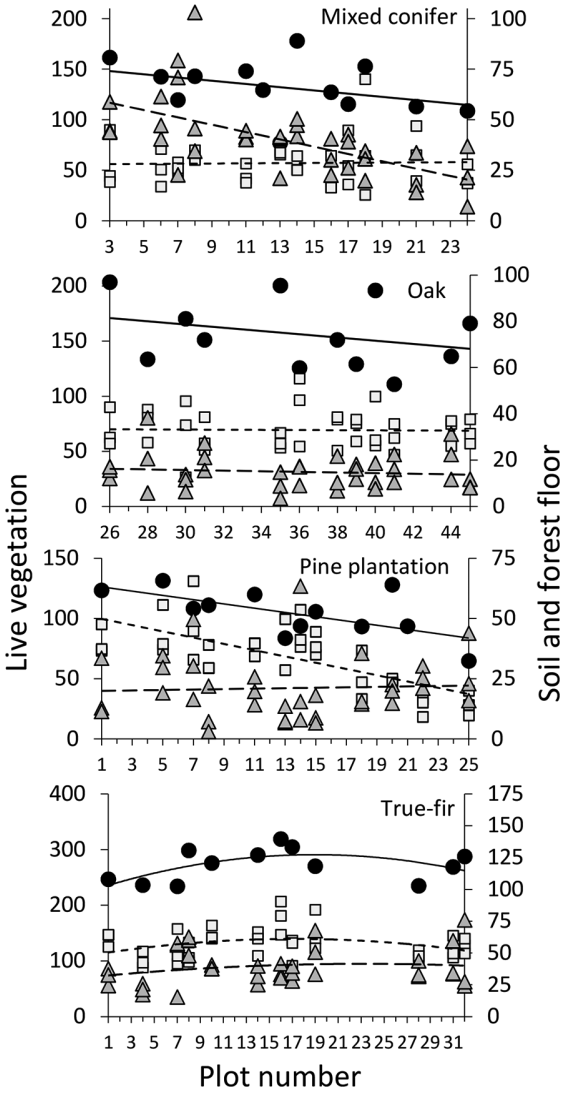

Fig. 8. Spatial patterns in carbon pools (Mg C/ha) in four forest stands in northern California. The plot numbers are surrogates for position within each stand. Solid circles, live vegetation; open squares, soil to 10 cm; and open triangles, forest floor. Each live vegetation data point is the stand C. Each forest floor and soil data point is one of three measurement points per plot located about 8–10 m apart.

Aboveground live stem C stored in our stands ranged from 105 to 272 Mg C/ha and was also higher than means estimated for forest stands in the National Forests in California or those on private lands. The summary of the Forest Inventory and Analysis for live vegetation in California for

the years 2001 to 2010 (Christensen et al. 2016) reports mean aboveground live C stores (in Mg C/ha) for a variety of similar stand types: mixed conifer 125, ponderosa pine 48, western oak 57, and high-elevation conifer forests 140. The California Air Resources Board (CARB 2015) has derived common practice levels of aboveground live C stocks on private lands for setting baseline C by which addition C is calculated and sellable as C offsets for forest projects. In the Southern Cascades supersection CARB common practice, mean C in aboveground live stems (in Mg C/ha) is substantially lower than that observed in this study: High-elevation forests are 49, mixed conifer are 58–86, and mixed oak woodlands are 33–54. However, very high carbon contents of 510 Mg C/ha have been reported in all pools above the mineral soil (e.g., live and dead stems, shrubs, woody debris, and forest floor) in old-growth *Abies magnifica* stands in Sierra Nevada (Gonzalez et al. 2010).

Woody debris accumulations

The less disturbed stands MC and TF had large accumulations of woody debris in all layers to 1 m soil depth (67 and 68 Mg C/ha, respectively) that was about twice that of the more disturbed stands OK and PP. The total dead wood C in MC accounted for 19% of the total C. High accumulations of woody debris appear to be a trait of conifer forests vs. broadleaf forests; dead wood in old-growth forests in the Pacific Northwest can exceed 150 Mg C/ha (Harmon and Hua 1991) in contrast to the less than 20 Mg C/ha for other forests (reviewed by Lambert and Cromack 1982). High accumulations in the Pacific Northwest are mostly due to slow decomposition rates, but wood can also accumulate in a forest by asynchronous inputs and episodic events (Lang 1985, Fahey et al. 2005). The dead wood pool can also be important sources of C to the forest floor as fragmentation inputs of the wood to the forest floor during the last stages of wood decay have been estimated to be as high as 40% of the original wood (Mattson and Swank 2014). McFee and Stone (1966) reported that up to 29% of the volume of forest floors was buried woody debris in old-growth hardwood forests in the Adirondack Mountains of New York. In our MC and TF stands, buried dead wood pieces comprised approximately 30% of the total forest floor C. Total buried dead wood in the forest floor and soil represented 37–50% of the aboveground dead wood. These patterns suggest a substantial C flux from aboveground dead wood may be occurring to the forest floor and to soils and they are mixed to a depth of at least 30 cm. Generally, wood pieces declined with depth (Table 2) and were not observed below 40 cm soil depths except MC which had wood down to 1 m depth (Table 4).

Live roots

The arithmetic means of all diameters of live root C to a 1 m depth (9.8 Mg C/ha, from Figs. 3–6) were over twice as great as the geometric means (3.8 Mg C/ha from Table 3), and this difference was greater in the deeper soils. The arithmetic and geometric means of the fine, live roots (≤1 mm diameter) to a 1 m depth were 4.8 and 2.4 Mg C/ha, respectively. Given the natural variability in root mass measures, either mean is similar to those reported in the literature. For example, fine, (<2 mm) live roots to a 1 m depth at an old-growth forest at Wind River, Washington, were 3.6 Mg C/ha (Harmon et al. 2004). Annual means for fine roots (<2 mm) to 30 cm soil depth ranged from 1.7 to 3.3 Mg C/ha for 15- to 100-yr-old stands of Scots pine in Finland (Makkonen and Helmisaari 2001). Fine-root (<2 mm) averaged 1.8 Mg C/ha among 17 stands of conifer species as reported in nine publications (summarized by Santantonio et al. 1977).

The 10–20 cm and the 20–30 cm soil layers had more live roots than the 0–10 cm soil layer. This may be an artifact of different methods as the sampling of the two lower layers was by cores and the top layer by pit excavation. Cores were reported to estimate 27% higher root contents than pits (Park et al. 2005). However, patterns of rooting depths are not well understood and root growth may follow the nutritional and moisture needs of the plant (Pierrt et al. 2016, reviewed by Cairns et al. 1996). Deep rooting may be another reason for the observations of relatively high soil C at depth in these stands and it may be the source of deep soil C. However, the source of this deep C is poorly known and is speculated to be more microbial products than plant compounds (Schmidt et al. 2011). Deep soil C also has long turnover times (Torn et al. 1997) and is not likely related to recent

disturbance to the vegetation or disturbance to top soils and may instead represent a pedogenic site difference.

Low soil C in MC

MC failed to store more total C to 1 m depth than either OK or PP as expected given its less disturbed status and greater forest mass. Physical soil disturbance and mixing with the forest floor that likely occurred in PP during the windrowing 50 yr ago has been considered to be a major cause of increased decomposition rates (Gholz and Fisher 1982, Jurgensen et al. 1986, Chapin et al. 2002, Powers et al. 2013). The fire disturbance to OK was expected to have burned the forest floor and possibly the top layers of the soil (Brown and Smith 2000, Bormann et al. 2008). Soil geochemical differences between MC vs. OK and PP may also be important as mineralogy has been shown to protect soil C (Doetterl et al. 2015, Mathieu et al. 2015) and young volcanic soils are typically high in such as non-crystalline soil minerals, which have been associated with greater soil C stores (Torn et al. 1997). Low accumulation of fine-soil C in MC was a result of low fine-soil bulk density combined with high rock content. The reason for such a difference is not apparent and warrants further consideration.

Gifford and Roderick (2003) have suggested soils be sampled for specific mass instead of to a specific depth. The total C content can be compared on the same masses of soil by collecting a second sample a couple of cm below the bottom of the core to allow interpolation of the added carbon for soils of low mass. By assuming the soil measures over the next lower 10 cm of soil change uniformly with depth, we made such an adjustment for soil mass following Gifford and Roderick. MC soil mass was 3.31 g/cm^2 for the top 10 cm layer vs. the mean of OK and PP of 4.58 g/cm^2. By including the next 3 cm of soil to the top 10 cm, the soil mass in MC was estimated to be 4.55 g/cm^2. Using interpolated carbon concentrations of 5.2% and multiplying it by the mass of soil in the top 13 cm in MC so as to compare the same masses of soil as OK or PP gave an additional 6.4 Mg C/ha for a total of 29.4 Mg C/ha for MC. This was equal to the accumulation than in OK or PP in their top 10 cm of soil. The same calculation for TF which had very low fine-soil bulk density would increase its soil carbon from 50 to 64 Mg C/ha. However, these comparisons essentially reflect the difference in soil C concentrations in MC and TF. While producing greater C estimates in the upper layer, the adjustment simply takes soil C from the next layer and does not necessarily mean there is more C in the entire soil profile.

Summary: Forest carbon storage

The TF stand at the higher elevation and the least disturbed for the longest time had the highest accumulations of C in both the live vegetation and detrital pool. MC, OK, and PP at lower elevations had undergone more recent disturbance but still had moderately high accumulations of C. The pattern of highest total C accumulations in TF supported our expectation of higher C in the least disturbed stand with the longest time since disturbance. However, TF was also at about 400 m higher elevation and the climate data from Humbug Summit suggest TF was 5°C cooler than the low-elevation stands during summer. We do not think that higher elevation of TF was a large cause of the greater accumulation of C. Most reviews of forest and elevation ascribe lower aboveground productivity with decreasing temperature (reviewed by Waring and Schlesinger 1985). Lower aboveground production was measured with increasing elevation at sites such as the Smoky Mountains in southeastern United States (Whittaker 1975). Lower aboveground C stores with increasing elevations have been shown in studies that have used LiDAR to measure C stocks (Swetnam et al. 2017). However, detrital pools have been shown to be higher at higher elevations. Twofold higher forest floor masses are thought to be due to slower decay rates at higher elevations approaching tree line at Hubbard Brook in the northeastern United States (Fahey et al. 2005). The highest total C stores were observed at the highest elevations site near tree line in Ecuador due to accumulations in organic horizons of the soil and a shift to greater root production (Moser et al. 2011). Considering these findings, it is perhaps best to say that greater C in live vegetation in TF is mainly the result of a longer time since disturbance and the greater C in detrital pools in TF is a combination

of a longer time since disturbance and lower decomposition rates from lower temperatures.

Our expected pattern in total ecosystem C to 1 m soil depth as MC > OK > PP was not observed and was partially observed to 30 cm soil depth where MC had more C than PP but not OK. MC failed to show larger accumulations of C because it had low amounts of soil C. Lower C stores in live vegetation, forest floor, woody debris, and mean soil C concentrations in OK and PP vs. MC did support the hypothesis of lower C associated with sites of greater disturbance. It is possible the site preparation on PP acted to increase soil bulk density. However, fine-soil bulk density is high in PP at all depths measured to 1 m and it is unlikely soils were compacted to these depths and instead indicates the soils at PP and OK are denser throughout or perhaps MC is the unusual soil type.

Other observed patterns were that the less disturbed stands were associated with greater forest floor and woody debris C. Spatial trends were observable in the forest floor plus soil C, both within plots and across plots and this followed the same trends in live C mass.

It is recognized that C in forests is not static but is a process of slow accumulation via internal processes absent disturbance (Luo and Weng 2011). C accumulation in live stems is a balance between gains via GPP and losses via respiration (Chapin et al. 2002, Pregitzer and Euskirchen 2004, Tang et al. 2014). In addition, C in forests can be set back by disturbance (Atiwill 1994, Luo and Weng 2011). Eddy flux studies show most forests are small to moderate C sinks of 0.4–4 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ (Luyssaert et al. 2007) and California FIA data of U.S. national forest show net growth after accounting for stem mortality to average 0.2 Mg $C \cdot ha^{-1} \cdot yr^{-1}$ between 2000 and 2010 (Christensen et al. 2016).

We think these stands represent typical stands and disturbance histories on national forests in this region. TF, given its high C stocks that approach old-growth stand in the U.S. Pacific Northwest, and its apparent long time since disturbance may be considered to be close to steady state and other high-elevation stands in the region may also be near steady state. Harvests of high-elevation stands are rare due to inaccessibility. Fire is also rare and in montane forests in the Sierra Nevada is strongly controlled by spring and summer temperatures (Keeley and Syphard 2017). However, fire frequency at high elevations has been increasing over the past century (Schwartz et al. 2015). The three low-elevation stands that have more frequent disturbance are in their recovery phases and are likely accumulating carbon in the live vegetation and possibly in detrital pools.

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