

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 $+50 \pm 47$ 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 (R_h) were not significantly different between stand types 2 years after fire. The ratio NPP/ R_h 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 ($P < 0.01$, $r^2 = 0.76$). 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 R_h , 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

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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 the release of carbon during this postfire period are ecosystem heterotrophic respiration (R_h) 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 R_h . The length of this pulse and timing of recovery of NPP describe the trajectory of change in NEP after disturbance.

In July 2002, lightning 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*), woolly 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 tridentate*) 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.

$$\text{NEP} = \text{NPP}_A - R_{\text{hWD}} + \text{NPP}_B - R_{\text{hsoil}},$$

where 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), 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 m² 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 CO₂ efflux, temperature and moisture

Soil CO₂ 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 CO₂ 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 CO₂ efflux from the subset of plots that were not accessible during winter, we used the average ratio of the soil CO₂ 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 CO₂ efflux based on the same plot's soil CO₂ 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 $Q_{10} = 1.18$, $SE = 0.04$) 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 Textronix 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 is easy to accept that differences between plot categories do not exist when in reality differences are present, but confounded by additional 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

Plot	Longitude	Latitude	Burn class	Age (years)	Trees (ha ⁻¹)	Median height (m)	LAI	Species composition	History
609	-121.531	44.601	M	15	621	4.6	0.67	Pipo, Cade	Sanitation salvage 1977, natural regeneration
611	-121.538	44.575	M	142, 36	414	4.3	1.15	Pipo, Cade, Psme	Shelterwood removal 1985, seed trees still present, natural regeneration
604	-121.504	44.559	M	49	573	5.5	0.58	Pipo, Cade, Juno	Overstory removal 1980, natural regeneration
601	-121.502	44.560	M	50	684	4.9	0.48	Pipo, Cade, Psme	Overstory removed 1980, natural regeneration
607	-121.535	44.574	M	216, 61	131	9.9	0.32	Pipo, Cade, Psme, Abgr	Two-layer canopy; Shelterwood removal 1986, natural regeneration
610	-121.526	44.569	M	232, 79	613	8.7	2.13	Pipo, Cade, Psme	No harvest, natural old growth stand
608	-121.529	44.595	S	15	664	4	0	Pipo, Cade, Psme	Shelterwood/sanitation removal 1977, overstory removal 1986, planted 1987
602	-121.513	44.580	S	18	113	3.6	0	Pipo, Cade, Psme	Thinning 1997, natural regeneration
612	-121.530	44.593	S	200, 41	995	6.7	0	Pipo, Cade, Psme	Sanitation salvage 1977, natural regeneration
605	-121.517	44.573	S	54	1268	7.2	0	Pipo, Cade, Psme	Thinning, Overstory removal 1970-1973, natural regeneration
603*	-121.501	44.580	S	57	251	7.2	0	Pipo, Cade, Psme	Thinning, Overstory removal 1970-1973, natural regeneration
606	-121.507	44.582	S	148, 77	852	6.1	0	Pipo, Cade, Psme	Thinning, Overstory removal 1970-1973, natural regeneration

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

Plot ages characterize the dominant cohort and are the median age or where two prominent cohorts were evident 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*, *Calocotrus decurrens*; *Pipo*, *Pinus ponderosa*; *Psme*, *Pseudotsuga menziesii*. For control plots refer to Table 1, Law *et al.* (2003).

stands for comparisons with the burned plots to make inferences about the role of fire severity on ecosystem carbon dynamics.

Total NPP in the severely burned plots 2 years after the fire was 47% that of unburned plots (Fig. 1a, $P = 0.03$); a trend of increasing total NPP with decreasing burn severity was evident. Fire of moderate severity killed 72% of all the trees; however, 91% of the killed trees were <20 cm in DBH, a category which only accounted for 22% of prefire bole wood production (Fig. 2). Fire of moderate severity killed only 34% of trees >20 cm DBH, resulting in a decline of only 18% of bole wood production for this size class compared with prefire productivity. We note prefire estimates of the counts of living trees were based on postfire surveys such that if complete combustion of a tree occurred it would not be included in estimates. We suspect complete combustion was rare and most likely limited to those individuals that were dead, and thus desiccated, before the fire.

Mean annual tree ring width on individuals that survived the fire in the moderately burned plots, detrended to remove nonfire related declines, showed no significant remaining patterns in growth with respect to time ($P = 0.39$, Fig. 3). The detrended mean annual ring width over the 4 years prefire was almost identical (to within <0.01 mm) of the mean annual ring width for the 2 years postfire (2.17 mm). In these nutrient limited ecosystems combustion releases nitrogen and fire may result in short-term enhanced growth rates during early succession, which would counter stress-induced decline in wood production. Forb and grass ANPP was over five times greater in severely burned plots compared with the unburned plots ($P = 0.04$) accounting for almost 30% of NPP in severely burned plots compared with <3% in the unburned plots (Fig. 1a).

Soil respiration

The seasonal patterns of soil CO₂ efflux on the severely and moderately burned plots, seasonal mean soil temperature at 5 cm depth and soil water content across the top 30 cm soil depth were not significantly different, although severely burned plots tended to have slightly lower soil respiration and higher soil temperature and moisture (Fig. 4). It is not surprising to observe similar soil temperatures because forests in this semiarid region have relatively open canopies, and solar radiation reaching the ground is high relative to closed-canopy forests. Differences in soil temperature were qualitatively more related to plot aspect rather than LAI. Soil CO₂ efflux peaked in mid-June, before maximum seasonal soil temperature, and declined subsequently until intermittent rainfall (19 mm total) between the middle

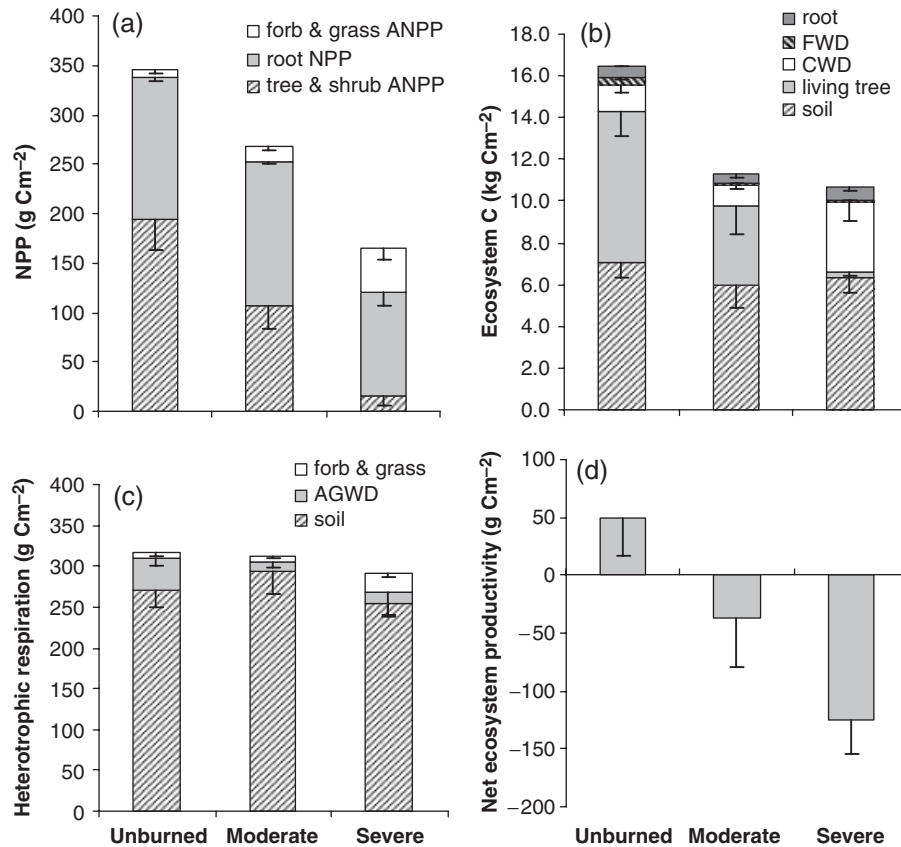


Fig. 1 Annual carbon fluxes (g C m^{-2} ground) and carbon pools (kg C m^{-2} ground) of severely burned (stand replacing fire, $n = 6$), moderately burned ($n = 6$) and unburned plots ($n = 12$). Bars indicate -1 SE. (a) Tree and shrub aboveground net primary production (ANPP) includes bole, branch and foliage. Root NPP includes fine and coarse roots. (b) Soil carbon is integrated to 1 m depth and includes charcoal and incorporated organic matter. Living tree includes bole, bark, branches and foliage. Coarse woody debris (CWD) comprises of logs and snags including branches and bark; fine woody debris (FWD) is material 0.6–10 cm in diameter. Roots include both live and dead pools (<2 cm diameter, to 1 m soil depth). (c) Aboveground woody debris (AGWD) includes both FWD and CWD. Forb & grass refers to the aboveground decomposition of this vegetation layer. Soil heterotrophic respiration includes the litter layer in the unburned plots. (d) Net ecosystem productivity (NEP).

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:

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

where R_{Hsoil} ($\mu\text{mol m}^{-2} \text{s}^{-1}$) is diel mean soil CO_2 efflux from six automated soil chambers kept free of vegetation. T_{15} ($^{\circ}\text{C}$) 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 (δ) 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 $198 \text{ g C m}^{-2} \text{ yr}^{-1}$. This compared with $351 \text{ g C m}^{-2} \text{ yr}^{-1}$

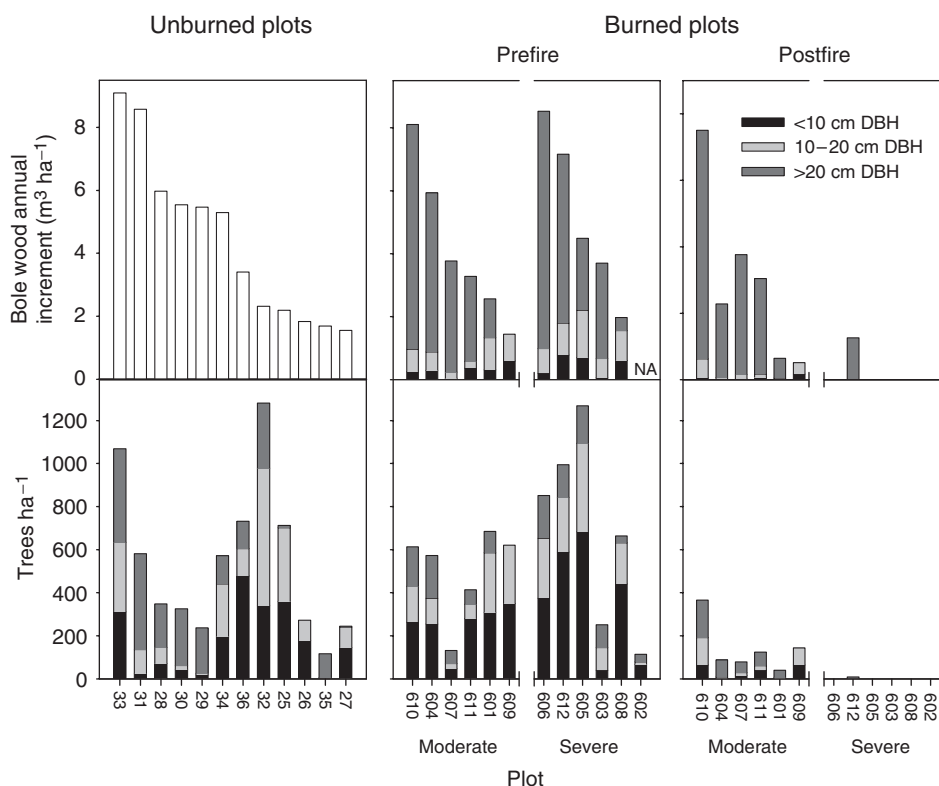


Fig. 2 Living trees per hectare and bole wood production prefire and postfire by tree diameter class (DBH, diameter at 1.3 m). Severely burned plots are those with no surviving trees postfire (and plot 612, having one living tree). Moderately burned plots account for the remainder. No prefire bole increment data were collected for plot 602.

Table 2 Allometric equations used for estimating woody biomass

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

*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.

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

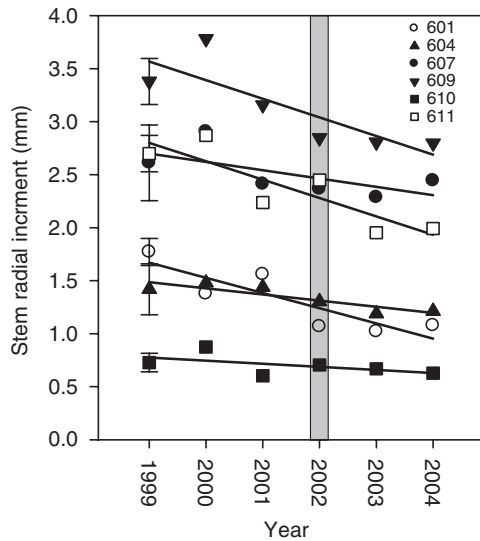


Fig. 3 Mean annual stem growth rates from increment cores taken from moderately burned plots. The vertical grey bar denotes the year of the fire, for clarity ± 1 SE is shown on the first data point for each plot.

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 into 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

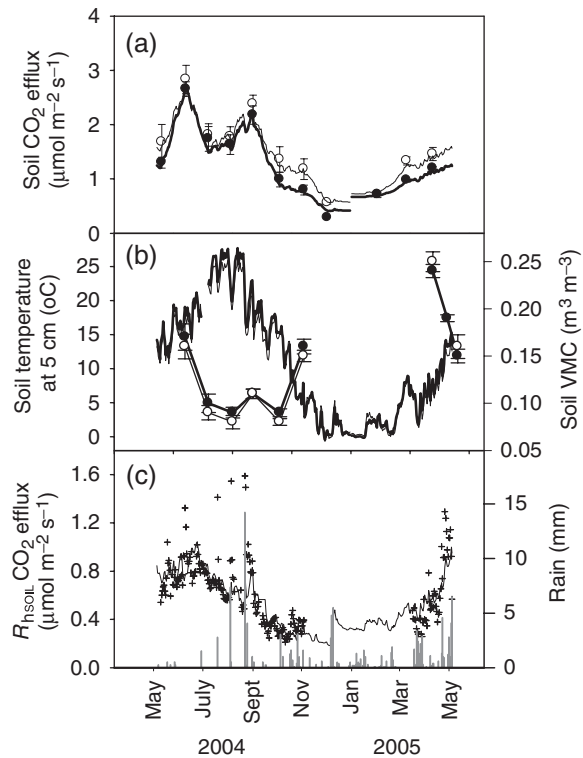


Fig. 4 Soil CO₂ efflux (a) and related variables (b) in moderately burned (open symbols, fine lines) and severely burned (closed symbols, heavy lines) plots between May 2004 and May 2005. Bars indicate ± 1 SE. Daily mean soil temperature was measured continuously, soil volumetric moisture content (VMC) periodically (b). Daily mean soil heterotrophic respiration (c) as measured with an automated chamber system (cross symbols) is shown in relation to daily total rainfall (vertical bars). Overlaid lines (a and c) refer to models fitted to data to determine annual CO₂ effluxes.

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.

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

Plot #	Burn class	NPP _A	NPP _B	R _{hSS}	R _{hLOG}	R _{hFWD}	R _{SOIL}	R _{hTOTAL}	NEP	LM _A	CWD	FWD	Soil C
609	M	58	54	1	4	4	373	228	-116	834	1837	111	3192
611	M	162	279	6	1	6	599	357	83	3172	346	146	8088
604	M	103	69	4	5	3	471	289	-117	1946	1847	81	8321
601	M	51	136	1	12	3	479	295	-108	467	1047	76	5314
607	M	143	236	5	1	7	495	301	78	4360	376	181	6073
610	M	255	101	1	3	4	699	402	-46	12874	266	105	1913
608	S	32	137	4	1	4	448	273	-104	21	691	116	4898
602	S	39	40	3	1	4	449	280	-202	355	1173	95	3918
612	S	97	138	9	4	3	540	333	-98	1609	4064	67	5915
605	S	67	132	11	4	3	451	295	-95	86	3244	90	7883
603*	S	44	29	5	0	1	351	227	-154	617	2246	30	5024
606	S	102	146	23	4	2	468	343	-95	132	8958	50	6935
S mean (SD)		64 (30)	104 (54)	9 (7)	2 (2)	3 (1)	451 (60)	292 (43)	-125 (44)	470 (599)	3396 (1224)	75 (32)	5762 (1456)
M mean (SD)		129 (76)	146 (92)	3 (2)	4 (4)	4 (2)	519 (114)	312 (60)	-38 (95)	3942 (4610)	953 (303)	117 (40)	5484 (2578)
Unburned mean (SD)		212 (109)	144 (56)	2 (3)	20 (15)	15 (10)	666 (202)	306 (81)	50 (47)	7373 (5523)	1188 (992)	393 (257)	7057 (2389)

*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_h 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 CO₂ 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.

Total annual soil respiration was strongly correlated with ANPP ($P < 0.01$) when data were pooled from burned and unburned plots (Fig. 5). Soil CO₂ 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

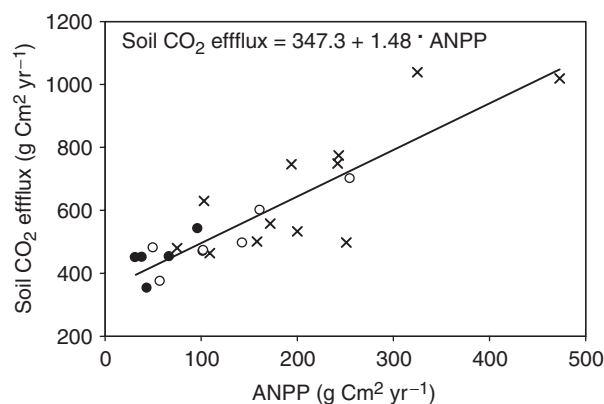


Fig. 5 Annual soil CO₂ efflux for severely burned (filled circles), moderately burned (open circles) and unburned (crosses) plots in relation to annual aboveground net primary productivity (ANPP). The regression shown is through all points ($P < 0.01$, $r^2 = 0.76$).

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

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 above-ground 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 $-125 \pm 44 \text{ g C m}^{-2} \text{ yr}^{-1}$ ($\pm 1 \text{ SD}$) in severely burned to -38 ± 96 and $+50 \pm 47 \text{ g C m}^{-2} \text{ yr}^{-1}$ 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 (*Picea 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 $-190 \text{ g C m}^{-2} \text{ yr}^{-1}$ (i.e. $65 \text{ g C m}^{-2} \text{ yr}^{-1}$ less) and $-47 \text{ g C m}^{-2} \text{ yr}^{-1}$ (i.e. $9 \text{ g C m}^{-2} \text{ yr}^{-1}$ 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 CO_2 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 fraction of the total soil CO₂ 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 $0\text{--}60 \text{ g C m}^{-2} \text{ yr}^{-1}$. While such changes are not insignificant, they are considerably less than the variability in estimates in 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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References

- Agee JK (1993) *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC.
- Bond-Lamberty B, Wang C, Gower ST (2004a) A global relationship between heterotrophic and autotrophic components of soil respiration? *Global Change Biology*, **10**, 1–11.
- Bond-Lamberty B, Wang C, Gower ST (2004b) Contribution of root respiration to soil surface CO₂ flux in a boreal black spruce chronosequence. *Tree Physiology*, **24**, 1387–1395.
- Campbell JL, Sun OJ, Law BE (2004a) Disturbance and ecosystem production across three climatically distinct forest landscapes. *Global Biogeochemical Cycles*, **18**, GB4017, doi: 10.1029/2004GB002236.
- Campbell JL, Sun OJ, Law BE (2004b) Supply-side controls on soil respiration among Oregon forests. *Global Change Biology*, **10**, 1857–1869.
- Cochran PH (1985) *Site index, height growth, normal yields and stocking levels for larch in Oregon and Washington*. USDA Forest Service. Pacific Northwest Forest and Range Experiment Station. Research Note PNW424.
- Curtis PS, Hanson PJ, Bolstad P, Barford C, Randolph JC, Schmid HP, Wilson KB (2002) Biometric and eddy-covariance based estimates of annual carbon storage in five eastern North American deciduous forests. *Agricultural and Forest Meteorology*, **113**, 3–19.
- Czimczik CI, Trumbore SE, Carbone MS, Winston GC (2006) Changing sources of soil respiration with time since fire in a boreal forest. *Global Change Biology*, **12**, 957–971.
- Dale VH, Joyce LA, McNulty S *et al.* (2001) Climate change and forest disturbances. *Bioscience*, **51**, 723–734.
- Donato DC, Fontaine JB, Campbell JL, Robinson WD, Kauffman JB, Law BE (2006) Post-wildfire logging hinders regeneration and increases fire risk. *Science*, **311**, 352.
- Everett RL, Lehmkuhl JF, Schellhaas R, Ohlson P, Keenum D, Riesterer H, Spurbeck D (1999) Snag dynamics in a chronosequence of 26 wildfires on the east slope of the cascade range in Washington state, USA. *International Journal of Wildland Fire*, **9**, 223–234.
- Franklin J, Harmon ME (2002) *Dendrometer studies for stand volume and height measurements (TV0009)*. Corvallis, Oregon:

- Forest Science Data Bank, Department of Forest Science, Oregon State University. <http://www.fsl.orst.edu/lter/data/abstract.cfm?dbcode=TV009>
- Gholz HL, Grier CC, Campbell AG, Brown AT (1979) *Equations for estimating biomass and leaf area of plants in the Pacific Northwest*. Research Paper 41. Forest research laboratory, Oregon State University, Corvallis, 37 pp.
- Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. *New Phytologist*, **147**, 13–31.
- Hanson PJ, Edwards NT, Garten CT, Andrews JA (2000) Separating root and soil microbial contributions to soil respiration: a review of methods and observations. *Biogeochemistry*, **48**, 115–146.
- Harmon M, Fasth B, Yatkov M, Sexton J (2005) *The fate of dead spruce on the Kenai peninsula, a preliminary report*. USDA-FS. Technical Report R10-TP-134.
- Harmon M, Ferrell W, Franklin JF (1990) Effects on carbon storage of conversion of old-growth forests to young forests. *Science*, **247**, 699–702.
- Harmon ME, Sexton J (1996) *Guidelines for measurements of woody detritus in forest ecosystems*, Publ. 20, U.S.LTER Network Office, University of Washington, Seattle.
- Irvine J, Law BE (2002) Contrasting soil respiration in young and old-growth ponderosa pine forests. *Global Change Biology*, **7**, 1183–1194.
- Janssens IA, Lankreijer H, Matteucci G *et al.* (2001) Productivity overshadows temperature in determining soil and ecosystem respiration across European forests. *Global Change Biology*, **7**, 267–278.
- Kurz WA, Apps MJ, Stocks BJ *et al.* (1995) Global climate change: disturbance regimes and biospheric feedbacks of temperate and boreal forests. In: *Biotic Feedbacks in The Global Climatic System. Will The Warming Feed The Warming?* (eds Woodwell GM, Mackenzie FT), 436 pp. Oxford University Press, New York, USA.
- Kuzyakov Y (2006) Sources of CO₂ efflux from soil and review of partitioning methods. *Soil Biology and Biochemistry*, **38**, 425–448.
- Law BE, Kelliher F, Baldocchi DD, Anthoni PM, Irvine J, Moore D, Van Tuyl S (2001a) Spatial and temporal variation in respiration in a young ponderosa pine forest during a summer drought. *Agricultural and Forest Meteorology*, **110**, 27–43.
- Law BE, Ryan MG, Anthoni PM (1999) Seasonal and annual respiration of a ponderosa pine ecosystem. *Global Change Biology*, **5**, 169–182.
- Law BE, Sun OJ, Campbell J, Van Tuyl S, Thornton PE (2003) Changes in carbon storage and fluxes in a chronosequence of ponderosa pine. *Global Change Biology*, **9**, 510–524.
- Law BE, Thornton PE, Irvine J, Anthoni PM, Van Tuyl S (2001b) Carbon storage and fluxes in ponderosa pine forests at different development stages. *Global Change Biology*, **7**, 755–777.
- Law BE, Turner D, Campbell J, Sun OJ, Van Tuyl S, Ritts WD, Cohen WB (2004) Disturbance and climate effect on carbon stocks and fluxes across Western Oregon USA. *Global Change Biology*, **10**, 1429–1444.
- Litvak M, Miller S, Wofsy SC, Goulden M (2003) Effect of stand age on whole ecosystem CO₂ exchange in the Canadian boreal forest. *Journal of Geophysical Research-Atmospheres*, **108**, No. D3, 8225, doi: 10.1029/2001JD000854.
- Majdi H, Pregitzer K, Moren AS, Nylund JE, Agren GI (2005) Measuring fine root turnover in forest ecosystems. *Plant and Soil*, **276**, 1–8.
- Means JE, Hansen HA, Koerper GJ, Alaback PB, Klopsch MW (1994) *Software for computing plant biomass: BIOPAK users guide*, Gen. Tech. Rep. PNW-GTR-340, Pacific Northwest Res. Stn., For. Serv., US Department of Agric., Portland, OR.
- Mokany KR, Raison J, Prokushkin AS (2006) Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biology*, **12**, 84–96.
- NIFC (2005) *National Intergency Fire Center; Wildland fire statistics 1960–2005*. www.nifc.gov/stats/wildlandfirestats.html
- Odum EP (1969) The strategy of ecosystem development. *Science*, **164**, 262–270.
- Pregitzer KS, Euskirchen ES (2004) Carbon cycling and storage in world forests: biome patterns related to forest age. *Global Change Biology*, **10**, 2052–2077.
- Reichstein M, Ray A, Freibauer A *et al.* (2003) Modelling temporal and large-scale spatial variability of soil respiration from soil water availability, temperature and vegetation productivity indices. *Global Biogeochemical Cycles*, **17**, No. 4, 1104, doi: 10.1029/2003GB002035.
- Ryan MG, Lavigne MB, Gower ST (1997) Annual carbon cost of autotrophic respiration in boreal forest ecosystems in relation to species and climate. *Journal of Geophysical Research-Atmospheres*, **102**, 28871–28883.
- Schulze ED, Wirth W, Heimann M (2000) Managing forests after Kyoto. *Science*, **289**, 2058–2059.
- Subke JA, Inglima I, Cotrufo MF (2006) Trends and methodological impacts in soil CO₂ efflux partitioning: a metaanalytical review. *Global Change Biology*, **12**, 1–23.
- Sun OJ, Campbell JL, Law BE, Wolf V (2004) Dynamics of carbon stocks in soils and detritus across chronosequences of different forest types in the Pacific Northwest, USA. *Global Change Biology*, **10**, 1470–1481.
- Van Tuyl S, Law BE, Turner DP, Gitelman AI (2005) Variability in net primary production and carbon storage in biomass across Oregon forests—an assessment integrating data from forest inventories, intensive sites, and remote sensing. *Forest Ecology and Management*, **209**, 273–291.