



# Fire, thinning, and the carbon economy: Effects of fire and fire surrogate treatments on estimated carbon storage and sequestration rate

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Received 5 October 2007; received in revised form 14 November 2007; accepted 20 November 2007

## Abstract

Changes in estimated standing stocks of carbon (C) in vegetation, forest floor, dead wood, and mineral soil for the fire and fire surrogate (FFS) network sites were evaluated in relation to the application of prescribed fire, mechanical treatments designed as surrogates for prescribed fire, and the combination of mechanical treatment and fire. Pre-treatment C stocks and changes in C stocks over two intervals (pre-treatment to first post-treatment year and first post-treatment to a 2nd, 3rd, or 4th post-treatment year, depending on site) were evaluated using meta-analytical methods. Total C storage across the network averaged  $185 \pm 8$  (standard error)  $\text{Mg C ha}^{-1}$ , of which 45% was in vegetation, 38% in soil organic matter, 10% in the forest floor and 7% in dead wood. C stored in vegetation was not significantly affected by prescribed fire, but decreased  $\sim 30 \text{ Mg ha}^{-1}$  as the result of mechanical or mechanical + fire treatment; in contrast, forest floor C storage was reduced by  $\sim 1\text{--}7 \text{ Mg ha}^{-1}$  by fire or mechanical + fire treatment, but unaffected by mechanical treatment alone. Neither dead wood C nor soil organic C was significantly affected by the treatments. At the network scale, total ecosystem C was not significantly affected by fire, though four individual sites did exhibit significant C losses to fire. Mechanical treatment, with or without fire, produced significant reductions of  $16\text{--}32 \text{ Mg ha}^{-1}$  during the first post-treatment year, but this was partially balanced by enhanced net C uptake of  $\sim 12 \text{ Mg ha}^{-1}$  during the subsequent 1–3 years. In terms of C storage and uptake, western coniferous forests responded differently to the FFS treatments than did eastern deciduous, coniferous, and mixed forests, suggesting that optimal management for fire, harvesting, and C sequestration may differ between regions.

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**Keywords:** Carbon budget; Fire surrogates; Mechanical treatment; Prescribed fire

## 1. Introduction

Growing concern over the impact of rising atmospheric carbon dioxide ( $\text{CO}_2$ ) on global climate has led to the search for sinks of  $\text{CO}_2$  that could be maximized for the duration of the conversion of the global economy from fossil fuels to carbon-free alternatives. One of the most widely discussed of these potential sinks is the sequestration of atmospheric carbon (C) in temperate forests, including their biomass, detritus, and soil components (Schimel et al., 2000; Myneni et al., 2001). Recent estimates suggest that terrestrial vegetation, soil, and detritus could be a sink equivalent to 15–30% of annual global emissions from fossil fuels and industrial activity (Myneni et al., 2001). Among the many uncertainties in such estimates are the effects of current and past land-use change, fire regimes, and forest management

practices on the rates of C flux through forests (Foster et al., 2003). For example, Houghton et al. (1999) suggested that fire suppression in North America over the last century had reduced the overall forest sink strength by  $0.5\text{--}2.0 \text{ Pg C year}^{-1}$ , while Dixon et al. (1994) advocated stronger fire suppression in Russia as a step that could increase the sink strength of the Eurasian forests by  $0.1\text{--}0.6 \text{ Pg C year}^{-1}$ . As large portions of the North American forests are in some stage of regrowth following fire, harvesting, or other disturbance, C sequestration estimates generated primarily from mature/old-growth forests are likely not sufficiently representative to be used for regional forest management (Chen et al., 2004). There is, therefore, a critical need to establish C inventories and sequestration rates for forests under different disturbance regimes and management strategies (Chen et al., 2004).

The fire and fire surrogate (FFS) network is composed of forest ecosystems arrayed across the coterminous United States from Washington and California in the west to Alabama, Ohio, and Florida in the east. All of the forest ecosystems represented

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in the FFS network share the attribute of having been converted by fire suppression and other management practices from forests that were subject to frequent, low-severity fires during pre-EuroAmerican settlement to forests that are currently subject to infrequent but catastrophic fires. The primary goal of the FFS Network Study was to assess the effectiveness and ecological consequences of three alternative manipulative management strategies designed to simultaneously reduce wildfire hazard and help restore ecosystem structure and function to a more sustainable condition. As such, the FFS Network Study presents a unique opportunity to assess storage and fluxes of C through selected North American forest ecosystems in relation to geography, fire suppression, and forest management strategies. The specific objectives of this portion of the broader FFS Network Study were to:

- characterize the variation in total C storage among selected North American forests in which fire suppression has affected ecosystem structure;
- characterize the distribution of stored C among ecosystem components in such forests;
- determine the proximate effects on C storage and distribution of three management modes intended to reduce wildfire hazard and restore pre-suppression forest structure: prescribed fire, mechanical treatment, and the combination of the two; and,
- compare rates of C sequestration in the first and subsequent growing seasons after treatment to those predicted by broad-scale modeling studies.

## 2. Methods

### 2.1. Study sites

The twelve FFS study sites ranged from Washington and California to Florida and Ohio (Table 1). The designated FFS experimental design was a randomized complete block, with three blocks and four treatments (control, prescribed fire, mechanical treatment, and the combination of mechanical treatment and prescribed fire) allocated at random to those three blocks. The sole exception to this treatment plan was at the Ca–S site, which was located in a U.S. National Park and therefore could not implement mechanical treatments. In this site, spring and autumn fires were compared to the untreated controls. Due to a variety of logistic constraints, three of the twelve FFS sites were established as completely randomized designs (Ca–N, Ca–S, WA), with the four treatments allocated at random among the twelve treatment units. One site (OR) established four replicates of each treatment in a completely randomized design.

Each treatment unit consisted of a minimum of 10 ha with a buffer zone of at least 4 ha surrounding it. Both the treatment unit and the buffer received the experimental treatment designated for that unit. Among the twelve FFS sites, the treatment units ranged in size from those approximating the minimum 10 ha to as large as 80 ha.

In the designated FFS design, each treatment unit was overlain with a 50 m grid and contained a minimum of 36 labeled grid points. Ten, 0.1-ha rectangular permanent

Table 1  
Geographic information for the twelve fire and fire surrogate network project study sites

Site	Geographic location	Facility	Forest type	Latitude	Longitude	Elevation (m)	Soil orders
CA-N	Southern Cascades Range, CA	Klamath National Forest	Western mixed conifer	41°57'	121°86'	1630	Alfisols, Entisols
CA-C	Central Sierra Nevada, CA	Blodgett Experimental Forest	Western mixed conifer	38°90'	120°65'	1255	Alfisols
WA	Northeastern Cascades Range, WA	Wenatchee National Forest	Ponderosa pine/Douglas-fir	47°26'	120°32'	950	Alfisols, Mollisols
CA-S	Southern Sierra Nevada, CA	Sequoia-Kings Canyon National Park	Western mixed conifer	36°59'	118°76'	2025	Inceptisols
OR	Blue Mountains, OR	Wallowa-Whitman National Forest	Ponderosa pine/Douglas-fir	45°65'	117°23'	1255	Mollisols, Inceptisols
MT	Northern Rocky Mts., MT	Lubrecht Experimental Forest	Ponderosa pine/Douglas-fir	46°90'	113°43'	1150	Alfisols, Inceptisols
AZ	Southwestern Plateau, AZ	Coconino & Kaibab National Forests	Ponderosa pine	35°21'	111°85'	220	Alfisols, Mollisols
AL	Gulf Coastal Plain, AL	Solon-Dixon Forestry & Education Center	Longleaf pine/slash pine	31°16'	86°68'	50	Ultisols, Entisols
OH	Central Appalachian Plateau, OH	Vinton Furnace Experimental Forest, Tar Hollow & Zaleski State Forests	Appalachian oak	39°30'	84°54'	250	Alfisols, Inceptisols
NC	Southern Appalachian Mts., NC	Green River Game Lands	Appalachian oak	34°67'	82°84'	600	Ultisols, Inceptisols
SC	Southeastern Piedmont, SC	Clemson University Forest	Loblolly pine/oak	35°21'	82°37'	250	Alfisols, Inceptisols
FL	Florida Coastal Plain, FL	Myakka River State Park	Florida slash pine	27°26'	82°28'	25	Spodosols

Sites are ordered by longitude from west to east.

sampling plots were located at random within each treatment unit with one corner anchored at a grid point. Two of the twelve FFS sites (Ca–C, OR) deviated from this base design. The Ca–C site utilized 20, 405-m<sup>2</sup> circular plots per unit and the OR site had an average of 24 circular plots of 200 m<sup>2</sup> for the pre-treatment sampling and 400 m<sup>2</sup> for the second post-treatment sampling.

Vegetation components, soil, and fuels were sampled during the pre-treatment growing season, the growing season immediately following the completion of the treatment implementation, and where logistically possible, an additional post-treatment year as late in the funding period as possible (usually the second year after treatment, but the third year for the NC and SC sites, and the fourth for the OH site). Two sites (Ca–N, OR) had incomplete pre-treatment sampling because their units and treatments had been installed before the designated FFS design was established, and logistic constraints resulted in pre-treatment sampling being incomplete in one additional site (Ca–S).

## 2.2. Field sampling methods

Each live and dead tree  $\geq 10$  cm diameter at breast height (dbh, 1.37 m) in each permanently marked vegetation plot was marked, identified, and measured (dbh, height, and various crown condition parameters) during the pre-treatment sampling year, and remeasured during each subsequent sampling. Stems growing into the tree size class were marked, identified, and measured the year they were  $\geq 10$  cm dbh, and followed thereafter. Saplings (stems  $> 1.37$  m height but  $< 10$  cm dbh), seedlings ( $\leq 1.37$  m height), and the cover of shrubs, forbs, and graminoids were measured in subplots nested within the larger vegetation plots in all sites. Shrub, forb, and graminoid biomass was only measured directly in sites where these components were judged to be significant fuel sources. The number and size of the subplots varied among FFS sites in relation to stem density and plant diversity (details for each site are given by McIver (2001)).

Standing dead wood was sampled using the same methods as were used for live vegetation. The mass of downed, dead wood  $\geq 75$  mm in diameter was estimated using the planar intercept method of Brown (1974) supplemented with strip plots. In most sites, two 20 m transects were run from each of the 36 grid points in each treatment unit, and the number of intercepts of woody materials in four size classes (0–6 mm, 6–25 mm, 25–75 mm, and 75–150 mm diameters) was tallied. To allow for unique situations, the number of transects or grid points was increased or decreased in selected sites (details given by McIver (2001)). To assess the mass and spatial distribution of larger woody debris, strip plots (4 m  $\times$  20 m) were established at a minimum of 50% of the grid points sampled by the planar intercept method. Within each strip plot, logs or parts of logs  $\geq 1$  m in length and  $> 150$  mm diameter at the larger end were identified, their length within the strip plots measured, and their diameters measured at their ends or at the point(s) whether they intercept the boundary of the strip plot. Materials in the 75–150 mm and  $> 150$  mm size classes were identified to

species where possible, and the decay condition of each was noted. Subsamples from each size class at each site were dried and weighed to produce mass and density estimates. Sampling of woody debris in all size classes was done during the pre-treatment year, the initial post-treatment year, and (where possible) a later sampling year.

The mass of the forest floor (organic horizon) was considered to be the sum of the Oi, Oe, and Oa (L, F, and H) subhorizons (where present) exclusive of woody materials. To estimate forest floor mass, 0.1 m<sup>2</sup> plots at the ends of each of the woody debris transect were excavated and the depth of each subhorizon was measured on all four faces of the excavated plot; each forest floor subhorizon was then sorted separately and transported back to the laboratory where they were dried at 70 °C and weighed. This resulted in 36–72 replicates for each forest floor subhorizon in each treatment unit. Regressions of forest floor mass on depth (by subhorizon where applicable) were then constructed for each treatment unit. In plots that were to be burned (fire and mechanical + fire), a series of eight “duff pins” were installed in each of the 0.1 ha vegetation sampling plots prior to the fire, and the depth of each forest floor subhorizon was determined both before and after the fire. The mass-depth regressions generated by destructive sampling were then used to estimate the pre-fire and post-fire forest floor horizon mass at each of those points.

Mineral soils were typically sampled either near the corners of the permanent sampling plots or in a subplot established within the permanent sampling plot. Mineral soils were sampled during the pre-treatment year in all sites, though not all sites took a complete set of pre-treatment samples. All sites sampled mineral soils during the first post-treatment growing season and eight of the twelve sampled again during a subsequent growing season.

The upper forest floor (Oi, Oe) subhorizons, if present, were removed prior to sampling the mineral soil. If no distinct boundary occurred between the Oa (H) subhorizon and the A horizon, the Oa was included in the sampling of the surface mineral soil and not in the sampling of the forest floor subhorizons. In sites where a distinct horizon boundary between the A/E and O was present, the Oa was sampled separately as part of the fuels assessment, and mineral soil samples were taken either for the full depth of the A horizon or to 15 cm, whichever was less. As the depths of the rooting zone varied from  $\sim 30$  to  $> 150$  cm among FFS sites and some sites reported soil C concentrations by horizon rather than depth, we calculated a single, weighted average (WSC) using the following equation from Johnson and Curtis (2001):

$$WSC = \frac{\sum(C_d(D))}{\sum D} \quad (1)$$

where  $D$  is the depth and  $C_d$  is the C concentration at depth  $D$ . We chose the modal depth of the rooting zone among the FFS sites (30 cm) as the arbitrary depth for pool size estimation, and then estimated soil organic C on an area basis using WSC and bulk density estimates.

The area of each treatment unit in which bare mineral soil was exposed at the surface was visually estimated at a minimum of 200 and maximum of 2000 points per treatment unit during each sampling year. Bulk density was determined on a minimum of 20 core samples per treatment unit or estimated from a minimum of 200 soil strength (penetrometer) measurements per treatment unit using site-specific regressions of bulk density on soil strength. Organic C concentration in mineral soil and forest floor subhorizons were determined by microDumas oxidation; corrections for inorganic C were made in sites where inorganic C may have been significant component of the total C pool.

To convert live and dead tree basal area and height measurements to aboveground biomass, allometric (regression) equations were obtained from the compilation of North American tree species biomass regressions of Jenkins et al. (2004). Although we initially employed species-specific equations for the dominant species where possible, inconsistencies among equations for a given species and among equations for closely related species led to our abandoning this approach in favor of the ten-species group equations given by Jenkins et al. (2004), all of which had  $r^2 > 0.938$ . Total dry biomass estimates from the species group equations were then allocated into foliage, stem + branch bark and stem + branch wood using the component ratio equations of Jenkins et al. (2003), cited in Jenkins et al. (2004). Within species groups, stemwood biomass estimates were adjusted using estimates of wood specific gravity derived from Jenkins et al. (2004) and the additional references listed in Appendix A.

For stems <10 cm dbh, we used a single biomass estimate for each species group as the geometric mean of the estimated biomass of a 2.5, 5.0, 7.5, and 10.0 cm dbh stems, and used that single estimate for all saplings of that group in the 2.5–10 cm dbh range. We validated these sapling estimates against outputs from a set of regressions that was based on stems that spanned those sizes (the *Cornus florida* equations from Boerner and Kost, 1986). The *Cornus* equations yielded a geometric mean of 8.45 kg stem<sup>-1</sup>, compared with geometric means of 8.44–8.59 kg stem<sup>-1</sup> for the species group equations.

As indicated above, C concentrations in mineral soil organic matter and forest floor subhorizons were determined empirically in each site. In contrast, analyses of C in vegetation and dead wood compartments were available for only a few sites; thus, we depended on literature sources for estimates of C in vegetation and dead wood in most sites. Estimates of the C concentration in various biomass components (i.e., wood, bark, and foliage) were difficult to obtain, and many C inventory studies rely on a general estimate of [C] of dry plant biomass being 50% C (Lalmon and Savidge, 2003). For species for which we could not obtain direct C concentrations from the literature, we combined the wood specific gravity estimates from Jenkins et al. (2004) with the estimates of C storage in dry wood in 18 species-by-geographic region groupings given by Skog and Nicholson (2000; Table 2). Carbon concentrations in foliage and bark for those species were then estimated from published estimates of carbon-to-nitrogen mass ratios and tissue nitrogen (N) concentrations.

### 2.3. Data analysis

Although analysis of the effects of the FFS treatments on C stocks within a site could be analyzed in a straightforward manner using analysis of variance approaches, we felt this was not the most appropriate manner to analyze the results at the network scale. First, the specifics of the experimental design varied in subtle though important ways among the twelve sites. For example, some sites had sufficient pre-treatment measurements to use pre-treatment conditions as covariates whereas others did not. Similarly, some sites established their treatment units in a spatial manner that would permit analysis as a split-plot or complete block design whereas others did not. In light of such differences, we judged that resorting to a least-common-denominator analysis of variance model would serve little purpose. Second, the absolute magnitude of the effects of the FFS treatments on C stores was relatively modest compared to the variations among network sites in total C stocks and distributions of C among vegetation, dead wood, forest floor, and mineral soil components; hence, any single, analysis of variance-based approach would tend to obscure the impact of these treatments across the network of sites.

Instead, we first took a meta-analytical approach, as this would allow us to treat each network site as a single experiment with  $n = 3$  for each treatment at each site (except OR in which  $n = 4$ ). For each study site, the effect size (ES) was estimated as

$$ES = \frac{\bar{X}_t - \bar{X}_c}{s_p} \quad (2)$$

where  $X_t$  is the mean for the treatment in question,  $X_c$  the mean for the control, and  $S_p$  is the pooled standard deviation for the two groups.

As the effect size calculated in this manner is biased when used with small sample sizes, we adjusted the effect size for the sample size of  $n = 3$  per treatment per site ( $n = 4$  for OR) using Hedge's  $d$ :

$$d_i = \left(1 - \frac{3}{4(n_t + n_c) - 9}\right) ES \quad (3)$$

where  $d_i$  is the adjusted effect size for each individual site and ES was the unadjusted effect size.

To calculate the cumulative effect size at the FFS network scale, we used a random effects model because we assumed that variability among effect sizes was due to both subject-level “noise” and true unmeasured differences across studies (Raudenbush, 1994; Rosenberg et al., 2000). This, in turn, required estimation of both the pooled study variance and the total heterogeneity of a given sample, with the latter being used to test the hypothesis that all effect sizes were equal using the Chi-squared distribution with  $k - 1$  degrees of freedom (Gurevitch and Hedges, 1993). Means and 95% confidence intervals of the FFS effect size were calculated using MetaWin 2.0, and effect sizes were considered statistically significant if the 95% confidence interval did not overlap 0 (Rosenberg et al., 2000). To allow for variations among sites in the time between

the initial and final post-treatment samplings, net effects during the later sampling period were calculated on an annual basis.

### 3. Results and discussion

#### 3.1. C storage patterns

Across the forests of the FFS Network, the patterns of C storage (both ecosystem totals and distribution of C among

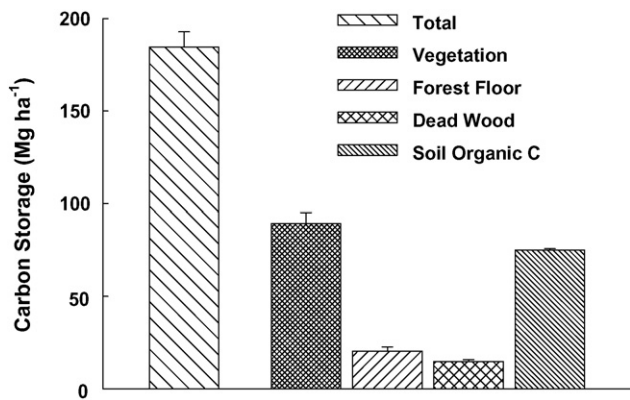


Fig. 1. Mean carbon storage in  $\text{Mg ha}^{-1}$  in various forest compartments for the twelve fire and fire surrogate (FFS) network sites. Error bars denote plus one standard error of the mean.

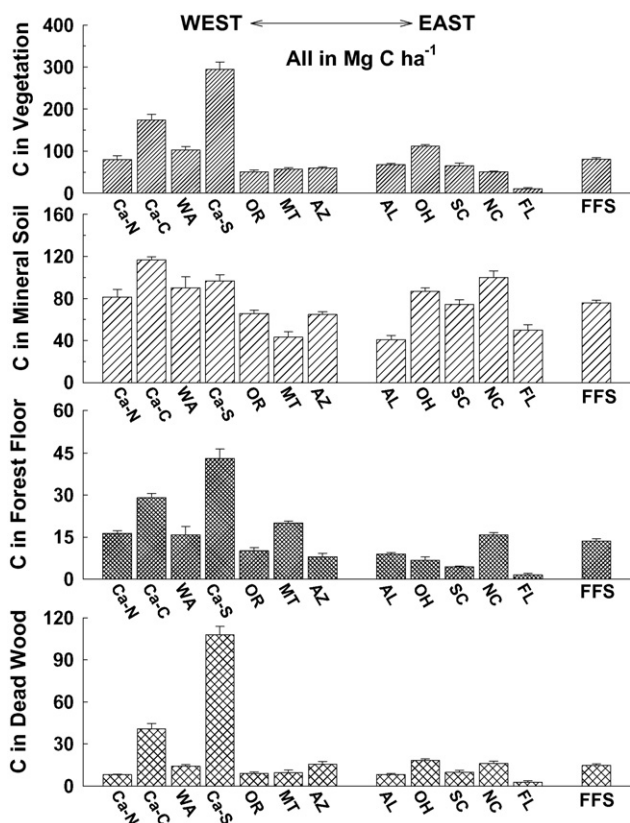


Fig. 2. Mean carbon storage ( $\text{Mg ha}^{-1}$ ) in four ecosystem compartments in the twelve FFS Network sites. Error bars denote plus one standard error of the mean. The bar at the extreme right represents the Network mean, excluding Ca-S and FL Site codes follow Table 1.

ecosystem compartments) were strikingly similar to patterns of C storage generated for forests of the coterminous U.S. in previous studies (Figs. 1 and 2; a full listing of carbon stocks by component, site, treatment, and year is published as an on-line supplement to this paper). Across the full FFS Network, estimated total ecosystem C storage (defined as C in above-ground vegetation + forest floor + dead wood + mineral soil to 30 cm) averaged  $185 \pm 8$  (standard error of the mean) -  $\text{Mg C ha}^{-1}$ . The six western sites used in the meta-analysis averaged  $171 \pm 6 \text{ Mg C ha}^{-1}$ , while the four eastern sites averaged  $196 \pm 12 \text{ Mg C ha}^{-1}$ . Using forest and soils inventory data, Heath et al. (2003) reported the average total C stored in forest ecosystems of the coterminous U.S. in 1997 was about  $203 \text{ Mg C ha}^{-1}$ . The average value from Heath et al. (2003) is higher than values from the FFS Network due, in part, to their inclusion of C stores up to a 1-m soil depth. The average C storage for all western forests (timberland only) across the coterminous U.S. in 1997 was about  $193 \text{ Mg ha}^{-1}$ , while the average C storage of all eastern forests (timberland only) was about  $210 \text{ Mg ha}^{-1}$  (Heath et al., 2003). These comparisons

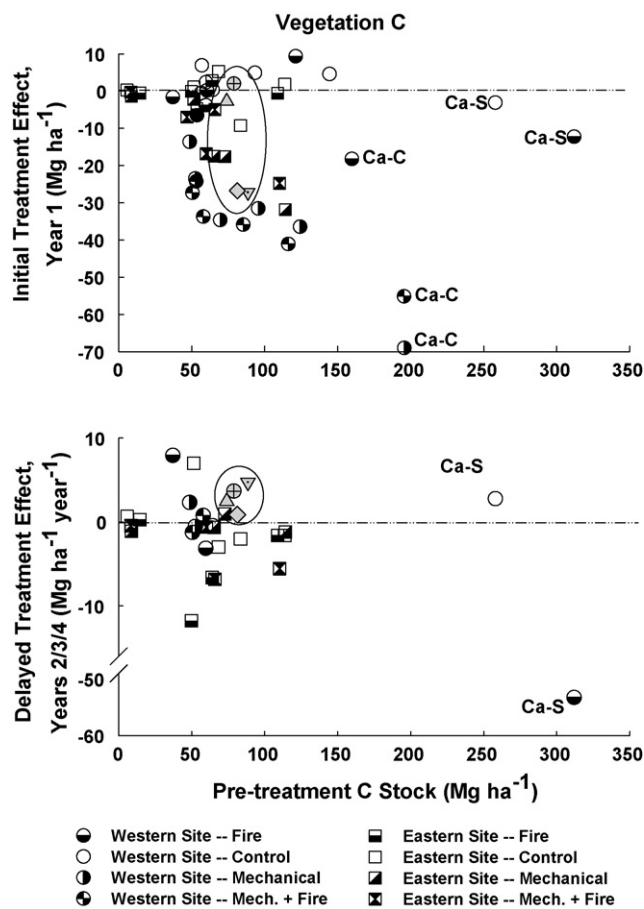


Fig. 3. Net changes in carbon storage ( $\text{Mg ha}^{-1} \text{ year}^{-1}$ ) in aboveground vegetation during the first post-treatment year (top) and subsequent sampling year (2nd, 3rd, or 4th growing season following treatment; bottom) relative to the pre-treatment aboveground vegetation carbon stock ( $\text{Mg ha}^{-1}$ ) for the fire and fire surrogate (FFS) sites. Net changes for the subsequent sampling year were estimated relative to values after the first post-treatment year. The ellipse in each panel encompasses the overall FFS network means. Site codes follow Table 1.

suggest that C storage in FFS Network forests was representative of forests across the coterminous U.S. in general, and they also increase our confidence in the accuracy of our estimates.

Based on our definitions, we estimate that across all twelve of these forests an average of 45% of the total ecosystem C was in vegetation, 38% in soil organic matter, 10% in the forest floor, and 7% in dead wood (both standing and downed; Fig. 1). This distribution of C among ecosystem compartments differs from previous estimates that indicate that the mineral soil contains about 50% (Turner et al., 1995; Heath et al., 2003) to 67% (Dixon et al., 1994; Johnson and Curtis, 2001) of total ecosystem C; however, as noted above, these differences are likely due to limiting our extrapolation of mineral soil C to a 30 cm soil depth, compared with depths of 1 m or more in other studies.

Estimated C stocks in live, aboveground vegetation among the ten sites used in the meta-analysis ranged from 50 to 174 Mg C ha<sup>-1</sup>, with an average of 81 ± 4 Mg C ha<sup>-1</sup> (Fig. 2). For comparison, Dixon et al. (1994), Turner et al. (1995), and Heath et al. (2003) estimate aboveground C storage in

forest vegetation across the coterminous U.S. averages 61–66 Mg C ha<sup>-1</sup>. The lower average value from these broad-scale estimates than our specific-site estimates is probably the result of our estimates not including young, early successional forests or forests in parts of the U.S. that typically have lower standing tree basal area (e.g., woodlands).

The two sites that were excluded from the meta-analysis because they did not have a full, replicated set of FFS treatments were also the network outliers in terms of vegetation C storage. The Florida Coast Plain (FL) site dominated by Florida slash pine (*Pinus ellioti* var *densa*) had vegetation C storage of only 11 Mg C ha<sup>-1</sup>, whereas the southern Sierra Nevada mixed-conifer (*Abies concolor*/*Pinus lambertiana*/*Pinus jeffreyi*) site in California (Ca-S) had 294 Mg C ha<sup>-1</sup> in vegetation. Heath et al. (2003) also reported a wide range in average C storage in vegetation among contrasting forest (timberland) types across the coterminous U.S. For instance, they estimated the average C storage in vegetation in piñon-juniper woodlands was ~25 Mg C ha<sup>-1</sup>, while on average 151 Mg C ha<sup>-1</sup> was stored in aboveground vegetation in redwood forests.

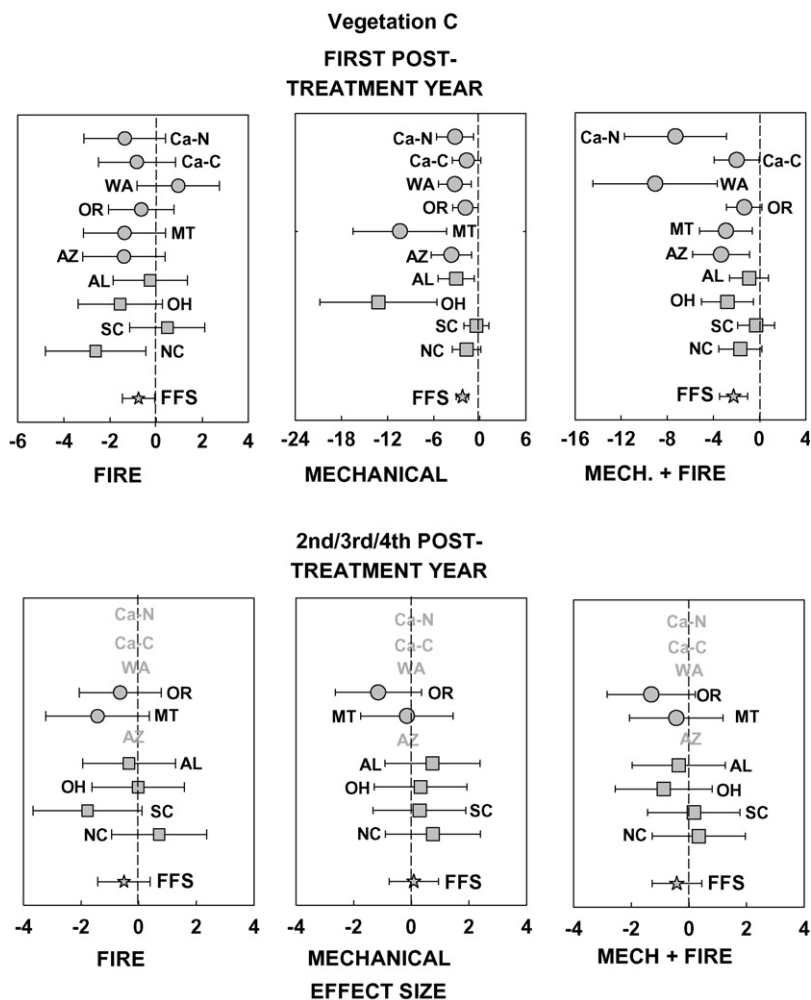


Fig. 4. Summary of the meta-analysis of the effects of three fire and fire surrogate (FFS) treatments on aboveground vegetation carbon stocks (Mg ha<sup>-1</sup>) during the first (top) and subsequent (2nd, 3rd, or 4th) growing season following treatment; bottom) sampling years. Symbols represent mean effect size, with error bars depicting the 95% confidence interval for the mean effect size. Sites for which insufficient data were available to test a given treatment-year combination are indicated by the site code in gray along the zero effect line. Site codes follow Table 1.

Given the coupling between vegetation and detritus in terrestrial ecosystems, it is not surprising that the amount of C stored in dead biomass (i.e., forest floor and dead wood) showed a similar pattern across the FFS Network sites as the amount of C stored in aboveground vegetation (adj.  $r^2 = 0.912$ ,  $p < 0.001$ ,  $n = 12$ ; Fig. 2). Across all FFS sites, C storage in dead biomass ranged from ~4 to 151 Mg C ha<sup>-1</sup>, which is similar in magnitude to the range of average values for different forest types in the U.S. reported by Heath et al. (2003); 2.9 to 73.0 Mg C ha<sup>-1</sup>). As has been found in regional analyses previously (e.g., Heath et al., 2003), western sites tended to have more C stored in dead biomass than eastern sites (averages of ~50 and ~18 Mg C ha<sup>-1</sup>, respectively), as well as more C stored in vegetation (Fig. 2).

Organic C storage in mineral soils varied less across the FFS Network than did the other measured ecosystem C compartments, and this finding was similar to the results from broad-scale analyses across the coterminous U.S. (e.g., Heath et al., 2003; Fig. 2). Across the entire FFS Network, soil organic C storage ranged from about 40–120 Mg ha<sup>-1</sup> in the upper 30 cm of mineral soil, and C stored in this pool was not as well correlated with the amount of C stored in vegetation (adj.  $r^2 = 0.295$ ,  $p = 0.040$ ,  $n = 12$ ) as was dead biomass. Across the ten sites of FFS network used in the meta-analysis, storage of C in soil organic matter averaged  $76 \pm 3$  Mg C ha<sup>-1</sup>. The two FFS sites that were excluded from the meta-analyses were also network outliers relative to the other sites in terms of soil organic C storage. The FL site had an exceptionally low amount of C stored in mineral soil (50 Mg C ha<sup>-1</sup>), while Ca-S had an exceptionally high amount of C stored in this pool (97 Mg C ha<sup>-1</sup>). We found that soil organic C content was highly variable within sites among both years and treatments. Similarly, Knoepp and Swank (1997) reported that soil organic C in their unmanaged reference stands in North Carolina varied by almost twofold over a 17-year period, with the variations random with respect to time. Whether such variability is the result of actual spatial and temporal heterogeneity or represents sampling artifacts is open to argument (Knoepp and Swank, 1997).

### 3.2. FFS treatment effects

#### 3.2.1. Vegetation

Across the network, C storage in aboveground vegetation changed little between pre-treatment and one-year post-treatment values in the control and the fire treatment units (Fig. 3). In contrast, the mechanical and mechanical + fire treatments resulted in a network-wide average loss of C of approximately 30 Mg ha<sup>-1</sup> during the first growing season following treatment, presumably dominated by removal of woody biomass during the treatment itself. Mechanical treatment prescriptions called for reductions of 20–45% in basal area among FFS sites, and the loss of this amount of C from the vegetation pool is consistent with this prescription (see Figs. 1 and 2 for pre-treatment vegetation C-pool estimate). There was somewhat greater removal of vegetation C from the western sites (34.8 and 36.3 Mg C ha<sup>-1</sup> for the mechanical and the mechanical + fire treatments, respectively) than from the

eastern sites (17.3 and 13.4 Mg C ha<sup>-1</sup>, respectively). At the network scale, estimated C storage in vegetation changed little between the first post-treatment growing season and the last sampling period (hereafter referred to as “subsequent sampling years”), with the exception of the fire treatment at the Ca-S site where approximately 18% of the vegetation C was lost during the second and third years after treatment (Fig. 3). Meta-analysis demonstrated significant, first year losses of vegetation C at the network scale in response to all three treatments (Fig. 4). Only one site exhibited a significant loss of C in vegetation as a result of prescribed fire alone (NC), whereas eight of the ten sites included in the meta-analysis exhibited significant losses of vegetation C as the result of mechanical treatment. The combination of mechanical treatment and fire resulted in significant, first year losses of vegetation C in five of ten sites. There were no significant changes in vegetation C during the subsequent sampling years at either the network or site levels.

#### 3.2.2. Forest floor, dead wood, and soil organic matter

During the first post-treatment year, controls and mechanically treated units exhibited little change in forest floor C (Fig. 5). In contrast, there was a significant, network-wide

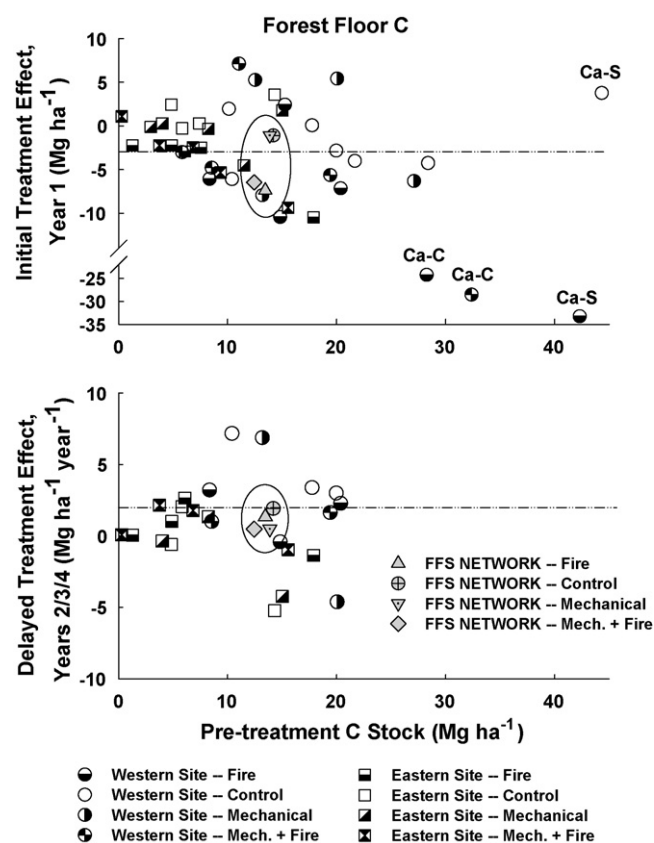


Fig. 5. Net changes in carbon storage (Mg ha<sup>-1</sup> year<sup>-1</sup>) in the forest floor during the first post-treatment year (top) and subsequent sampling year (2nd, 3rd, or 4th growing season following treatment; bottom) relative to the pre-treatment aboveground vegetation carbon stock (Mg ha<sup>-1</sup>) for the fire and fire surrogate (FFS) sites. Net changes for the subsequent sampling year were estimated relative to the first post-treatment year. The ellipse in each panel encompasses the overall FFS network means. Site codes follow Table 1.

reduction in forest floor C during the first post-treatment year by an average of 7.3 Mg C ha<sup>-1</sup> from fire alone and 6.5 Mg C ha<sup>-1</sup> from the combination of the mechanical treatment and fire. However, most of these losses were from the relatively fast-turnover litter rather than the more persistent “duff” (Oe + Oa) layer (data not shown). The exceptions to this pattern were the fire units at the Ca-S and Ca-C sites (the two sites with the greatest total estimated C storage and greatest fire severity, where flame lengths of 3 m or more were reported) and the mechanical + fire units at the Ca-C site, which lost 25–35 Mg C ha<sup>-1</sup> during the initial post-treatment year. At the network scale, none of the treatments resulted in significant change in forest floor C over the subsequent sampling years (Fig. 5), though a few individual site-by-treatment combinations exhibited gains or losses on the order of 5–8 Mg C ha<sup>-1</sup> year<sup>-1</sup>. Meta-analysis revealed significant first year losses of forest floor C as a result of the fire and mechanical + fire treatments at the network scale, but not the mechanical treatment alone (Fig. 6). There were no significant network-wide effects of any of the treatments during the

subsequent sampling years, and significant site-level effects were uncommon.

Pre-treatment C storage in dead wood was generally <20 Mg ha<sup>-1</sup> and was similar at the first post-treatment year in most of the FFS sites. Notable exceptions were increases of 100–150% in dead wood C storage after mechanical and mechanical + fire treatments at the WA site (in which helicopter logging was employed), and losses of ~20 Mg C ha<sup>-1</sup> after fire at the Ca-S and Ca-C sites (in which fire severity was at the high end of the network range; Fig. 7). During the subsequent sampling years, there were average increases in dead wood C on the order of 40% in the fire and mechanical + fire treatments, but little change in the control and mechanical treatments (Fig. 7). Meta-analysis revealed no significant, network-wide effect of fire or mechanical treatment on dead wood C, either in the first post-treatment year or during subsequent sampling years, or the mechanical + fire treatment during the subsequent sampling years (Fig. 8). In contrast, the combination of mechanical treatment and fire did result in a significant, network-wide first year gain of ~2.5 Mg ha<sup>-1</sup> in dead wood C,

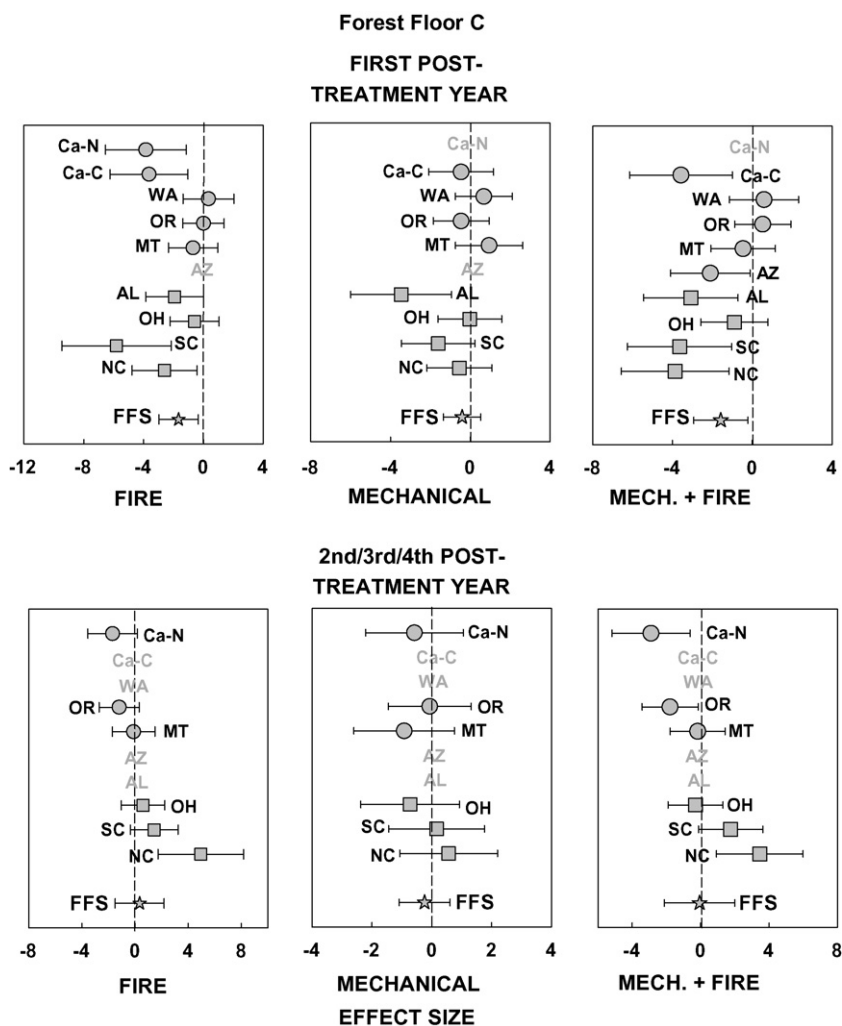


Fig. 6. Summary of the meta-analysis of the effects of three fire and fire surrogate (FFS) treatments on forest floor carbon stocks (Mg C ha<sup>-1</sup>) during the first (top) and subsequent (2nd, 3rd, or 4th growing season following treatment; bottom) sampling years. Symbols represent mean effect size, with error bars depicting the 95% confidence interval for the mean effect size. Sites for which insufficient data were available to test a given treatment-year combination are indicated by the site code in gray along the zero effect line. Site codes follow Table 1.

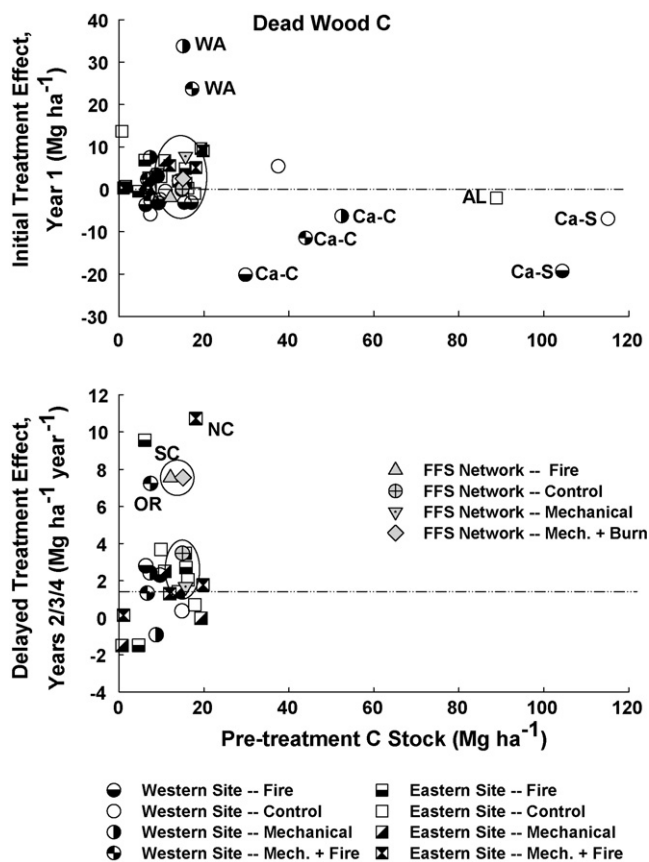


Fig. 7. Net changes in carbon storage ( $\text{Mg ha}^{-1} \text{ year}^{-1}$ ) in dead wood (standing and downed) during the first post-treatment year (top) and subsequent sampling year (2nd, 3rd, or 4th growing season following treatment; bottom) relative to the pre-treatment aboveground vegetation carbon stock ( $\text{Mg ha}^{-1}$ ) for the fire and fire surrogate (FFS) sites. Net changes for the subsequent sampling year were estimated relative to values after the first post-treatment year. The ellipse in each panel encompasses the overall FFS network means. Site codes follow Table 1.

primarily the result of an increase of  $>20 \text{ Mg C ha}^{-1}$  at the ponderosa pine/Douglas-fir (*Pinus ponderosa/Pseudotsuga menziesii*) site in the northeastern Cascades Range of WA.

Soil organic C was highly variable from year to year, both within and among network sites (Fig. 9). Across the network, changes in soil organic C averaged  $<10\%$  of pre-treatment stocks during both the initial post-treatment year and the subsequent sampling years; however, individual site-by-treatment combinations exhibited considerably larger changes during the first post-treatment year (as much as  $\pm 30 \text{ Mg C ha}^{-1}$ ; Fig. 9). Meta-analysis demonstrated no significant, network-wide effect of any of the FFS treatments on soil organic C during either sampling period (Fig. 10). Significant site-level effects were uncommon and appeared to be idiosyncratic.

The forest floor, particularly the litter (Oi) layer, is one of the most dynamic C pools in forests (Yanai et al., 2003). Prescribed fire, either alone or in combination with mechanical treatment, significantly reduced C stores in this ecosystem compartment the first year following treatment across the FFS Network. Page-Dumroese et al. (2003) suggest that this C pool (including highly decayed dead wood) is the most susceptible to loss via

prescribed or wildfire, accounting for the vast majority of ecosystem C loss both during and subsequent to the fire. However, our results and others (Hall et al., 2006) indicate that this C pool rapidly returns to its pre-disturbance state unless vegetation biomass is substantially reduced for extended periods of time (Dore et al., 2008).

In many forests, dead wood represents a substantial storehouse for terrestrial ecosystem C (Harmon et al., 1990). We found that this C pool changed significantly across the network of sites only in the mechanical + fire treatment and only during the first growing season following treatment. This result suggests that, under the fuel management or restoration treatments designed to reduce the likelihood of stand-replacing wildfire or return ecosystem structure or function to pre-EuroAmerican conditions in ecosystems such as those we studied, C stored in dead wood compartments are not likely to change substantially. This pattern is in contrast to other more major disturbances such as stand-replacing wildfire where dead wood can continue to accumulate for over a century (Hall et al., 2006).

Results of previous studies of the effects of prescribed fire on mineral soil organic C in coniferous forests vary as much in magnitude and direction as they do in geography, soil types, fire severity, and tree species. Most of the available studies indicate that repeated prescribed fire has little impact on soil organic C (e.g., Moehring et al., 1966; McKee, 1982; Richter et al., 1982), and in a recent study in a longleaf pine (*Pinus palustris*) ecosystem, Wilson et al. (2002) found that soil organic C varied more strongly as a function of landscape position than with fire. Some studies have demonstrated significant decreases in soil organic C as the result of repeated prescribed burns (e.g., Hunt and Simpson, 1985; Mabuhay et al., 2003), while other studies show an increase in soil organic C after prescribed fire (e.g., Wells, 1971).

Fire severity is an important factor regulating the effect of fire on soil organic C. For example, Groeschl et al. (1990) found that areas of a Virginia Table Mountain pine (*Pinus pungens*) forest that experienced low-severity fires had 11% more soil organic C than unburned reference stands, whereas areas that experienced high-severity fire had 19% less soil organic C than the unburned stands. They attributed the difference to their low-severity stands having some combusted forest floor left to contribute charcoal and fine organic matter to the soil, whereas their high-severity burn had lost the entire forest floor and had experienced significant post-fire erosion.

Despite a rich literature from coniferous ecosystems that demonstrates the potential for significant losses of soil organic matter during and after fire, few studies have demonstrated major changes in soil organic matter content following fire in oak-rich forests of the eastern U.S. (Boerner, 2006). Knighton (1977) and Knoepp et al. (2004) observed no significant changes in soil organic C as the result of one to three fires in Wisconsin oak (*Quercus* spp.) forests and oak-pine (*Quercus-Pinus*) stands in North Carolina, respectively. Only slight increases in soil organic C were observed in Ohio oak-hickory (*Quercus-Carya*) sites subjected to one to four prescribed fires (Boerner et al., 2000, 2004).

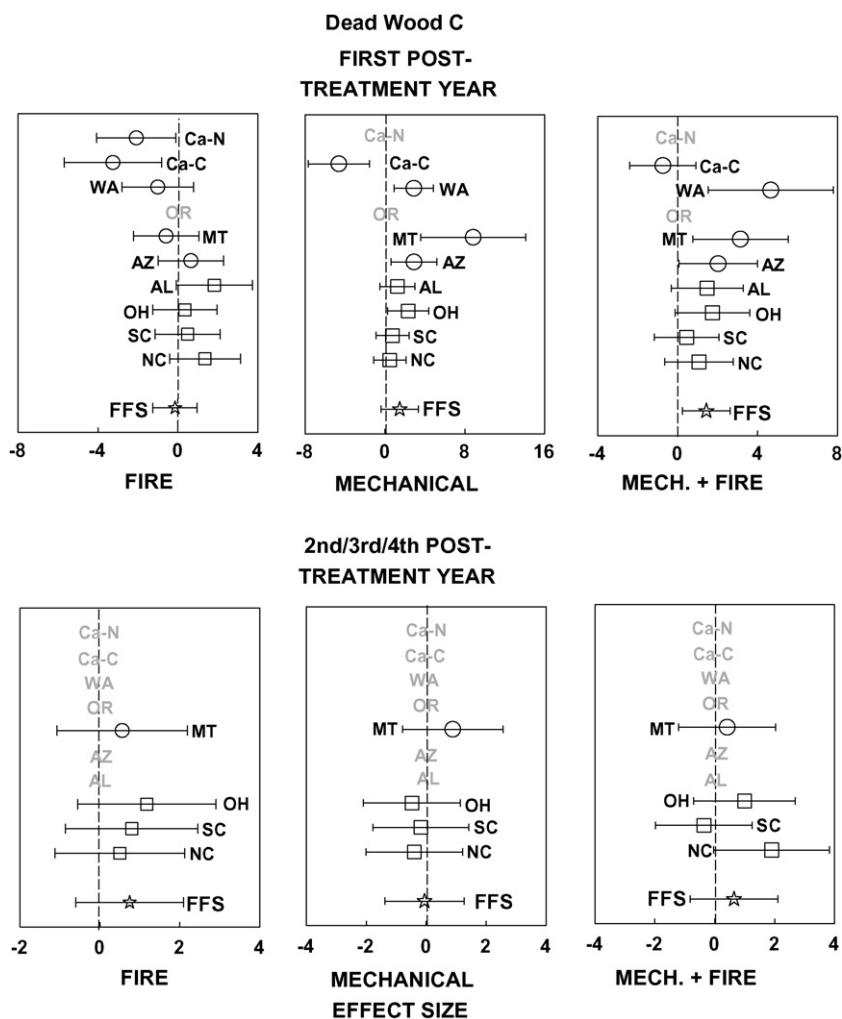


Fig. 8. Summary of the meta-analysis of the effects of three fire and fire surrogate (FFS) treatments on dead wood (standing and downed) carbon stocks ( $\text{Mg ha}^{-1}$ ) during the first (top) and subsequent (2nd, 3rd, or 4th growing season following treatment; bottom) sampling years. Symbols represent mean effect size, with error bars depicting the 95% confidence interval for the mean effect size. Sites for which insufficient data were available to test a given treatment-year combination are indicated by the site code in grey along the zero effect line. Site codes follow Table 1.

Mineral soil C may increase after harvesting as the result of incorporation of forest floor materials into the soil, and return to pre-harvest C levels may take from  $<4$  to  $>20$  years (compare Smethurst and Niambiar, 1990 with Knoepp and Swank, 1997; Black and Hardon, 1995). Most of the available literature that considers the effects of harvesting on forest floor and soil organic C are based upon much more intensive harvesting than is represented by our mechanical treatments. For example, Carter et al. (2002) reported significant, short-term losses of soil organic C after clearcutting of loblolly pine plantations in Texas and Louisiana.

Similarly, prior studies of the effect of the combination of mechanical treatment and prescribed fire on soil organic C also focus primarily on more intense harvesting practices. For instance, Knoepp et al. (2004) attempted restoration of degraded pitch pine-mixed oak (*Pinus rigida-Quercus* spp.) stands in western North Carolina by cutting all woody material and burning in late summer when intensity would be at a maximum. They observed no effect of this treatment on soil organic C. In contrast, Gholz and Fisher (1982) observed a

short-term doubling of soil organic C after clearcutting, burning, and site preparation in a Florida slash pine (*Pinus elliotti* var. *densa*) plantation. As the added organic C was highly labile, it was rapidly degraded and pre-harvest soil organic C levels were restored within five years (Gholz and Fisher, 1982).

In an extensive meta-analysis of the effects of forest management on soil C and N, Johnson and Curtis (2001) noted no overall net effect of fire on mineral soil C; however, studies that examined soils  $>10$  years after fire show increases in soil C whereas studies performed during the first 10 years after fire demonstrated no significant change in soil C. More relevant to the FFS network was their conclusion that prescribed fire generally produced decreases in soil organic C, broadcast slash burning had no significant effect, and wildfire generally resulted in increased soil organic C. The fires applied in the FFS treatments would fall, for the most part, in the first two categories, and the network-wide results of those fires are generally consistent with the trends reported by Johnson and Curtis (2001).

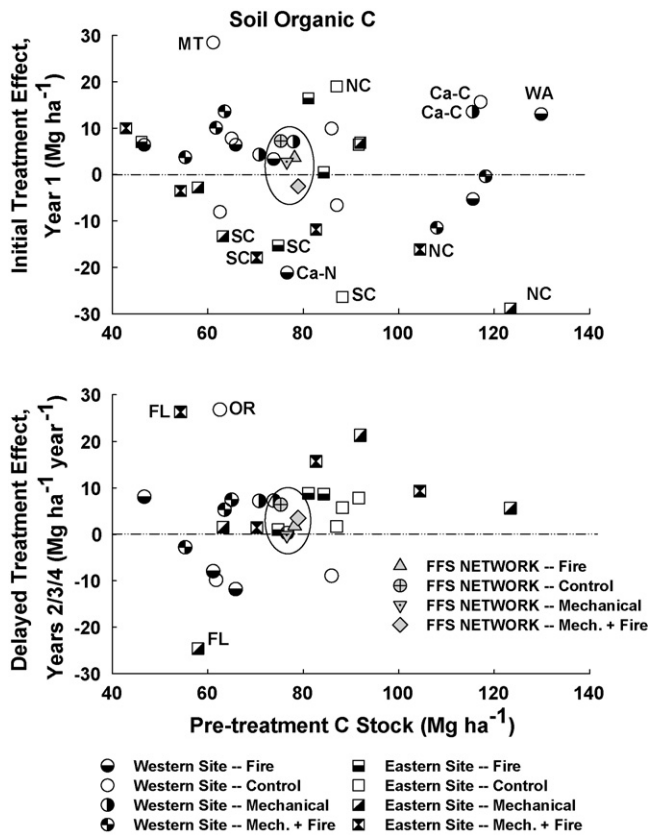


Fig. 9. Net changes in carbon storage (Mg ha<sup>-1</sup> year<sup>-1</sup>) in mineral soil (0–30 cm depth) during the first post-treatment year (top) and subsequent sampling year (2nd, 3rd, or 4th growing season following treatment; bottom) relative to the pre-treatment aboveground vegetation carbon stock (Mg ha<sup>-1</sup>) for the fire and fire surrogate (FFS) sites. Net changes for the subsequent sampling year were estimated relative to values after the first post-treatment year. The ellipse in each panel encompasses the overall FFS network means. Site codes follow Table 1.

One factor that could influence differentially the trajectory of soil C and N, both during and after the period covered by this study, is colonization by N-fixing shrubs and/or herbs. In western coniferous forests, a significant portion of N lost during and shortly after fire may be offset by N-fixation (Agee, 1993). Although the presence of N-fixing shrubs such as *Ceanothus* spp. has been noted in some of the western sites, overall shrub and forb cover changed little in those sites in response to the FFS treatments (pre-treatment shrub and forb cover: 8.0 ± 0.9% and 5.8 ± 0.5%, respectively; first year-post treatment: 5.7 ± 0.6% and 10.4 ± 1.1%; 2nd/3rd year post-treatment: 9.0 ± 1.0% and 15.3 ± 1.3%; unpublished data, FFS Network Data Base). Although it is possible that relative cover of N-fixers increased while that of non-N-fixers decreased, the resolution of the FFS vegetation data base does not permit us to evaluate this possibility.

In the eastern forests, the N-fixing tree *Robinia pseudoacacia* (black locust) and the N-fixing herb genera *Desmodium* and *Lespedeza* are both common and widespread (Boring and Swank, 1984; Hendricks and Boring, 1999). *R. pseudoacacia* was almost absent from the FFS treatment units and its abundance did not increase as a result of the treatments

(unpublished data, FFS Network Data Base); similarly, total forb cover did not change significantly over the three points in time for which we have estimates (pre-treatment: 3.5 ± 0.5%; first year post-treatment 4.9 ± 0.5%; 2nd/3rd/4th year post-treatment 5.7 ± 0.9%), though, once again, we cannot determine whether a shift in forb community composition towards greater abundance of N-fixers took place.

The meta-analysis of management effects on forest mineral soil C of Johnson and Curtis (2001) concluded that harvesting had little net effect on soil organic C. When summed over many studies, the effects of harvesting centered on 0% change, and the 95% confidence interval (CI) for the mean overlapped zero; however, rare individual studies did indicate changes as much as ±20–30%. Johnson and Curtis (2001) did note, however, that harvesting in conifer forests resulted in net increases in soil C whereas harvesting in hardwood stands did not. Overall, the results from the FFS study are consistent with the patterns derived in the meta-analysis of Johnson and Curtis (2001), suggesting that single mechanical treatments conducted in forests do not significantly alter mineral soil C pools.

### 3.2.3. Ecosystem C storage

At the network scale, estimated total ecosystem C storage (defined here as the sum of C storage in vegetation, forest floor, dead wood, and soil organic C to 30 cm depth) decreased modestly during the first year after all three of the treatments, but changed little during subsequent post-treatment years (Fig. 11). Once again, there were notable exceptions, including first year decreases of >20% after all three treatments at the Ca–C site, and increases during the subsequent years of >25% in the fire and mechanical + fire treatments at the NC site and the control at the OR site (Fig. 11). Meta-analysis revealed no significant effect of prescribed fire alone on total ecosystem C at the network scale during the first post-treatment year, though four of ten individual sites showed significant first year effects (decreases at the Ca–N, Ca–C, and MT sites and an increase at the OR site; Fig. 12). In contrast, the mechanical and the mechanical + fire treatments resulted in significant first year losses in total ecosystem C at the network scale (Fig. 12). The network-wide effect of the mechanical treatment was driven by significant losses of C at the AL and NC sites, whereas the mechanical + fire treatment effect was the result of significant losses at the Ca–C, MT, AL, and OH sites (Fig. 12). There were no significant, network-wide effects of the FFS treatments on total ecosystem C during the subsequent sampling years, and only one significant, site-level effect (fire treatment at the OR site; Fig. 12).

Prescribed fire alone produced no significant change in net C uptake rates, either across the full network or among eastern and western site groups. During the subsequent sampling period, estimated network-wide ecosystem C uptake rates in sites given the fire treatment were positive and similar to those in controls. In contrast, at the network scale and among the eastern sites, mechanical treatment, with or without prescribed fire, resulted in net losses of ecosystem C in the first post-treatment year and net uptake of C during the subsequent sampling period. Among the western sites there were no

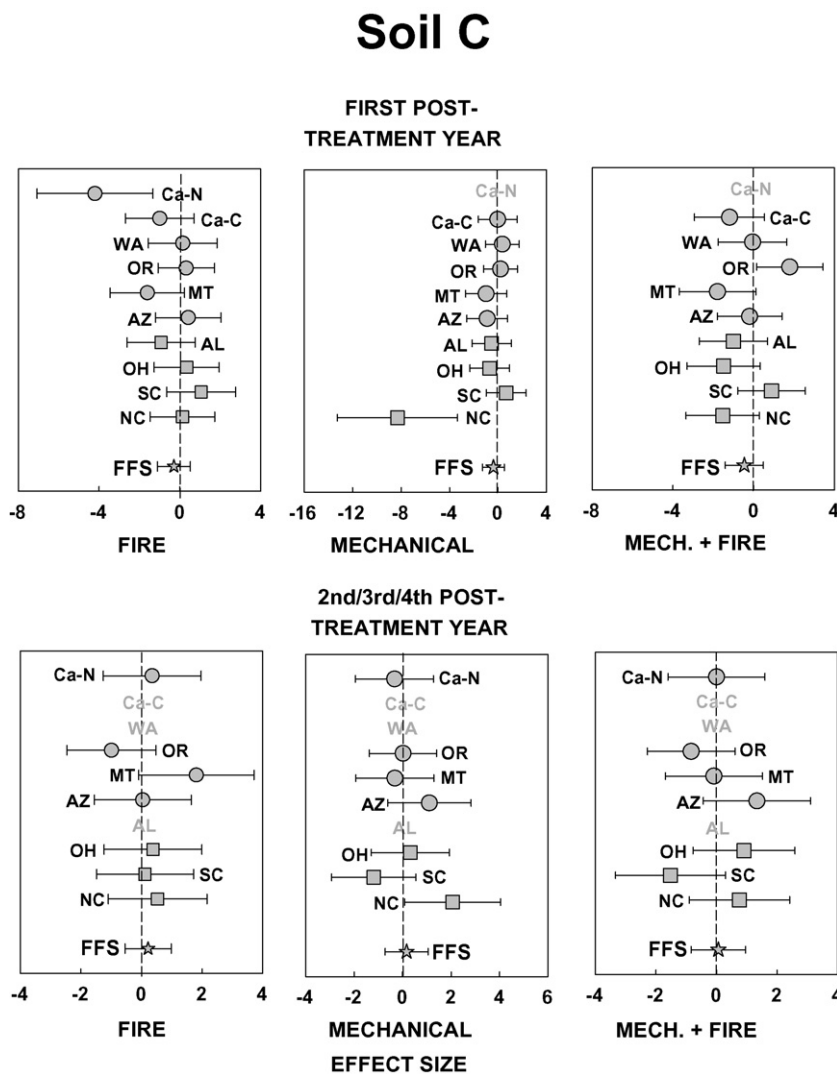


Fig. 10. Summary of the meta-analysis of the effects of three fire and fire surrogate (FFS) treatments on mineral soil (0–30 cm depth) carbon stocks ( $\text{Mg ha}^{-1}$ ) during the first (top) and subsequent (2nd, 3rd, or 4th growing season following treatment; bottom) sampling years. Symbols represent mean effect size, with error bars depicting the 95% confidence interval for the mean effect size. Sites for which insufficient data were available to test a given treatment-year combination are indicated by the site code in gray along the zero effect line.

significant, group-wide changes in ecosystem C following mechanical treatment during either sampling interval.

As all of the ecosystems in the FFS Network had a history of frequent, low-severity fire and an abundance of fire-tolerant tree species, the lack of significant, network-wide reductions in either vegetation C or total ecosystem C pools following prescribed fire was expected. Effective fire suppression in ecosystems with a history of frequent, low-severity fires has been in place for as much as a century in some parts of the U.S. What the C consequences of continued or even expanded fire suppression are remains uncertain. Houghton et al. (1999) noted that prior to EuroAmerican settlement, fire (both wildfire and intentional burning) was responsible for both the largest instantaneous point sources and the largest, broad-scale chronic sinks of C in North America. They estimate that fire suppression may have reduced the net C sink by  $0.05\text{--}0.20 \text{ Pg C year}^{-1}$ . If one uses a median estimate of  $250 \times 10^6 \text{ ha}$  of forest in the

coterminous U.S. (Heath et al., 2003), this equates to an average reduction of  $0.06\text{--}0.24 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . Similarly, Hurtt et al. (2002) estimate that under continued fire suppression, the U.S. C sink-strength will decrease to  $0.21 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  by 2050 and to  $0.13 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  by 2100 as both encroachment of forest into recently burned lands and regrowth of post-fire forests decrease. Consistent with this view that long-term fire suppression will lead to broad-scale reductions in forest C sink-strength is the study by Law et al. (2003) conducted in ponderosa pine forests in central Oregon. They estimated that stands 9–23 years since fire or harvesting were net C sources of  $\sim 1.2 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ , while stands ranging in age from 56 to 106 years were net C sinks of approximately the same magnitude. Old growth forests of  $>190$  years were weak C sinks, averaging  $0.35 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  (Law et al., 2003). This pattern is also supported by results from ponderosa pine forests in the southwestern U.S. following stand-replacing

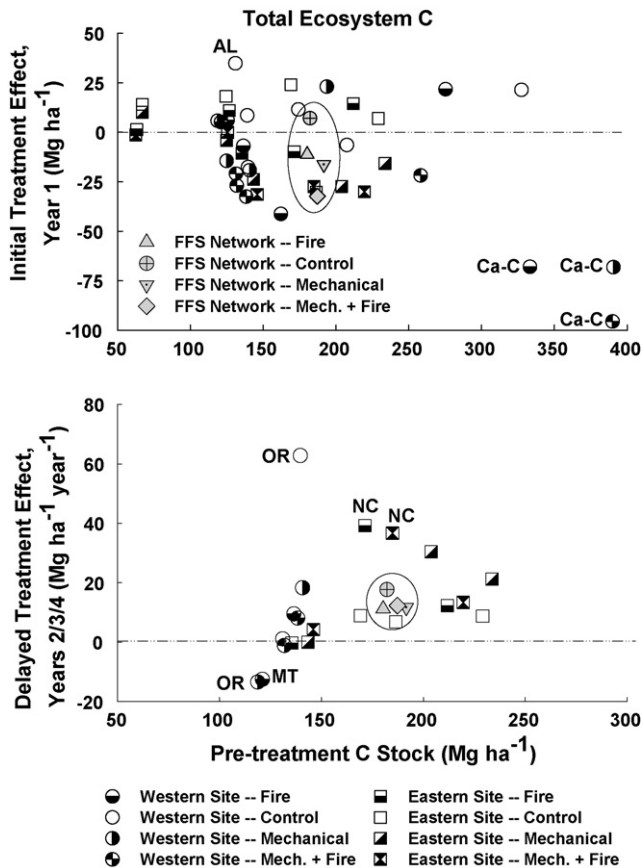


Fig. 11. Net changes in total ecosystem carbon storage ( $\text{Mg ha}^{-1} \text{ year}^{-1}$ ) during the first post-treatment year (top) and subsequent sampling year (2nd, 3rd, or 4th growing season following treatment; bottom) relative to the pre-treatment aboveground vegetation carbon stock ( $\text{Mg ha}^{-1}$ ) for the fire and fire surrogate (FFS) sites. Net changes for the subsequent sampling year were estimated relative to values after the first post-treatment year. The ellipse in each panel encompasses the overall FFS network means. Site codes follow Table 1.

wildfire. Dore et al. (2008) found that a decade after a high-severity fire, the burned forest was still a net source of C ( $1.1 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ), while an unmanaged mature forest, that had not experienced fire in over a century and was similar to the burned forest prior to the wildfire, was a net sink ( $1.6 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ). Because even after 10 years there still was no tree regeneration in the burned forest, it is possible that this forest and other forested sites in the southwestern U.S. experiencing high-severity wildfire may remain net C sources for decades after the wildfire (Dore et al., 2008). In contrast, Dixon et al. (1994) estimated that instituting effective suppression to forests in Russia could increase their sink strength by  $\sim 0.68 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . What is clear from these conflicting estimates is that a sudden cessation of fire suppression in forests of the U.S. would produce a net source of C to the atmosphere for some period of time as wildfires go unfought, with a stronger C sink than is present today developing as post-fire forest development proceeds.

When all ecosystem components are taken together, the loss of vegetation C to mechanical treatment in our twelve forest sites is somewhat ameliorated by increases in C in forest floor,

dead wood, and soil organic matter. The net change across the network in total ecosystem C from mechanical treatment averaged  $-16.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  the first year post-treatment, but the 95% CI about that mean ranged from  $-42.6$  to  $1.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ; thus, extrapolation of that mean C loss rate should be tempered by the realization that the actual, site-specific change could be either slightly positive or non-significant. In contrast, the net change in estimated total ecosystem C from the combination of mechanical and fire treatments averaged  $-32.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ , and the 95% CI about that mean ranged from  $-18.9$  to  $-45.6 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . Therefore, our results suggest that the combination of mechanical and prescribed fire treatments will result in considerable first year losses of total ecosystem C, even though mechanical and fire treatments when applied alone produce smaller or non-significant losses. It should be noted, however, that during subsequent sampling years the overall response of the site network was an increase in total ecosystem C storage at a rate of  $11.7 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  (95% CI range of 0.6 to 22.9) following mechanical treatment and  $12.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  (95% CI range of 4.2 to 20.4) following mechanical plus fire treatments. Hence, short-term losses in ecosystem C from the immediate impacts of site disturbance and tree removal are offset over time by increases in C storage over the longer term.

### 3.3. Net gains/losses and C sequestration rates.

The untreated controls sites exhibited a net gain of  $7.1 \pm 5.9 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  during the first post-treatment year, with the eastern sites averaging  $4.7 \pm 7.9 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  and the western sites averaging  $8.7 \pm 8.5 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . As a result of considerable variation among sites, none of these network-wide average rates of net C uptake were significantly different from zero. In contrast, net annual C uptake during the subsequent sampling period, which varied from 2 to 4 years among sites, averaged  $17.7 \pm 7.6 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  for the full network and  $8.2 \pm 3.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  for the eastern sites, both of which were significantly greater than zero. Only two of the western sites estimated net annual uptake after the first post-treatment year: MT reported a net C gain of  $1.1 \pm 0.9 \text{ Mg C ha}^{-1} \text{ year}^{-1}$  and OR reported a net gain of  $62.8 \pm 22.4 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ . The latter was, to some degree, an artifact of a change in sample plot size from year 1 to year 3 that may have added sample area with considerably greater tree density than the original sample area.

Comparing biometrically generated estimates of net C uptake, such as those we report here, with estimates generated by other methods is difficult as rates calculated from broad-scale modeling approaches (e.g., Schimel et al., 2000; Pacala et al., 2001), micrometeorological methods (e.g., eddy covariance studies), and biometric approaches seem to generate estimates for the same region that vary by as much as an order of magnitude. For example, the models employed by Myneni et al. (2001) estimated net C uptake by eastern deciduous forests at  $0.3 \text{ Mg C ha}^{-1} \text{ year}^{-1}$ ; in contrast, Barford et al. (2001) estimated total ecosystem C uptake for an eastern deciduous

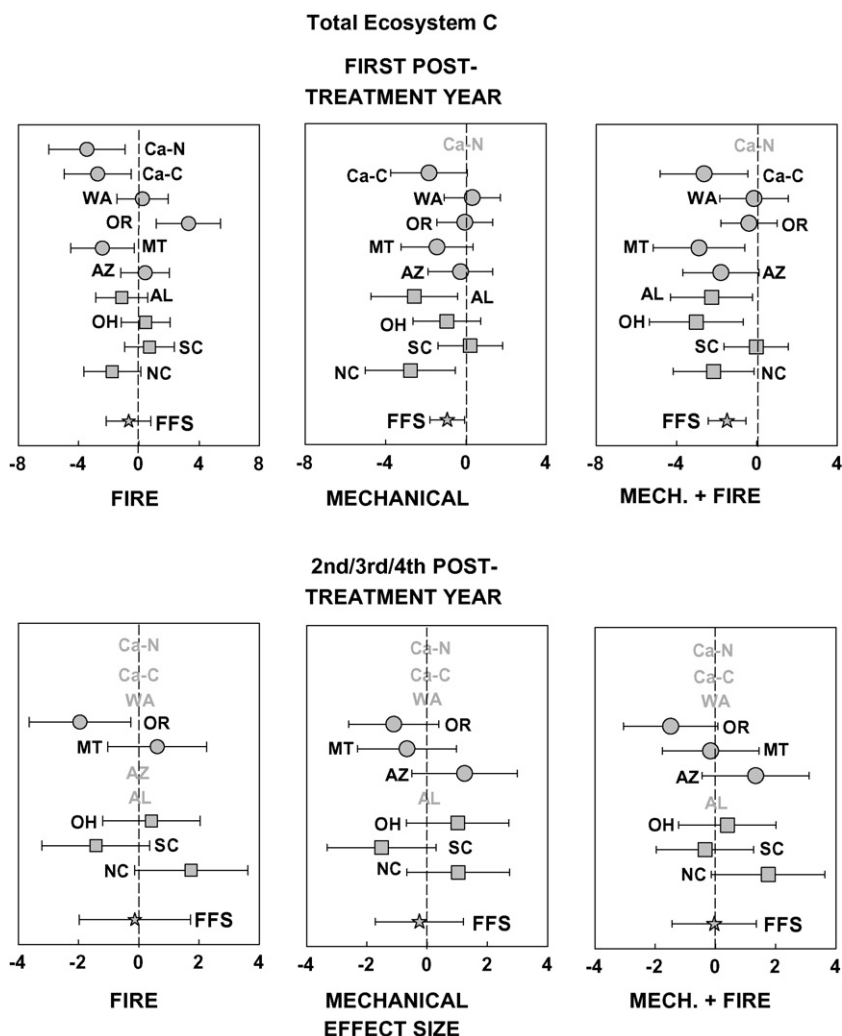


Fig. 12. Summary of the meta-analysis of the effects of three fire and fire surrogate (FFS) treatments on total ecosystem carbon stocks ( $\text{Mg ha}^{-1}$ ) during the first (top) and subsequent (2nd, 3rd, or 4th growing season following treatment; bottom) sampling years. Symbols represent mean effect size, with error bars depicting the 95% confidence interval for the mean effect size. Sites for which insufficient data were available to test a given treatment-year combination are indicated by the site code in gray along the zero effect line. Site codes follow Table 1.

forest to be  $2.0 \pm 0.4 \text{ Mg ha}^{-1} \text{ year}^{-1}$  based on micrometeorological methods and  $1.6 \pm 0.4 \text{ Mg ha}^{-1} \text{ year}^{-1}$  based on biometric methods similar to the ones we employed in this study. Similarly, Ehman et al. (2002) estimated that a deciduous forest in Indiana took up  $2.4\text{--}2.9 \text{ Mg ha}^{-1} \text{ year}^{-1}$  when estimated by micrometeorological methods and  $2.7\text{--}3.8 \text{ Mg ha}^{-1} \text{ year}^{-1}$  when estimated biometrically. For the western US, Myneni et al. (2001) estimated net C uptake to range between  $0.0$  and  $0.15 \text{ Mg ha}^{-1} \text{ year}^{-1}$ , whereas Law et al. (2003, 2004) estimated net C uptake of  $0.7 \text{ Mg ha}^{-1} \text{ year}^{-1}$  for ponderosa pine forests in central Oregon and  $1.7 \text{ Mg ha}^{-1} \text{ year}^{-1}$  for all Oregon forests.

Results from the FFS study indicate that prescribed fire has little impact on forest C budgets in the subset of eastern forests we examined; however, mechanical treatments (either alone or in combination with fire) converted these forests from net C sinks to C sources, at least for the first year following treatment. In contrast, in the subset of western forests we analyzed neither mechanical treatments nor prescribed fire resulted in wide-

spread, significant changes in total forest ecosystem C budgets. Previous studies have concluded that the North American forest biomass sink is mostly in the eastern forests (Turner et al., 1995; Myneni et al., 2001; Hurtt et al., 2002), where regrowth after fire, harvesting, or land-use change causes rapid C uptake, and the second largest sink is mostly in the western forests where fire suppression has led to increased detrital C (Hurtt et al., 2002). When combined with the data presented here, those conclusions suggest that management strategies designed to maximize C sequestration by forests of the conterminous U.S. will need to approach western and eastern forests differently.

#### Acknowledgements

This is publication number 156 of the fire and fire surrogate network project, funded by the Joint Fire Sciences Program. We thank Mark Lewis for data base management, Jim McIver for network coordination, and a legion of research cooperators at

the twelve FFS sites for their assistance. S.C. Hart was supported by Joint Venture Agreements 00-JV-1122165-233, 03-JV-11221605-036, 04-JV-11221615-089, and 06-JV-11221615-228 with the U.S. Forest Service Rocky Mountain Research Station during this research.

## Appendix A

See Table A.1.

Table A.1  
Sources for wood specific gravity and/or carbon concentration estimates

Genus	Species	Sources
<i>Abies</i>	<i>concolor</i> <sup>a</sup>	<a href="http://edis.ifas.ufl.edu/ST001">http://edis.ifas.ufl.edu/ST001</a> ; <a href="http://waynesword.palomar.edu/plsept99.htm#specific">http://waynesword.palomar.edu/plsept99.htm#specific</a>
<i>Abies</i>	<i>grandis</i> <sup>a</sup>	Jenkins et al. (2004)
<i>Abies</i>	<i>magnifica</i> <sup>a</sup>	Jenkins et al. (2004)
<i>Acer</i>	<i>rubrum</i>	Clark and Schroeder (1986) Clark et al. (1986) Martin et al. (1998) Woodson (1976) Bendtsen and Ethington (1975)
<i>Acer</i>	<i>saccharum</i>	<a href="http://hort.ufl.edu/trees/ACESACD.pdf">http://hort.ufl.edu/trees/ACESACD.pdf</a> ; <a href="http://www.rook.org/earl/bwca/nature/trees/acersac.html">http://www.rook.org/earl/bwca/nature/trees/acersac.html</a>
<i>Calocedrus</i>	<i>decurrens</i> <sup>a</sup>	<a href="http://hort.ufl.edu/trees/CALDECA.pdf">http://hort.ufl.edu/trees/CALDECA.pdf</a>
<i>Carya</i>	spp.	Clark and Schroeder (1986) Clark et al. (1986) Martin et al. (1998) Woodson (1976) Manwiller (1979)
<i>Cornus</i>	<i>florida</i>	Boerner and Kost (1986) Elliott et al. (2002)
<i>Cornus</i>	<i>nuttalli</i> <sup>a</sup>	<a href="http://waynesword.palomar.edu/plsept99.htm#specific">http://waynesword.palomar.edu/plsept99.htm#specific</a>
<i>Fagus</i>	<i>grandifolia</i>	<a href="http://hort.ufl.edu/trees/FAGGRAA.pdf">http://hort.ufl.edu/trees/FAGGRAA.pdf</a> ; Boggs et al. (2005) Merrill and Cowling (1966)
<i>Fraxinus</i>	<i>americana</i>	Clark and Schroeder (1986) Woodson (1976) Manwiller (1979) Bendtsen and Ethington (1975)
<i>Ilex</i>	<i>opaca</i> <sup>a</sup>	<a href="http://hort.ufl.edu/trees/ILEOPAA.pdf">http://hort.ufl.edu/trees/ILEOPAA.pdf</a>
<i>Juniperus</i>	<i>virginiana</i> <sup>a</sup>	<a href="http://hort.ufl.edu/trees/JUNVIRA.pdf">http://hort.ufl.edu/trees/JUNVIRA.pdf</a>
<i>Larix</i>	<i>occidentalis</i> <sup>a</sup>	Jenkins et al. (2004)
<i>Lithocarpus</i>	<i>densiflorus</i> <sup>a</sup>	Jenkins et al. (2004)
<i>Liquidambar</i>	<i>styraciflua</i>	Clark et al. (1986) Woodson (1976) Manwiller (1979) Bendtsen and Ethington (1975)
<i>Liriodendron</i>	<i>tulipifera</i>	Clark et al. (1986) Woodson (1976) Manwiller (1979) Bendtsen and Ethington (1975) Martin et al. (1998)
<i>Magnolia</i>	sp.	Woodson (1976) Manwiller (1979) Bendtsen and Ethington (1975)
<i>Nyssa</i>	<i>sylvatica</i>	Clark and Schroeder (1986) Woodson (1976) Manwiller (1979) Bendtsen and Ethington (1975)

Table A.1 (Continued)

Genus	Species	Sources
<i>Oxydendrum</i>	<i>arboreum</i> <sup>a</sup>	Jenkins et al. (2004)
<i>Pinus</i>	<i>contorta</i>	Jenkins et al. (2004) Little and Shainsky (1992)
<i>Pinus</i>	<i>echinata</i> <sup>a</sup>	Gibson et al. (1986)
<i>Pinus</i>	<i>elliotti</i> <sup>a</sup>	Gibson et al. (1986)
<i>Pinus</i>	<i>jeffreyi</i> <sup>a</sup>	Jenkins et al. (2004)
<i>Pinus</i>	<i>lambertiana</i> <sup>a</sup>	Jenkins et al. (2004)
<i>Pinus</i>	<i>palustris</i> <sup>a</sup>	Gibson et al. (1986)
<i>Pinus</i>	<i>ponderosa</i>	Jenkins et al. (2004) Little and Shainsky (1995)
<i>Pinus</i>	<i>rigida</i>	Jenkins et al. (2004)
<i>Pinus</i>	<i>strobus</i>	Wahlgren et al. (1968)
<i>Pinus</i>	<i>taeda</i>	Booker and Maier (2001) Gibson et al. (1986) McMillin (1973)
<i>Pinus</i>	<i>virginiana</i> <sup>a</sup>	<a href="http://hort.ufl.edu/trees/PINVIRA.pdf">http://hort.ufl.edu/trees/PINVIRA.pdf</a>
<i>Populus</i>	<i>grandidentata</i>	Jenkins et al. (2004)
<i>Prunus</i>	<i>serotina</i> <sup>a</sup>	<a href="http://waynesword.palomar.edu/plsept99.htm#specific">http://waynesword.palomar.edu/plsept99.htm#specific</a>
<i>Pseudotsuga</i>	<i>menziesii</i>	<a href="http://hort.ufl.edu/trees/PSEMENA.pdf">http://hort.ufl.edu/trees/PSEMENA.pdf</a>
<i>Quercus</i>	<i>alba</i>	Clark and Schroeder (1986) Day and Monk (1977) Manwiller (1979) Bendtsen and Ethington (1975) Martin et al. (1998)
<i>Quercus</i>	<i>coccinea</i>	Clark et al. (1986) Woodson (1976) Manwiller (1979) Bendtsen and Ethington (1975) Martin et al. (1998)
<i>Quercus</i>	<i>falcata</i>	Clark et al. (1986) Woodson (1976) Manwiller (1979) Bendtsen and Ethington (1975) Martin et al. (1998)
<i>Quercus</i>	<i>gambelii</i> <sup>a</sup>	<a href="http://www.fs.fed.us/database/feis/plants/tree/quegam/all.html">http://www.fs.fed.us/database/feis/plants/tree/quegam/all.html</a>
<i>Quercus</i>	<i>kelloggi</i> <sup>a</sup>	<a href="http://waynesword.palomar.edu/plsept99.htm#specific">http://waynesword.palomar.edu/plsept99.htm#specific</a> ; Martinelli et al. (1999)
<i>Quercus</i>	<i>laurifolia</i> <sup>a</sup>	Manwiller (1979) Bendtsen and Ethington (1975)
<i>Quercus</i>	<i>marilandica</i> <sup>a</sup>	Woodson (1976) Manwiller (1979)
<i>Quercus</i>	<i>nigra</i> <sup>a</sup>	Woodson (1976) Manwiller (1979) Bendtsen and Ethington (1975)
<i>Quercus</i>	<i>prinus</i>	Clark and Schroeder (1986) Clark et al. (1986) Martin et al. (1998)
<i>Quercus</i>	<i>rubra</i>	Clark and Schroeder (1986) Manwiller (1979) Bendtsen and Ethington (1975) Martin et al. (1998)
<i>Quercus</i>	<i>stellata</i> <sup>a</sup>	Woodson (1976) Manwiller (1979)
<i>Quercus</i>	<i>velutina</i>	Clark and Schroeder (1986) Manwiller (1979) Bendtsen and Ethington (1975)
<i>Quercus</i>	<i>virginiana</i> <sup>a</sup>	<a href="http://hort.ufl.edu/trees/QUEVIRA.pdf">http://hort.ufl.edu/trees/QUEVIRA.pdf</a>
<i>Robinia</i>	<i>pseudoacacia</i>	Clark and Schroeder (1986)
<i>Sassafras</i>	<i>albidum</i>	<a href="http://hort.ufl.edu/trees/SASALBA.pdf">http://hort.ufl.edu/trees/SASALBA.pdf</a>
<i>Tilia</i>	<i>americana</i>	Clark and Schroeder (1986)
<i>Tsuga</i>	<i>canadensis</i> <sup>a</sup>	Wahlgren et al. (1968) Pardo et al. (2005) Rutkowski and Stottleyer (1993)

Table A.1 (Continued)

Genus	Species	Sources
<i>Ulmus</i>	<i>americana</i>	Clark et al. (1986) Manwiller (1979) Bendtsen and Ethington (1975)

All internet sources were accessed 25 June 2007.

<sup>a</sup> Species for which estimates of wood carbon concentration were estimated from specific gravity and carbon concentration in stored wood products.

## Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.foreco.2007.11.021.

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