Postfire carbon pools and fluxes in semiarid ponderosa pine in Central Oregon

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Abstract
Forest fire dramatically affects the carbon storage and underlying mechanisms that control the carbon balance of recovering ecosystems. In western North America where fire extent has increased in recent years, we measured carbon pools and fluxes in moderately and severely burned forest stands 2 years after a fire to determine the controls on net ecosystem productivity (NEP) and make comparisons with unburned stands in the same region. Total ecosystem carbon in soil and live and dead pools in the burned stands was on average 66% that of unburned stands (11.0 and 16.5 kg C m⁻², respectively, P < 0.01). Soil carbon accounted for 56% and 43% of the carbon pools in burned and unburned stands. NEP was significantly lower in severely burned compared with unburned stands (P < 0.01) with an increasing trend from −125 ± 44 g C m⁻² yr⁻¹ (±1 SD) in severely burned stands (stand replacing fire), to −38 ± 96 and +50 ± 47 g C m⁻² yr⁻¹ in moderately burned and unburned stands, respectively. Fire of moderate severity killed 82% of trees <20 cm in diameter (diameter at 1.3 m height, DBH); however, this size class only contributed 22% of prefire estimates of bole wood production. Larger trees (>20 cm DBH) suffered only 34% mortality under moderate severity fire and contributed to 91% of postfire bole wood production. Growth rates of trees that survived the fire were comparable with their prefire rates. Net primary production NPP (g C m⁻² yr⁻¹, ±1 SD) of severely burned stands was 47% of unburned stands (167 ± 76, 346 ± 148, respectively, P < 0.05), with forb and grass aboveground NPP accounting for 74% and 4% of total aboveground NPP, respectively. Based on continuous seasonal measurements of soil respiration in a severely burned stand, in areas kept free of ground vegetation, soil heterotrophic respiration accounted for 56% of total soil CO₂ efflux, comparable with the values of 54% and 49% previously reported for two of the unburned forest stands. Estimates of total ecosystem heterotrophic respiration (Rₜₜ) were not significantly different between stand types 2 years after fire. The ratio NPP/Rₜₜ averaged 0.55, 0.85 and 1.21 in the severely burned, moderately burned and unburned stands, respectively. Annual soil CO₂ efflux was linearly related to aboveground net primary productivity ANPP with an increase in soil CO₂ efflux of 1.48 g C yr⁻¹ for every 1 g increase in ANPP (P < 0.01, r² = 0.76). There was no significant difference in this relationship between the recently burned and unburned stands. Contrary to expectations that the magnitude of NEP 2 years postfire would be principally driven by the sudden increase in detrital pools and increased rates of Rₜₜ, the data suggest NPP was more important in determining postfire NEP.

Keywords: carbon cycling, CO₂ efflux, heterotrophic respiration, net ecosystem production, net primary production, Pinus ponderosa, soil respiration, wildfire

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Introduction
With current interest in determining the role of forests in the terrestrial carbon cycle and their potential to sequester anthropogenic carbon emissions, widespread
efforts are being made to measure and synthesize data that quantifies the net carbon balance of forested ecosystems across a range of climatic and disturbance regimes (Schulze et al., 2000; Curtis et al., 2002; Law et al., 2004; Pregitzer & Euskirchen, 2004). Forest disturbance is often directly attributed to human activity through land conversion or timber extraction, but in most ecosystems natural events such as insect outbreaks and wildfires play an integral role. Indirect human activities including fire suppression and climate change have recently contributed to increases in fire probability and insect infestations (e.g. Kurz et al., 1995; Dale et al., 2001). In the United States during the last decade there has been on average an increase of almost 10% a year in land area consumed by wildfire compared with the previous decade (NIFC, 2005). This has been partially driven by the suppression of fire throughout western North America during the last century resulting in high fuel accumulations with the consequence that in the dry coniferous forests larger intense fires are more likely in the future (Agee, 1993). Compared with the gradual storage of carbon in forests over decades to centuries as they grow and mature, intense wildfire can result in a huge and immediate release of carbon to the atmosphere followed by smaller releases during the following years to decades. The processes controlling ecosystem heterotrophic respiration (Rh) and net primary production (NPP), the balance of which is annual net ecosystem productivity (NEP) or annual carbon storage. The nature of these carbon fluxes immediately following fire has seen little study in the semiarid regions of the western United States. Yet, describing the trajectory of carbon storage during this period is essential to allow scaling of patterns of carbon sequestration across the landscape.

Forest recovery following disturbance is generally considered to follow a systematic progression based on the balance between carbon gains by regenerating vegetation and losses from decomposing organic matter (Odum, 1969; Law et al., 2003; Litvak et al., 2003). However, the rate of this recovery during the initial stages is likely to depend on the nature of the disturbance event. For example, we can reasonably suggest that following logging, a considerable quantity of fine woody debris (FWD) and coarse woody debris (CWD) is likely to be left on site (Harmon et al., 1990). Whereas, following a high severity wildfire, fine litter may be combusted, but coarse woody material and large dead superficially combusted tree boles may remain (Donato et al., 2006). The sizes and rates of decomposition of these various carbon pools will play an important role in the rate the site transitions from being a source of carbon to the atmosphere to becoming a carbon sink which is likely to differ between the harvested compared with burned stand.

Heterotrophic respiration rates are somewhat uncertain in the first few years after wildfire. In previous studies on forested sites that have seen little recent disturbance, soil CO2 efflux can account for the majority of ecosystem respiration (Law et al., 1999; Janssens et al., 2001). Separating this respiratory flux into autotrophic (live root respiration) and heterotrophic (decomposition) fractions is challenging (Hanson et al., 2000). However, a recent meta-analysis of data from studies that used a variety of separation approaches suggested that the heterotrophic fraction declines with increasing total soil CO2 efflux (Subke et al., 2006). It would seem likely that immediately following wildfire, such a correlation may no longer hold. Following fire, root mortality is likely to occur to some degree, resulting in decreased autotrophic respiration and an increased pool of detritus for microbial decomposition. The removal of the canopy may result in increased soil temperatures and increased soil water content as transpirational demand may have been reduced due to tree mortality. All these factors may increase the rates of heterotrophic respiration relative to autotrophic respiration resulting in a large pulse of Rh. The length of this pulse and timing of recovery of NPP describe the trajectory of change in NEP after disturbance.

In July 2002, lightening ignited the Eyerly fire and burned approximately 9500 ha of forest about 20 miles north of Sisters in central Oregon. The fire included extreme fire behavior with 55% of the burned area categorized as stand replacing fire. In 2001 within the same area, although not within the perimeter of the subsequent Eyerly fire, numerous forest plots were surveyed as part of a study examining the effect of forest age on carbon storage and fluxes (Law et al., 2003). Thus, an opportunity arose to study postfire carbon dynamics and contrast results with data collected on forest stands that represented the prefire conditions. The objectives of the current study were to measure carbon pools and key carbon fluxes in forest stands subject to moderate and high severity fire, 2 years postfire, in this semiarid region in order to estimate NEP and compare carbon pools and underlying processes with unburned stands.

**Methods**

**Study design**

Twelve 1 ha plots were selected from within the perimeter of the Eyerly fire (44°37′N, 121°30′W) which burned late summer 2002 in central Oregon, USA. Six plots were categorized as severely burned and had no
living trees (a single living tree was subsequently found on one plot during detailed survey) and six plots were classified as moderately burned and had some degree of tree survivorship of highly variable proportions. Ground vegetation 2 years postfire comprised of numerous forbs and grasses including common yarrow (Achillea millefolium), nine-leafed desert parsley (Lomatium triternatum), wooly sunflower (Eriophyllum lanatum), arrow leaf balsamroot (Balsamorhiza sagittata), low beardtongue (Penstemon humilis), big deer vetch (Lotus crassifolius), Idaho fescue (Festuca idahoensis), blue bunch wheat grass (Pseudoroegneria spicata) and cheat grass (Bromus tectorum). Resprouting shrubs included ceanothus (Ceanothus spp.), bitterbrush (Purshia tridentata) and manzanita (Arctostaphylos patula). For unburned plots, we used data from the east Cascade study sites described in Law et al. (2003) and Campbell et al. (2004a) which are within ~15 km of the Eyerly fire in this ponderosa pine (Pinus ponderosa Dougl. Ex P. Laws) dominated ecosystem. The 12 unburned plots were part of a study that covered a wide range of age classes. The principle factor of interest in the current study is the role of fire on ecosystem NEP, and forest age was viewed as a potentially confounding factor. To minimize this issue, plots were selected within each of the burn severity classes to cover the same age distribution as the unburned plots. This study design is a space for treatment substitution, which could introduce confounding spatial variation due to factors such as elevation or water table depth. To determine whether the unburned plots could be used to sensibly represent the prefire condition of the burned plots, we reconstructed prefire bole NPP on the burned plots using tree cores to compare with bole NPP on unburned plots.

**Estimating NEP**

NEP was estimated using a combination of biometric surveys, allometric relationships, biomass decay constants and assessment of the heterotrophic fraction of soil respiration.

\[
\text{NEP} = \text{NPP}_A - R_{hWD} + \text{NPP}_B - R_{hsoil}
\]

where \(\text{NPP}_A\) is aboveground NPP (trees, shrubs, forbs and grasses), \(R_{hWD}\) is the heterotrophic respiration of aboveground woody debris (decomposition of CWD and FWD, snags and stumps), \(\text{NPP}_B\) is belowground NPP (fine and coarse root growth) and \(R_{hsoil}\) is the fraction of total soil \(CO_2\) efflux that can be attributed to heterotrophic sources (decomposition of soil organic matter). Protocols for assessing the various components of NEP on the twelve 1 ha unburned plots have been presented in detail by Law et al. (2003), Campbell et al. (2004a) and Sun et al. (2004). The survey protocols used on the 12 burned plots largely followed these published methods. Here, we present a summary of the methods, and details where methods differed from the published approaches.

**Biomass and NPP\(_A\)**

On each of the twelve 1 ha burned plots, four regularly spaced circular subplots were surveyed, ranging in radius between 8 m (for higher tree density plots) and 15 m (for lower tree density plots). Tree species, diameter, height, decay class and increment cores were collected to age individuals and provide wood density information for conversion of wood volume to wood mass. A conversion factor of 0.51 was used to convert wood mass into carbon mass. Within each plot and species, we observed no distinct tree size related patterns in increment ring widths over the past several years and used mean ring width by species for scaling. Tree dimensions together with mean wood increment over individual years were used with species-specific allometric equations (Table 2) obtained from the BIO-PAC database (Means et al., 1994). On plots with living trees, leaf area index (LAI) was determined optically using a LAI-2000 (LI-COR Inc., Lincoln, NE, USA), which together with average leaf mass per unit area and an average leaf retention time of 4 years (typical for ponderosa pine in this region) was used to determine foliage NPP. To quantify forb and grass NPP\(_A\), four 0.25 m\(^2\) quadrats per subplot (total of 12 quadrats) were clipped to ground level following onset of senescence and the material was dried and weighed. If quadrats intercepted living shrubs, only the current year’s growth was harvested to quantify shrub NPP\(_A\). This does not account for woody increment of previous year’s shrub growth and will result in a small underestimate of NPP\(_A\). Shrub NPP\(_A\) estimated in this manner accounted for 14% and 9% of total NPP\(_A\) in the severely and moderately burned plots, respectively and thus, this error was considered to be of little consequence. The tree cores taken from individuals that survived the fire (i.e. moderately burned plots) were also used to assess whether tree bole growth in the 2 years following the fire was significantly different from prefire growth rates. Mean annual ring widths between 1999 and 2004 were used in this analysis. This period, including the prefire period, exhibited a decreasing trend in ring width with time, which was detrended with a linear function. To examine whether there remained any significant variability over time that coincided with the fire, the detrended ring widths were viewed as separate, but correlated variables and tested using multivariate ANOVA.
Woody debris and $R_{hWd}$

Four 75 m long transects per plot were used to measure woody debris with a line intercept method. The diameter of all CWD (>10 cm diameter and 1 m length) crossing each transect was measured and given a decay class (five classes). FWD was divided into three size classes (0.6–2.5, 2.5–7.6 and 7.6–10 cm diameter). The smallest class was recorded along 4 m of each transect whereas the two larger size classes were recorded along 15 m of each transect. The diameter and decay class were recorded for the largest FWD size class. The diameter of each piece was converted into volume per unit area and annual decomposition losses were calculated using species specific decay constants and decay class specific wood densities (Harmon & Sexton, 1996, M. Harmon, personal communication). Forest floor litter was generally absent and not quantified on the burned plots. Decay constants for snags were assumed 10% the value for CWD (see ‘Discussion’). The diameter, height and decay class of all stumps were measured in all subplots and included in the decomposition calculations. To estimate decay rates of forbs and grasses, an additional 12 quadrats (0.25 m²) were clipped on plot 603 six months following the assessment of herb and grass NPP. Based on the weight difference (~27%) between the clippings we assumed an annual loss of 50% of forb and grass ANPP.

Belowground carbon pools and NPP$_B$

Soil cores were extracted using a 7.3 cm diameter auger at predetermined intervals along three 36 m transects per plot. In total 30 cores 0–20 cm depth, seven cores 20–50 cm depth and three cores 50–100 cm depth were taken per plot where soil depth allowed. Samples were sifted through a 2 mm sieve, air dried, mixed by transect and depth before a ground subsample was analyzed for total carbon and nitrogen with a LECO CNS 2000 analyzer (Leco Corp., St. Joseph, MI, USA). The volume of all stones was measured by displacement. The organic matter, roots and rocks that did not pass through the sieve were washed in a hydropneumatic elutriation system (Gillison’s Fabrication Inc., Benzonia, MI, USA). Ten of the 0–20 cm depth samples and all samples from greater depths were separated into fine roots (0–2 mm), coarse roots (2–20 mm), other organic matter and charcoal before being oven dried and weighed. On one-third of the plots, the fine roots were further separated into forb/grass roots and trees roots.

To determine fine root NPP, we assumed that trees killed by fire had no living roots; this was confirmed on one of the severely burned plots from soil cores. The ratio of plot level postfire to prefire NPP of tree boles was used as a measure of the effective fraction of living trees. This fraction was multiplied by total measured fine root biomass (i.e. including dead and alive roots of unknown proportion) to determine the effective root pool (i.e. the fine root pool after excluding those roots killed as a consequence of fire). This effective root pool was considered to have both live and dead root fractions that would be typical of an unburned stand due to normal root turnover. Live fine root fraction was on average 61% (SD = 7%) of total fine root fraction across the unburned plots (O. Sun, unpublished data). Fine root (0–2 mm) turnover from rhizotron studies in two of the unburned plots was estimated as 0.6 when expressed as fraction of standing crop (Law et al., 2003). Fine root NPP was computed as the live fine root biomass of the effective root pool multiplied by root turnover. Coarse root NPP was estimated using an allometric equation (Gholz et al., 1979) and annual tree diameter growth as described by Van Tuyl et al. (2005). NPP of forb/grass roots was assumed to be equal to the total forb/grass root pool (i.e. all forb/grass roots were produced and turned over once during the year). On those plots where roots were sorted between forb/grass and trees, the average ratio of forb/grass to total root biomass in the top 20 cm of soil was 36% (SD = 9%), this value was used to estimate forb/grass root biomass for the remaining plots.

Soil CO$_2$ efflux, temperate and moisture

Soil CO$_2$ efflux was measured using a Li-6400 with Li-6000-9 soil chamber (LI-COR Inc.). Measurements were made using 12 PVC collars (10.7 cm in diameter) at each site that were installed across three transects in April 2004. We considered the small diameter collars and shallow insertion depth (~25 mm) would not prevent roots of any emerging grasses and forbs surrounding the collar to grow into the soil volume beneath the collars, vegetation that germinated inside the collar itself was removed each month. Soil CO$_2$ efflux was measured at each of the burned plots between mid-May and early November 2004 at monthly intervals. In December 2004, January and March 2005 measurements were made on only four of the plots due to limited winter accessibility. Soil temperature was recorded next to the collar at 5 cm depth during the measurement. To fill the missing values of soil CO$_2$ efflux from the subset of plots that were not accessible during winter, we used the average ratio of the soil CO$_2$ efflux that was measured on a specific plot to that same plot’s most recently measured value at a time when all the plots were measured, this ratio was used to predict the unmeasured plot’s soil CO$_2$ efflux based on the same plot’s soil CO$_2$ efflux at the last time measured before the winter.
period. This approach was necessary as the response of soil CO₂ efflux to temperature was weak (average Q₁₀ = 1.18, SE = 0.04) due to seasonal soil water limitations and, therefore, the temperature response could not be used to extrapolate and fill missing values during the winter period. Soil water content measurements were made at monthly intervals across the season when soil surface temperatures were above freezing using time-domain-reflectometry (TDR). Four sets of 30 cm long probes were installed vertically in each plot and measurements were made using a Tektronix cable-testing oscilloscope (1502B, Tektronix Corp., Beaverton, OR, USA) in conjunction with a CR10X data logger and SMD1502 interface (Campbell Scientific, Logan, UT, USA). Soil temperature was continuously measured at 5 cm depth at eight locations in each plot using two Hobo-H8 loggers (Onset Computer Corp., Bourne, MA, USA). Annual estimates of soil CO₂ efflux for each of the 12 plots were computed by generating plot-specific exponential relationships between soil CO₂ efflux and temperature. These relationships and the residuals, (i.e. the seasonality in soil CO₂ efflux not accounted for by temperature), were employed as described by Ryan et al. (1997) using plot specific daily average soil temperatures to generate daily estimates of soil CO₂ efflux.

On one severely burned plot, an automated soil respiration system as described by Irvine & Law (2002) was installed in early May 2004 that measured soil CO₂ efflux continuously during the nonwinter months. Six chambers (0.21 m² sampling area each) were dedicated to monitoring soil heterotrophic respiration, where all initially present vegetation was removed and the chambers were subsequently kept free of vegetation by periodic weeding. There were no living trees or shrubs on this plot. The data set generated by this system covered a wide range of soil temperature and soil water contents that allowed the mathematical fitting of a function to predict daily mean soil heterotrophic respiration from daily mean values of soil temperature and soil water content as measured next to the automated chambers. The annual estimate of heterotrophic respiration was compared with the annual estimate of total soil CO₂ efflux estimated from the periodic manual measurements to determine the fraction of soil CO₂ efflux that can be attributed to decomposition. We have previously shown good agreement when comparing total soil CO₂ efflux measured using this automated system and manual measurements (Irvine & Law, 2002).

**Statistical analysis and uncertainty**

We used an analysis of variance (ANOVA) to test for significant differences in the measured or computed variables using PROC GLM (SAS Institute Inc., 1988). In many cases variances were inhomogeneous and PROC MIXED was used to allow analysis with unequal variance.

We take a pragmatic view of uncertainty in estimating NEP and the underlying component carbon pools and fluxes in this study. Quantifying variability in the response of NEP to levels of fire severity can be achieved by measuring replicated plots within that fire severity. Finding such plots can be problematic as stands within the Eyerly fire have uneven age structure, tree size distribution and varied management histories. Thus, between plot variability within a single burn severity may be influenced by these plot specific factors. Care needs to be taken when making statistical inferences as it easy to accept that differences between plot categories do not exist when in reality differences are present, but confounded by addition factors. In this respect, the trends and proportionalities of the various carbon pools and fluxes between the plot categories rather than the absolute values should be of most interest. An additional and important source of uncertainty relates to our ability to take survey measurements and scale them to the plot level. Many assumptions are necessary to scale forest level carbon pools and fluxes. For example, allometric equations taken from the literature to calculate biomass lacked statistics to add uncertainty to aboveground biomass (Van Tuyl et al., 2005). Equations were used consistently across all the plots so ANPP comparisons between plot categories should be unbiased. Measuring and modeling belowground processes is a challenging area of research and we provide a simple but practical sensitivity analysis of changing the estimates of fine root turnover and the fraction of soil respiration attributed to decomposition on our estimates of NEP.

**Results and discussion**

**NPP**

Bole NPP for 2001, the year before the fire, was not significantly different (P = 0.91) between severely burned (108 g C m⁻² yr⁻¹, SD 68), moderately burned (100 g C m⁻² yr⁻¹, SD 58) and unburned plots (108 g C m⁻² yr⁻¹, SD 65). Concerns that a wide range of forest ages (Table 1) were included in all plot categories and that burned and unburned plots may have unique plot age to bole NPP to relationships was considered by adding plot age as a covariate. There was no significant interaction between bole NPP for 2001 and plot age suggesting a consistent plot age to bole NPP relationship. Based on these analyses we considered the unburned plots as suitable reference.
Table 1  Stand characteristics of moderately (M) burned and severely burned (S, stand replacing fire) plots

<table>
<thead>
<tr>
<th>Plot</th>
<th>Longitude</th>
<th>Latitude</th>
<th>Burn class</th>
<th>Age (years)</th>
<th>Trees (ha⁻¹)</th>
<th>Median height (m)</th>
<th>LAI</th>
<th>LAI species composition</th>
<th>History</th>
</tr>
</thead>
<tbody>
<tr>
<td>609</td>
<td>-121.531</td>
<td>44.601</td>
<td>M</td>
<td>15</td>
<td>621</td>
<td>4.6</td>
<td>0.67</td>
<td>Pipo, Cade</td>
<td>Sanitation salvage 1977, natural regeneration</td>
</tr>
<tr>
<td>611</td>
<td>-121.538</td>
<td>44.575</td>
<td>M</td>
<td>142, 36</td>
<td>414, 43</td>
<td>4.3</td>
<td>1.15</td>
<td>Pipo, Cade, Psme</td>
<td>Shelterwood removal 1985, seed trees still present, natural regeneration</td>
</tr>
<tr>
<td>604</td>
<td>-121.504</td>
<td>44.559</td>
<td>M</td>
<td>49</td>
<td>573</td>
<td>5.5</td>
<td>0.38</td>
<td>Pipo, Cade, Juno</td>
<td>Overstory removal 1980, natural regeneration</td>
</tr>
<tr>
<td>601</td>
<td>-121.502</td>
<td>44.560</td>
<td>M</td>
<td>50</td>
<td>684</td>
<td>4.9</td>
<td>0.48</td>
<td>Pipo, Cade, Psme</td>
<td>Overstory removed 1980, natural regeneration</td>
</tr>
<tr>
<td>607</td>
<td>-121.535</td>
<td>44.574</td>
<td>M</td>
<td>216, 61</td>
<td>131</td>
<td>9.9</td>
<td>0.32</td>
<td>Pipo, Cade, Psme, Abgr</td>
<td>Two-layer canopy; Shelterwood removal 1986, natural regeneration</td>
</tr>
<tr>
<td>610</td>
<td>-121.526</td>
<td>44.569</td>
<td>M</td>
<td>232, 79</td>
<td>613</td>
<td>8.7</td>
<td>2.13</td>
<td>Pipo, Cade, Psme</td>
<td>No harvest, natural old growth stand</td>
</tr>
<tr>
<td>608</td>
<td>-121.529</td>
<td>44.595</td>
<td>S</td>
<td>15</td>
<td>664</td>
<td>4</td>
<td>0</td>
<td>Pipo, Cade, Psme</td>
<td>Shelterwood/sanitation removal 1977, overstory removal 1986, planted 1987</td>
</tr>
<tr>
<td>602</td>
<td>-121.513</td>
<td>44.580</td>
<td>S</td>
<td>18</td>
<td>113</td>
<td>3.6</td>
<td>0</td>
<td>Pipo, Cade, Psme</td>
<td>Thinning 1997, natural regeneration</td>
</tr>
<tr>
<td>612</td>
<td>-121.530</td>
<td>44.593</td>
<td>S</td>
<td>200, 41</td>
<td>995</td>
<td>6.7</td>
<td>0</td>
<td>Pipo, Cade, Psme</td>
<td>Sanitation salvage 1977, natural regeneration</td>
</tr>
<tr>
<td>605</td>
<td>-121.517</td>
<td>44.573</td>
<td>S</td>
<td>54</td>
<td>1268</td>
<td>7.2</td>
<td>0</td>
<td>Pipo, Cade, Psme</td>
<td>Thinning, Overstory removal 1970-1973, natural regeneration</td>
</tr>
<tr>
<td>603*</td>
<td>-121.501</td>
<td>44.580</td>
<td>S</td>
<td>57</td>
<td>251</td>
<td>7.2</td>
<td>0</td>
<td>Pipo, Cade, Psme</td>
<td>Thinning, Overstory removal 1970-1973, natural regeneration</td>
</tr>
<tr>
<td>606</td>
<td>-121.507</td>
<td>44.582</td>
<td>S</td>
<td>148, 77</td>
<td>852</td>
<td>6.1</td>
<td>0</td>
<td>Pipo, Cade, Psme</td>
<td>Thinning, Overstory removal 1970-1973, natural regeneration</td>
</tr>
</tbody>
</table>

*This plot was a short-term eddy-covariance site with continuous automated chamber measurements of soil heterotrophic respiration.

Plots are characterized by the dominant cohort and are the median age or where two major cohorts evidenced the 90th percentile age followed by the median age. Age for plot 602 was estimated from DBH and height (no increment cores taken). Plots sorted by increasing median age. Leaf area index (LAI) of the tree canopy was set to zero on severely burned plots because there was no living canopy present. Species codes: Abgr, Abies grandis; Cade, Calocedrus decurrens; Pipo, Pinus ponderosa; Psme, Pseudotsuga menziesii. For control plots refer to Table 1, Law et al. (2003).
and end of August 2004 resulted in a transient increase in efflux from all the plots. Modeled annual soil efflux (Fig. 4a, overlaid lines) was not significantly different between the two burn intensities ($P < 0.22$), however, fluxes from the severely burned plots were on average $32\%$ lower ($P < 0.01$) than from the unburned plots (Table 3). If we compare soil efflux estimates between plots in the two burn intensities, excluding data from the period during the winter when data were filled for a subset of plots that were not accessible, the difference between the two burn intensities still remains insignificant.

Continuous measurements of soil heterotrophic respiration on one severely burned plot (Fig. 4c, plot number 603 in tables) showed a similar seasonal pattern to total soil CO$_2$ efflux as measured across the 12 burned plots. However, the automated measurements better demonstrate the influence of precipitation events on soil $R_h$. We note due to rain gauge problems rainfall data from between days 126 and 210 was substituted with data from a site 10 km away. Daily soil heterotrophic respiration was estimated using:

$$R_{hsoil} = 0.27 \exp (0.077T_{15})(1 - (0.005 \exp (5.052\delta\theta_{30\text{ cm}})))$$

where $R_{hsoil} ($umol m$^{-2}$ s$^{-1}$) is diel mean soil CO$_2$ efflux from six automated soil chambers kept free of vegetation. $T_{15}$ ($^\circ$C) is the diel mean soil temperature at 15 cm depth and $\delta\theta_{30\text{ cm}}$ is the soil volumetric water content deficit over the top 30 cm soil depth. Soil water deficit ($\delta$) is expressed relatively between 0 and 1 (minimum and maximum water deficit, respectively) using $\delta = (\theta_{\text{max}} - \theta) / (\theta_{\text{max}} - \theta_{\text{min}})$ where the subscripts max and min refer to the maximum and the minimum values across the year. Total annual soil heterotrophic respiration estimated using this model on the severely burned plot (Fig. 4c, solid line, $P < 0.001$, $n = 215$) was 198 g C m$^{-2}$ yr$^{-1}$. This compared with 351 g C m$^{-2}$ yr$^{-1}$

![Fig. 1](image-url)
for modeled total soil CO₂ efflux based on manual measurements from the same plot, thus soil heterotrophic respiration accounted for 56% of total soil CO₂ efflux. For two of the unburned plots, using a root separation technique (defined as ‘root excision’ Subke et al., 2006) at three times across the season, we have

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**Table 2** Allometric equations used for estimating woody biomass

<table>
<thead>
<tr>
<th>Equation</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Bole volume</strong></td>
<td></td>
</tr>
<tr>
<td>Douglas fir (Pseudotsuga menziesii)</td>
<td>exp ((-5.8785 + 1.8357 \times (\log (DBH_{\text{m}})) + 1.0279 \times (\log (\text{height}_{\text{m}}})) \times 0.0283) Cochran (1985)</td>
</tr>
<tr>
<td>Ponderosa pine (Pinus ponderosa)</td>
<td>exp ((-6.0336 + 1.8715 \times (\log(DBH_{\text{m}})) + 1.1066 \times (\log (\text{height}_{\text{m}})) \times 0.0283) Cochran (1985)</td>
</tr>
<tr>
<td>Incense cedar (Calocedrus decurrens)</td>
<td>0.2149 \times \text{height}<em>{\text{m}} \times DBH</em>{\text{m}}^2 \times 2 Franklin &amp; Harmon (2002)</td>
</tr>
<tr>
<td><strong>Branch volume</strong></td>
<td></td>
</tr>
<tr>
<td>Douglas fir (P. menziesii)</td>
<td>exp ((-3.6941 + 2.1382 \times (\log (DBH_{\text{cm}}))) \times 1000) Gholz et al. (1979)</td>
</tr>
<tr>
<td>Ponderosa pine (P. ponderosa)</td>
<td>exp ((-5.3855 + 2.7185 \times (\log (DBH_{\text{cm}}))) \times 1000) Gholz et al. (1979)</td>
</tr>
<tr>
<td>Incense cedar (C. decurrens)*</td>
<td>exp ((3.2261 + 2.0877 \times (\log (DBH_{\text{cm}}))) \times 1000) Gholz et al. (1979)</td>
</tr>
<tr>
<td><strong>Coarse root volume</strong></td>
<td></td>
</tr>
<tr>
<td>All species</td>
<td>exp ((-4.6961 + 2.6929 \times (\log (DBH_{\text{cm}}))) \times 1000) Gholz et al. (1979)</td>
</tr>
</tbody>
</table>

*Equation developed for Alaska cedar (Chamaecyparis nootkatensis).

Equations are given in same units (subscript) as the original publications. One grand fir (Abies grandis) and one juniper (Juniperus occidentalis) were identified throughout all burned plots, allometric equations for Douglas fir and incense cedar were used for these two individuals respectively.
previously reported the contribution of soil heterotrophic respiration to total respiration to be on average 54% and 49% for an old-growth and young stand, respectively (Law et al., 2001b). Hence, when comparing a plot that suffered a stand replacing fire 2 years previously with stands that have had no burning or management activities in the last 15 years there appears to be a fairly conservative fraction of soil respiration that originates from heterotrophic sources. Few studies have partitioned soil CO2 efflux in to autotrophic and heterotrophic components immediately following fire. In cold boreal forests 3 years after stand replacing wildfire Bond-Lamberty et al. (2004b) found the heterotrophic fraction was >95%, however, by age six this fraction had declined to values comparable with those for mature stands. In our study in the warmer climate it appears that recovery from the immediate imbalance between soil heterotrophic and autotrophic respiration following wildfire is far quicker. At the severely burned plots there were no living trees however an extensive ground cover of grasses and forbs, often knee deep, rapidly grew during spring and early summer. Although we did not measure the LAI of this layer it was substantial especially considering the LAI of unburned forests in this area rarely exceeds three. The root to shoot ratios of shrubs and grasses can be large (Mokany et al., 2006) and the rapid recovery of fraction of soil CO2 efflux attributed to autotrophic respiration was evidently due to this rapidly colonizing layer of ground vegetation. Czimczik et al. (2006) found that during early stand development (5–40 years) following stand replacing fire in boreal forests, that soil CO2 efflux originates mainly from autotrophic sources. They also attributed this to the invasion of forbs and the resprouting of shrubs and deciduous trees. The importance of understory vegetation on soil respiration was also noted by Campbell et al. (2004b); they measured soil respiration across numerous unburned forest plots and concluded that several forest plots that had a notably higher fraction of understory vegetation exhibited higher soil respiration rates. In addition, Law et al. (2001a) found soil respiration was significantly higher under N-fixing shrubs (Pursia tridentata) compared with under trees and they were lowest in large areas of bare soil. The relatively dense layer of forbs and grasses in the severely burned plots in our study would also have offset the lack of transpiring tree canopy and thus may be responsible for the similar rates of soil moisture depletion in the severely and moderately burned plots. Results such as these perhaps highlight the importance of understanding the role of early successional vegetation in the carbon balance of recovering forests.
Total annual soil respiration was strongly correlated with ANPP ($P < 0.01$) when data were pooled from burned and unburned plots (Fig. 5). Soil CO$_2$ efflux showed an increase of 1.48 g C yr$^{-1}$ for every 1 g increase in ANPP ($r^2 = 0.76$). There was no difference in the relationship ($P = 0.55$) between burned and unburned plots. It should be noted that this relationship was generated from plots where sources of ANPP were associated with highly contrasting life forms within the same vegetation type and climate zone. On the severely burned plots 74% of ANPP was contributed by forbs and grasses compared to only 4% in the unburned plots. Considering the annual nature of forb and grass NPP, this relationship highlights the importance of considering autotrophic sources of carbon in developing dynamic models of soil respiration. Clearly over longer timescales it is logical that soil respiration is related to forest productivity as greater productivity results in both greater detritus inputs to the soil and larger live root pools. Over large spatial scales Reichstein et al. (2003) demonstrated that including LAI, a correlate of NPP, improved models of soil respiration. However, it is noteworthy that in these semiarid sites, the severely burned plots fit the same relationship as moderately or unburned sites. No such relationship was found when unburned forests were compared across a wide climatic gradient (Campbell et al., 2004b) likely due to differing patterns of above to belowground carbon allocation and turnover rates in the different ecoregions.

**Carbon pools and wood decomposition**

Soil carbon to 1 m depth was the largest, albeit most stable, carbon pool across all plot types (Fig. 1b). There were no significant differences in this pool between plot categories. Carbon stored in living trees accounted for 44%, 34% and 2% of total ecosystem carbon in the

**Table 3** Major annual carbon fluxes (g C m$^{-2}$ yr$^{-1}$) and carbon pools (g C m$^{-2}$) of moderately burned (M) and severely burned (S, stand replacing fire) plots, sorted by increasing median age

<table>
<thead>
<tr>
<th>Plot #</th>
<th>Burn class</th>
<th>NPP$_A$</th>
<th>NPP$_B$</th>
<th>$R_{SS}$</th>
<th>$R_{LOG}$</th>
<th>$R_{FWD}$</th>
<th>$R_{TOTAL}$</th>
<th>NEP</th>
<th>LM$_A$</th>
<th>CWD</th>
<th>FWD</th>
<th>Soil C</th>
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<tr>
<td>609</td>
<td>M</td>
<td>58</td>
<td>54</td>
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<td>4</td>
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<td>228</td>
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<td>834</td>
<td>1837</td>
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<td>132</td>
<td>8958</td>
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</tbody>
</table>

*Automated chamber measurements of soil heterotrophic respiration were made in this plot.

Means and standard deviations for the 12 unburned plots also given (see Law et al., 2003 for details). NPP$_A$, aboveground net primary productivity; NPP$_B$, belowground net primary productivity; $R_S$, refers to heterotrophic respiration of (subscript); SS, snags and stumps; LOG, coarse woody debris on ground; FWD, fine woody debris; TOTAL, sum of all heterotrophic fluxes; $R_{SOIL}$, total soil CO$_2$ efflux; NEP, net ecosystem productivity; LM$_A$, aboveground live mass including trees, shrubs, forbs and grasses; CWD; includes snags, logs and stumps; soil C to 1 m depth.

**Fig. 5** Annual soil CO$_2$ efflux for severely burned (filled circles), moderately burned (open circles) and unburned (crosses) plots in relation to annual aboveground net primary productivity (ANPP). The regression shown is through all points ($P < 0.01$, $r^2 = 0.76$).
unburned, moderately burned and severely burned plots, respectively. Total ecosystem carbon, the sum of all components shown in Fig. 1b was not significantly different between severely and moderately burned plots. The total average ecosystem carbon for burned plots was 66% that of unburned plots ($P<0.01$). The breakdown of carbon pools in the severely burned compared with moderately burned plots was principally a switch from live stems to snags as fire severity increased.

The FWD pools in both severely and moderately burned plots were comparable and on average only 24% of that in the unburned plots ($P<0.01$), implying that about 76% of the FWD may have been combusted in the fire. The CWD pool (standing and downed wood) in the severely burned plots was on average 3.5 times that of moderately burned plots and 2.9 times that of unburned plots ($P<0.05$). The fraction of CWD in the form of logs was significantly different between burned and unburned plots ($P<0.05$). The fraction of CWD that was logs was only 3% and 16% in the severely and moderately burned plots compared with 78% in the unburned plots. Snags accounted for 77%, 54% and 13% of CWD in the severely burned, moderately burned and unburned plots, respectively. Root biomass, alive and dead to 1 m depth, was not significantly different between the plot categories ($P=0.40$).

Soil heterotrophic respiration accounted for between 71% and 91% of $R_h$ (Fig. 1c). We note these values are based on a fixed, but apparently relatively stable fraction of total annual soil respiration (see ‘Soil respiration’ for details). Heterotrophic respiration of the aboveground woody debris pools based on decay constants was proportional to pool size.

NEP and sources of uncertainty

Combining the trend of decreasing NPP with increasing burn severity and stable $R_h$ across all plot types resulted in significantly lower NEP in burned compared with unburned stands ($P<0.01$, Fig. 1d), with an increasing trend in NEP from $-125 \pm 44$ g C m$^{-2}$ yr$^{-1}$ ($\pm 1$ SD) in severely burned to $-38 \pm 96$ and $+50 \pm 47$ g C m$^{-2}$ yr$^{-1}$ in moderately and unburned plots, respectively. Although NEP was assessed during different years in burned and unburned plots, NEP at the unburned plots was computed using 10-year average bole wood increment thereby minimizing the confounding effect of time. In addition, the coefficient of variation of eddy covariance estimates of annual NEP on one unburned plot between 2002 and 2005 was 16% (D. Vickers, in review), considerably smaller than differences in NEP between the plot categories in this study.

The ratio NPP/$R_h$ averaged 0.55, 0.85 and 1.21 in the severely burned, moderately burned and unburned plots. Compared with unburned plots, NPP declined 53% and 23% in the severely and moderately burned plots, respectively, where as $R_h$ was comparable among all plots. Thus, even though the fraction of carbon that moves into dead pools after an intense fire is substantial (Fig. 1b), the relatively slow rates of decay of the woody debris did not result in a huge pulse of heterotrophic respiration in the period 2 years following the fire. The litter layer (material finer than 0.6 cm) was absent and assumed combusted on the burned plots. On the unburned plots if we assume the quantity of litterfall that decomposes annually is equivalent to annual litterfall (i.e. the litter pool is at steady state), then litter decomposition contributes on average 20% of total $R_h$.

Decomposition of CWD was calculated with species-specific decay constants. For the species present at the study sites, decay rates ranged from approximately 0.5–3% yr$^{-1}$. On the severely burned plots, fire scorched snags, principally ponderosa pine, accounted for the majority of CWD yet published information for decay rates for this type of material is lacking. Everett et al. (1999) described the snag decay class transition for a range of species including ponderosa pine but did not report decay constants. Harmon et al. (2005) reported that snags of Lutz spruce (Picus lutzii Little) had almost zero rates of decay compared to logs. In hydric ecosystems, we might expect greater decay rates for snags than for logs of the same species, however, in the semiarid sites in this study it is likely that rates of decomposition for snags will be considerably lower than wood that is touching the ground due moisture limitations on microbial processes. In this study, we assumed the rates of decomposition for snags of ponderosa pine was approximately 0.3% a year, one-tenth the decay rate of downed CWD. If we were to assume that snag decay rates were the same as that of downed CWD, then NEP would decrease to $-190$ g C m$^{-2}$ yr$^{-1}$ (i.e. 65 g C m$^{-2}$ yr$^{-1}$ less) and $-47$ g C m$^{-2}$ yr$^{-1}$ (i.e. 9 g C m$^{-2}$ yr$^{-1}$ less) in the severely and moderately burned plots respectively, but this is not a reasonable assumption.

Soil heterotrophic respiration accounts for the greatest proportion of $R_h$ (71%, 91%, 86% in high severity, moderate severity and unburned stands) yet is probably one of the more difficult components of NEP to quantify. Numerous approaches to partition soil CO2 efflux in heterotrophic and autotrophic components have been tried and the range of variability of the relative fractions reported in the literature probably reflects the difficulty of the task (for reviews see Hanson et al., 2000; Bond-Lamberty et al., 2004a; Kuzyakov, 2006; Subke et al., 2006). In this study, we put effort into quantifying the
seasonality and annual total of soil heterotrophic respiration in one plot and used this information when expressed as a fraction of the total soil CO$_2$ efflux to estimate the soil R$_h$ for the remaining plots. Sensitivity of NEP to uncertainty in soil R$_h$ is substantial; if we assume that the fraction of soil R$_h$ was 10% greater, then estimated NEP would decrease to $-150 \text{g C m}^{-2} \text{yr}^{-1}$ (i.e. $25 \text{g C m}^{-2} \text{yr}^{-1}$ less) and $-67 \text{g C m}^{-2} \text{yr}^{-1}$ (i.e. $29 \text{g C m}^{-2} \text{yr}^{-1}$ less) in the severely and moderately burned plots, respectively.

Calculations of belowground NPP in the intensively and moderately burned plots were based on estimates of live fine root biomass and turnover. Various methods have been developed in the last decade for estimating fine root turnover rates and values seem to vary according to the method used (Majdi et al., 2005). The estimate used in this study is consistent with a meta-analysis of forest fine root turnover rates for roots smaller than 2 mm in diameter (Gill & Jackson, 2000); however, it is instructive to determine the sensitivity of NEP calculated in this study to estimates of root turnover. If we assume root turnover is 50% greater than the measured value of 0.6 on one of the unburned plots NEP would increase to $-123 \text{g C m}^{-2} \text{yr}^{-1}$ (i.e. $2 \text{g C m}^{-2} \text{yr}^{-1}$ more) and $-8 \text{g C m}^{-2} \text{yr}^{-1}$ (i.e. $30 \text{g C m}^{-2} \text{yr}^{-1}$ more) in the severely and moderately burned plots, respectively.

It is valuable to note that in these simple sensitivity analyses, aimed at those components we consider are likely to have the greatest uncertainty that the changes in NEP resulting from significant changes in each variable resulted in changes in NEP on the order of 0–60 g C m$^{-2}$ yr$^{-1}$. While such changes are not insignificant, they are considerably less than the variability in estimates of NEP between plots in either burn severity (Table 3). This suggests the unpredictable nature of fire when combined with a range of forest development stages results in large landscape scale variability in NEP that is important to adequately sample.

Summary

Data on tree ring width pre- and postfire illustrates that moderate severity fires in this type of ecosystem have a direct effect on postfire production through mortality rather than changes in the growth rates of the surviving trees. It seems likely that during the postfire year, before the start of this study, that dead fine root biomass may have rapidly decomposed and subsequently been replaced with fine root biomass from colonizing forbs and grasses. The NPP of early successional vegetation is significant, especially in intensely burned plots. Our initial expectation that we would observe a large heterotrophic respiratory flux from the soil in the severely burned plot 2 years after the fire was unfounded. NEP 2 years postfire in this semiarid ecosystem appears more controlled by declines in NPP rather than increases in R$_h$.

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